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Same-Sex Socio-Sexual Interactions Among a Group of Captive Bottlenose Dolphins (*Tursiops truncatus*)

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SAME-SEX SOCIO-SEXUAL INTERACTIONS AMONG A GROUP OF CAPTIVE BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

by

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A Thesis
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ABSTRACT

SAME-SEX SOCIO-SEXUAL INTERACTIONS AMONG A GROUP OF CAPTIVE MALE BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

by Natalia Botero Acosta

December 2015

Bottlenose dolphins (*Tursiops truncatus*) frequently engage in non-reproductive sexual behavior, including homosexual encounters. In order to better understand the nature and function of these interactions, a longitudinal study of the patterns of association and the dynamics of initiator/recipient role exchange was conducted. Underwater video footage of a colony of bottlenose dolphins housed at the Roatan Institute for Marine Sciences (RIMS), collected between March of 2010 and May of 2013, was analyzed. Associations occurring during homosexual interactions were transitory for most individuals. Nonetheless, subsequent analyses allowed the rejection of the null hypothesis of random association, suggesting the existence of preferred associations. A symmetry analysis showed that most pairs shared a symmetric relationship, as only five of 22 dyads were significantly asymmetric. Evidence of association preferences and overall symmetry suggest that homosexual interactions in this population promote social bonding. Alternative explanations, including reconciliation, dominance assertion, tension reduction, and practice for future mating, might also play a role in the occurrence and maintenance of these interactions.

DEDICATION

To my parents and my pup-

Ma, Pa, and Dante: You are the greatest support system someone could ask for. Thank you for ALWAYS being there for me, for encouraging me, believing in me, and loving me unconditionally. I can only hope to be as good of a person and a professional as you think I am. I love you.

To my Grandma-

Amacita: As you may know, I need to see and study instead of believing, but you have always gifted me with your prayers and loving thoughts. I love you.

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CHAPTER I

INTRODUCTION

Same-sex socio-sexual interactions have traditionally been considered as problematic for the theory of natural selection (Bagemihl, 1999; Bailey & Zuk, 2009; Poiani, 2010a; Vasey & Sommer, 2006). Currently, after more than 30 years of active research within the behavioral ecology field, homosexual behaviors are considered fairly common for a wide range of taxa. The role of same-sex socio-sexual behaviors depends on many factors, including the pattern of distribution of resources, the developmental ontogeny of social behavior, and the particularities of the social and mating systems, among others (MacFarlane, Blomberg, Kaplan, & Rogers, 2007; Poiani, 2010b). The study of same-sex socio-sexual behaviors in cetaceans is limited, mainly due to the challenges associated with the study of wide-ranging species that spend a great amount of time underwater. In this context, a longitudinal study of the patterns of association and the symmetry of homosexual behaviors in a captive colony, like the one housed at the Roatan Institute for Marine Sciences, allowed for the generation and testing of predictions regarding the function of these behaviors within the behavioral repertoire of the species.

CHAPTER II

REVIEW OF RELATED LITERATURE

Same-Sex Socio-Sexual Interactions

Sexual reproduction is a costly activity. Individuals invest time, energy, and resources to find a mate, defend it against potential rivals, and then engage in courtship and copulatory behavior (Andersson & Simmons, 2006). Nonetheless, sexual reproduction has considerable benefits, including the production of genetically variable offspring who are potentially more successful in ecologically variable habitats (Bailey & Zuk, 2009; Vasey & Sommer, 2006; Williams, 1975a, 1975b).

As a result of sexual selection, males of many species have elaborate ornaments and display complex courtship behaviors during the mate selection process (Arnqvist & Locke, 2005; Emlen & Oring, 1977; Kirkpatrick, 1982; Shuster & Wade, 2003; Waser, 1993). Females, in turn, use a combination of visual, olfactory, auditory, and behavioral cues to indicate the period of time when they are receptive. In this sense, it would seem that sexual activity is rarely separated from fertilization. However, for a wide variety of taxa, evidence suggests that not all sexual encounters lead to the production of offspring. It seems likely that sex plays an important role in the social lives of animals; perhaps involved in dominance assertion, social bonding, and tension regulation (Bagemihl, 1999; Bailey & Zuk, 2009; Furuichi, Connor, & Hashimoto, 2014; Poiani, 2010a; Vasey & Sommer, 2006; Wickler, 1972).

Same-sex socio-sexual interactions can be defined as behavioral displays that are sexual in nature and involve individuals of the same sex. Notably, the same behaviors observed as part of homosexual interactions also occur between males and females in the context of reproduction. Some form of, or a combination of, same-sex courtship, mounting, copulation, and even long-term pair bonding has been reported in a wide range of taxa, including mollusks, insects, amphibians, reptiles, birds and mammals (Bagemihl, 1999; Bailey & Zuk, 2009; Dagg, 1984; Furuichi et al., 2014; Mann, 2006; Östman, 1991; Poiani, 2010a; Vasey & Sommer, 2006; Vasey, 2004).

Same-sex socio-sexual interactions are non-reproductive acts. If the adaptedness of a behavioral trait is measured by the reproductive success it confers, homosexual behaviors seem to fall outside of functional evolutionary explanations (Bagemihl, 1999; Bailey & Zuk, 2009; Poiani, 2010a). Attempts to provide an evolutionary framework for same-sex socio-sexual behavior include the following hypotheses: (1) It facilitates the establishment, maintenance and strengthening of social relationships; (2) It is the result of differences in social status and mediates interactions between dominant and subordinate individuals; (3) It provides young animals with practice for behaviors related to reproduction; (4) It provides a mechanism to handle intra-sexual aggression and conflict; and (5) It promotes reconciliation of individuals following agonistic interactions (Bagemihl, 1999; Bailey & Zuk, 2009; Hohmann & Fruth, 2000; Mann, 2006; Vasey & Sommer, 2006; Vasey, 1995; Vasey, 2004).

While for bottlenose dolphins and bonobos the social bonding hypothesis has received considerable support (Mann, 2010; Smuts & Watanabe, 1999), behavioral studies conducted with different non-human primates, including Langur Monkeys (*Prebytis entellus*) and Pygmy Chimpanzees (*Pan Paniscus*) support the role of homosexual behavior as a mechanism to mediate interactions between dominant and subordinate individuals (Hohman & Fruth, 2000; Sommer, Schauer, & Kyriazis, 2010; Smuts & Watanabe, 1990; Wickler, 1972b). Conversely, considerable parenting demands in flamingos are thought to promote the practice of reproductive behaviors. Same-sex pairs who associate to nest or rear chicks gain experience that could enhance their long-term reproductive success (King, 2010). Additionally, according to Vervaecke & Roden (2010), calves and juveniles also performed a greater proportion of homosexual interactions in male bison (*Bison bison*) in comparison to older bulls, presumably because these age classes were the ones in need of practice for future mating activity. Finally, studies on female Bonobos (*Pan paniscus*) indicated that rates of post-conflict genital contact exceeded pre-conflict rates. Genital contacts were common when food could be monopolized, and tension was high, suggesting that homosexual behaviors were used in the context of negotiation of benefits or reconciliation (Hohmann & Fruth, 2000).

Same-sex socio-sexual interactions occur in the contexts of social play, social bonding, aggression, reconciliation, sexual excitement and non-playful physical contact (Bagemihl, 1999; Dagg, 1984; Poiani, 2010b; Vasey & Sommer, 2006). In this way, these interactions might be linked to multiple behavioral domains. The extent to which those domains influence the execution of homosexual behaviors may vary according to the species, and as a function of age and reproductive status. Between species, the role of same-sex socio-sexual behavior might also depend on the pattern of resource distribution, the developmental ontogeny of social behavior, and particularities of social and mating systems (MacFarlane et al., 2007; Poiani, 2010b).

Association Patterns

Within social groups, social preferences can be defined as patterns of interaction in which individuals are more likely to remain in close spatial proximity and direct their social behavior toward particular conspecifics (Connor, Smolker, & Richards, 1992; Lusseau et al., 2003; Whitehead, 2008a). Traditionally, social preferences have been described based on physical proximity and/or social interactions (Green, Griswold, & Rothstein, 1989; Horwich, Cogswell, Burrows, & Mitchell, 1982; L'Heureux, Lucherini, Festa-Bianchet, & Jorgenson, 1995).

When social preferences are maintained over time, they can be considered a relationship (Bashaw, Bloomsmith, Maple, & Bercovitch, 2007; Whitehead, 2008a). Social relationships can be distinguished from simple aggregation on the basis of the frequency, content, quality, and consistency of interactions (Whitehead, 2008b). Rates of interactions and association indices are considered good indicators of the content and quality of a relationship because they not only indicate that two individuals spend time together, but also inform how they spend this time. Two individuals that maintain a close relationship will associate more frequently and will show a distinctive pattern of social interactions. Additionally, since relationships can change over time, the temporal patterning of social relationships can provide additional detail on the functionality of the social bond. Measuring the behavioral and temporal properties of relationships is important because those properties most likely have an impact on survival and/or reproduction (Durrell, Sneddon, O'Connell, & Whitehead, 2004; Silk, 2002; Whitehead, 1997).

One approach to evaluate the extent to which preferential relationships occur within a social group consists in the calculation of a coefficient of association (COA). COA measures the proportion of time that two individuals spend in close proximity (Cairns & Schwager, 1987). The underlying assumptions are that physical proximity implies, to some extent, social affiliation, and that amount of time together correlates with the strength of affiliation (Bejder, Fletcher, & Bräger, 1998). An important consideration for the use of association coefficients is that individuals must be easily identified. Bottlenose dolphins fit this criterion since individuals can be recognized based on temporal characteristics, like rake marks; and also by more permanent features, like coloration and notches in dorsal fins and/or flukes (Bräger, Würsig, Acevedo, & Henningsen, 1994; Connor, Wells, Mann, & Read, 2000; Lusseau et al., 2003; Smolker, Richards, Connor, & Pepper, 1992).

The majority of association indices are defined so that they range between zero (two individuals never seen together) and one (two individuals always seen together). The higher the value of the index, the greater the level of association between the dyad (Whitehead, 2008a). A test of random association can be performed using permutation methods, in which testing is carried out using simulated data sets. Data sets are randomly generated to retain important features of the original data. This type of analysis highlights those dyads for which the association index is higher than would be expected from random association (Manly, 2007).

Bottlenose dolphins (*Tursiops truncatus*) live in fission-fusion societies characterized by sex segregation and frequent changes in group membership (Connor et al., 2000). Some males form first-order alliances to facilitate access to estrous females (Connor et al., 1992). Some of these alliances remain stable for long periods of time, up to 20 years (Connor & Krützen, 2015). First-order alliances typically pair with another alliance to form second-order alliances, which cooperate to guard their respective females or steal females from other alliances (Connor, Heithaus, & Barre, 2001; Connor, Read, & Wrangham, 2000; Whitehead & Connor, 2005).

A potential relationship between male-male socio-sexual behavior and alliance formation might be important for understanding same-sex displays in bottlenose dolphins (Bagemihl, 1999; Connor, Wells, et al., 2000; Mann, 2006). Same-sex socio-sexual interactions in male bottlenose dolphins are often observed in a dyadic or triadic context, implying that individuals could potentially show preferences (or avoidances) in their partner selection (Mann, 2006). In this scenario, same-sex socio-sexual interactions could mediate the establishment of key social bonds by providing a mechanism for testing the suitability of potential social partners. These associations will most likely have an impact on each individual's reproductive fitness; therefore, a mechanism that selects an appropriate partner out of a pool of potential candidates would be favored by natural selection (Mann, 2006).

Symmetry of Same-Sex Socio-Sexual Relationships

Social relationships can be described in many ways. One basic distinction differentiates between symmetrical and asymmetrical relationships (Bateson, 1972). An asymmetrical relationship is one in which the members of a dyad interact with one another at "significantly" different rates. Symmetric relationships are those in which both individuals direct similar behaviors toward one another and show mutual attraction (Bateson, 1972; Whitehead, 2008a). Because symmetry requires both individuals to be "responsible" for the relationship, reciprocity is often used as a measure of the strength of a relationship (Hemelrijk, 1990).

According to de Waal & Luttrell (1988), reciprocity can be recorded in three basic forms: 1) Symmetry-based reciprocity: based on features inherent to the dyadic relationship (e.g. kinship, age). This requires no score keeping because it is based on pre-existing attributes, 2) Attitudinal reciprocity, which is based on the mirroring of social attitudes between partners, and 3) Calculated reciprocity, the most cognitively advanced form of reciprocity, requires a sense of memory from previous interactions which leads to score keeping of given and received interactions (de Waal & Luttrell, 1988). Alternatively, Bagemihl (1999) proposed that reciprocity could be observed in two basic forms: simultaneous and sequential. In simultaneous reciprocity, partners exchange roles during a single bout of interactions, whereas in sequential reciprocity, partners trade roles at different points in time (Bagemihl, 1999).

However, even when the relationships are described as symmetrical or asymmetrical within any given time period, the influence of developmental and social processes may promote changes in the way animals interact with each other (Bateson, 1972). Asymmetry could be either an indication of social dominance or it could suggest that the relationship is still unstable (Bateson, 1972). Conflict might be evidenced in a temporary breaking down of the behavioral mechanisms that initially established the role exchange (or lack of it). The resulting relationship may either establish a new dynamic or consolidate the pre-existing one (Wade, 1977).

Asymmetry in relationships can have biological significance. Mating opportunities might be skewed so that only some individuals within the social group have access to receptive mates (Whitehead, 2008b; Yamagiwa, 2006). For example, if by engaging in homosexual behavior with B, A reduces the chances of its partner to copulate, A increases its reproductive fitness at the expense of B (Albonetti & Dessi-Fulgheri, 1990; Birkhead & Møller, 1992; Perry, 1998).

Studies on the social behavior of cetaceans are usually based on the animals' surface behavior. Most long-term research platforms have adopted photo-identification techniques to study patterns of social structure and behavior in such high mobility species (Connor & Krützen, 2015; Quintana-Rizzo & Wells, 2001; Würsig & Würsig, 1977). Although the application of the association coefficients methodology using surface-based observations has proven successful in bottlenose dolphins, very few attempts have been made to monitor underwater behavior so that it is possible to identify the initiators and recipients of social interactions (Mann, 2006; Sakai, Wang, Wang, Li, & Akamatsu, 2011).

According to Bagemihl (1999), same-sex socio-sexual displays in bottlenose dolphins are often symmetrical. Moreover, he indicated that partners often switch positions, alternating during the same socio-sexual bout or exchanging roles over a longer period of time. It is suggested that reciprocity would be part of the normal development of social interactions between individuals of different age classes. In this way, if two males of different age classes interact, either may penetrate the other (Bagemihl, 1999). A recent study on the ontogeny of male homosexual behavior in bottlenose calves in Shark Bay (Australia) explored the symmetry patterns of interactions for male calves and their primary male sexual partners. Some, but not all, of the male-male interactions involving calves were symmetrical, with regular role exchanges (Mann, 2006). If homosexual interactions act as a mechanism to establish trust via reciprocity of socio-sexual behavior, role exchange should be an important component in the establishment of trust between allies.

Proposed Study

The current study describes the patterns of association and dynamics of initiator/receiver role exchange for same-sex socio-sexual interactions in a captive colony of bottlenose dolphins in Honduras, based on underwater videos recorded between March of 2010 and May of 2013. Research hypotheses include: 1. Males have association preferences within same-sex socio-sexual interactions; 2. Association preferences are influenced by the age class of individuals, with higher association measures within versus between age classes; 3. Relationships will be predominantly symmetrical reflecting frequent role exchange; 4. The probability of adopting an active role within same-sex socio-sexual interactions will not depend on the age class and/or dominance status of participants.

CHAPTER III

METHODOLOGY

Subjects and Study Site

The Roatan Institute for Marine Sciences (RIMS) is situated on the northwest coast of Roatan, approximately 27 miles north of mainland Honduras. The dolphins' enclosure encompasses approximately 300m^2 in surface area (Figure 1). The sea floor is covered with corals, sand and sea-grass beds, with depths ranging from the shoreline to approximately 8 meters (Dudzinski et al., 2012; Dudzinski, Gregg, Paulos, & Kuczaj, 2010).

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

For the present study, four age classes were defined: calves, juveniles, subadults, and adults. Calves are defined as still nursing and less than 1/3 of adult body size; juveniles are weaned but still pre-reproductive and about 2/3 of adult body size; subadults may have achieved full length but are still pre-reproductive; and adults are fully reproductive and have reached full length (Mann, 2006). Details of the age class of male bottlenose dolphins housed in the facility can be found in Appendix A. It has been suggested by Dudzinski (2010, 2012) that the age and sex classes of the dolphins housed in this captive colony, who range in age from neonate to 30+ years, match those of coastal wild populations (Connor, Smolker, & Bejder, 2006; Dudzinski et al., 2012, 2010; Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004). During the study period, the population continuously grew. In 2010, one male calf was born, so the colony then housed 13 males. Two male calves were born in the summer of 2012, so as of March 2013 the population included 15 males.

Data Collection

High definition underwater videos were filmed opportunistically by Dr. Stan Kuczaj between March of 2010 and May of 2013. Recordings began when animals came into view and terminated when they swam away. Sketches for each data collection period were used to help identify individual dolphins. This allowed for temporary identifiers such as rake marks to be used for short time periods. Dolphins were also identified using permanent features like notches and coloration on flukes and dorsal fins (Würsig & Würsig, 1977).

Data Processing

Video footage, including same-sex socio-sexual interactions, was broken into three-minute segments, similar to the method employed by Dudzinski and colleagues (2010) in a comparison on pectoral fin contact in bottlenose dolphins (Dudzinski et al., 2010). Sample periods were then processed using a modification of the symmetric 1:0 method to describe association patterns (Whitehead, 2008b). All dyads received a score of 1 when they were seen within one body length of each other and given a 0 if only one of the individuals was sighted as part of a same-sex socio-sexual bout while the other was not (Table 1). Additionally, observers, dolphins located within a body length of the focal group, orienting to and following its participants, were also noted in the association sheet.

Table 1

Coding system for associations via the 1:0 method.

	Anthony	Bill	Mickey	Paya	Vin
Anthony	■	1	0	0	0
Bill	1	■	0	0	0
Mickey	0	0	■	0	1
Paya	0	0	0	■	0
Vin	0	0	1	0	■

Note. Adapted from (Whitehead, 2008b).

The current study recorded six types of socio-sexual behaviors: mounting, goosing, push-ups, petting, mouthing, and interference occurring between males (Mann, 2006). The operational definitions for each behavior and examples extracted from video data can be found in Appendix B and C respectively. Actor and recipient roles were defined to assess the direction of interactions (Altmann, 1974; Mann, 2006). Males would occasionally lie passively, exhibiting their ventral area to other dolphins (presenting), approach another male and began body contact (initiating), or rejected other males' advances and oriented belly up close to the water surface (avoiding). Each of those cases was recorded during video analysis.

An independent observer coded 20% of data in order to calculate an inter-observer reliability. A Spearman Correlation Index was calculated, and a minimum agreement of 80% was required to continue with data analyses.

Data Analysis

General Features of Same-Sex Socio-Sexual Interactions

A X^2 test compared the overall frequencies in which each individual adopted the actor and recipient roles within homosexual interactions. The purpose of this procedure was to assess the significance of presumed differences on the adoption of actor and recipient roles within male-male socio-sexual interactions, based on the age class and dominance status of individuals. The null hypothesis, no difference between the frequencies of actor and recipient roles, was rejected if the observed value for one of the categories was unexpectedly high. An additional X^2 was completed to determine if the age class of receivers influenced their chance of presenting, initiating, or avoiding interactions. The null hypothesis, no influence of age class, was rejected if the observed frequencies were unexpectedly high.

Association Preferences

In order to determine if individuals showed preferences for their partner selection within same-sex socio-sexual interactions, simple ratio index association (COAs) were calculated for every dyad using SOCPROG for MATLAB (Whitehead, 2009). COAs were calculated for: actor/receivers only and, including observers.

The simple ratio index, which ranges from zero to one, is commonly used in studies of captive animals to calculate the number of time periods that individual A and B are sighted together, divided by the number of periods that A is seen without B, and vice versa. The simple ratio index assumes that the scored associations are symmetric, the identifications are accurate, and all individuals are equally likely to be identified whether they are associated or not (Cairns & Schwager, 1987). It is considered a very accurate and statistically unbiased index because it neither double counts nor uses averages (Ginsberg & Young, 1992).

The calculation of the simple-ratio index was restricted to those individuals who were sighted in at least five sampling periods (same as Félix, 1997; García-Vital, Morteo, Martínez-Serrano, Delgado-Estrella, & Bazúa-Durán, 2015; Wells, Scottand, & Irvin, 1987). Different studies have used a range of sighting criteria for the calculation of COAs, from two sightings per individual (Slooten, Dawson, & Whitehead, 1993) to ten (Quintana-Rizzo & Wells, 2001). An intermediate value of five permitted the inclusion of enough individuals in the analysis, while omitting those animals that were sighted so infrequently that their inclusion might cause misleading results. Association coefficients were grouped into five categories: 1. Low: 0.01-0.20; 2. Moderate-Low: 0.21-0.40; 3. Moderate: 0.41-0.60; 4. Moderate-High: 0.61-0.80; 5. High: 0.81-1.00 (Quintana-Rizzo & Wells, 2001).

The coefficients of association were represented in a sociogram using Netdraw® (Borgatti, 2002). This allowed visualization of all the males in the population while connecting them by lines representing the strengths of the relationships between each dyad. Dyads with stronger relationships were connected through thicker lines and placed closer together (Whitehead, 2008b).

Preferred/avoided associations were tested with a variation of the permutation test implemented by Bejder and colleagues (1998). The null hypothesis is that all individuals associate with the same probability. For the alternative hypothesis to be supported, the distribution of association indices calculated from the real data should be significantly different from the distribution of association indices from permutated data sets (Bejder et al., 1998; Manly, 2007; Whitehead, 2008a). Preferred companionships were indicated by a significantly high standard deviation of the real association indices, while avoidance was inferred from a higher proportion of non-zero association coefficients in the random data (Whitehead, 2008a).

A Mantel test was conducted to compare patterns of association between and within age class categories. The test computed a matrix correlation by comparing a matrix of real association indices to randomly permutated matrices based on the age class distribution of the study population (Schnell, Watt, & Douglas, 1985).

Symmetry of Same-Sex Socio-Sexual Interactions

A symmetry index (α_{AB}) was calculated to test whether the actor and recipient roles were interchangeable within male same-sex sexual interactions. Considering that interactions were not independent, a modification of the index proposed by Beilharz and Cox (1967) was calculated based on sampling periods instead.

$$\alpha_{AB} = \frac{I_{AB} - I_{BA}}{I_{AB} + I_{BA}}$$

where I_{AB} included the number of sampling periods where A assumed the actor role more frequently than B. Likewise, I_{BA} encompassed the number of sampling periods where B was the actor more frequently than A. Sampling periods where A and B equally assumed the actor role were disregarded (Beilharz & Cox, 1967). This measure of asymmetry varies between $\alpha_{AB} = 0.0$, indicating equal rates in both directions and a symmetric relationship, and $\alpha_{AB} = 1.0$ in which case A is always the actor, or $\alpha_{AB} = -1.0$ when B is always the actor. The Standard Error was calculated using a simplification of the Delta method (Tietjen, 1986).

$$SE(\alpha_{AB}) = \frac{2\sqrt{I_{AB} I_{BA} (I_{AB} + I_{BA})}}{(I_{AB} + I_{BA})^2}$$

The statistical significance of the asymmetry was assessed using a chi-squared test:

$$\chi^2 = \frac{(I_{AB} - I_{BA})^2}{I_{AB} + I_{BA}}$$

The chi-squared statistic was compared to the X^2 distribution with one degree of freedom. The null hypothesis, of a symmetrical relationship, was rejected if the observed value was unexpectedly high (Whitehead, 2008b).

CHAPTER IV

ANALYSIS OF DATA

Same-sex socio-sexual interactions

A total of three hours of video, out of 44 hours filmed between March of 2010 and May of 2013, included male homosexual behavior. As a result, 1,872 interactions were recorded during 195 sampling periods. In contrast, male-female and female-female interactions were recorded during 31 and 7 sampling periods, respectively.

When males engaged in homosexual behavior, bouts included a median of three participants (Range: 2-4; SD = 0.66). When observers were considered, median group size remained stable (Range: 2-10; SD = 1.54). Same-sex socio-sexual bouts had an average duration of 53 seconds (Range: 1-362s; SD = 59s).

Most interactions were mounts (N = 1137) and gooses (N = 372). Socio-sexual pettings (N = 235) and push-ups (N = 102) were less frequent. This pattern held true on both, the group and the individual level of analysis. Two additional behaviors, interference (N = 22) and mouthing (N = 4), were recorded 1.2% and 0.2% of times respectively. Figure 2 depicts the frequency of each behavior.

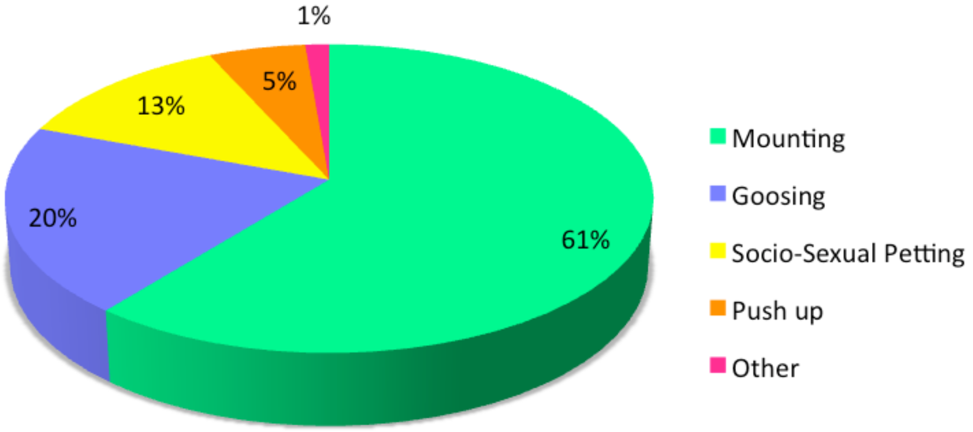


Figure 2. Frequency of same-sex socio-sexual behaviors

Approximately 12.4% of mounts were attempts, where body arching was observed, but the approach was not completed, or the actor was not able to position its genital area respect to the one of the recipient. The ratio of completed vs. attempted mounts differed according to the age class of actors (Table 2). While calves and juveniles exhibited the highest ratios of completed mounts, the frequency of completed mounts was lower for adults and subadults.

Table 2

Frequency of completed/attempted mounts by age class

Age class	Completed	Attempted	% Completed	% Attempted
Calves	235	34	87.4%	12.6%
Juveniles	416	46	90.0%	10.0%
Subadult	218	39	84.8%	15.2%
Adult	107	19	84.9%	15.1%

In the current study, all age classes were recorded as participants of homosexual interactions (Table 3). Juveniles were the actors of 40% of observed events. Subadults and calves followed (27.1% and 21.1% respectively). Lastly, adults were the least common age class within homosexual interactions (11.8%).

Table 3

Frequency of male-male socio-sexual events by age class of participants

	Recipient				
Actor	Calf	Juvenile	Subadult	Adult	Total
Calf	171	93	119	2	385
Juvenile	153	144	320	11	728
Subadult	50	166	225	53	494
Adult	27	27	104	56	215

All males within the RIMS captive colony were identified as observers within homosexual bouts, although individual differences were obvious. Ronnie, a subadult that transitioned to adult during the study, was the most common observer (21 bouts).

Han (19 bouts) and Bill (18 bouts), two adult males, were the second and third most frequent observers. In contrast, younger males, Cortez (6 bouts), Champion and Lenca (1 bout each) were detected as observers the least amount of times.

The frequencies at which each individual adopted the actor and recipient roles within same-sex socio-sexual interactions exhibited considerable variability. A total of four males adopted the actor role significantly more often than what was expected by chance ($X^2 \geq 3.84$, $p < 0.05$). With the exception of Dixon, these males were considered dominant over conspecifics of similar age. Conversely, six males, of various age classes and dominance status, acted as recipients significantly more often than what was expected by chance ($X^2 \geq 3.84$, $p < 0.05$). Lastly, five males, including Paya (the oldest and highest ranked male in the dominance hierarchy) displayed very similar frequencies for both roles ($X^2 < 3.84$, $p > 0.05$).

Recipients initiated homosexual interactions 1.2% of times. A similar pattern was found with avoidance, where 3.8% of recipients evaded sexual contact with other males. In contrast, 34.5% of receivers presented previous to the occurrence of male-male socio-sexual events. Adults and juveniles presented more often than expected by chance ($X^2 \geq 7.81$, $p < 0.05$). Adults also initiated interactions more often than expected by chance ($X^2 \geq 7.81$, $p < 0.05$). No significant differences were detected for avoidance of male-male socio-sexual interactions ($X^2 < 3.84$, $p > 0.05$).

Patterns of Association

Simple ratio association coefficients were calculated within three-minute sampling periods (Appendices D & E). A total of 25 videos were excluded from the analysis, since they were recorded less than three minutes from the previous clip, or participants could not be identified due to reduced visibility. Conversely, 15 video clips were long enough to include more than one sampling period.

When the analysis was restricted to the actor/receivers, the majority (91%) of COAs fell into the Low category. The remaining 9% corresponded to the Moderate-Low class. When observers were included, 70.5% of the dyads still fell into the Low category. The Moderate-Low category now included 26.9% of COAs, while 2.6% of dyads shared a moderate COA. A graphic representation of the association patterns was achieved with sociograms (Appendices F and G).

For the current study, the average association coefficient for males engaging in same-sex socio-sexual interactions was 0.08, which implies a low-level association. The highest coefficient of association (0.39) corresponds to adult males Han and Hector. The second highest coefficient (0.37) involved two male calves, Vin and Mickey, which transitioned to juveniles during the study. Vin and Dixon, who transitioned to subadult in 2013, shared the third highest association index (0.36). When observers were included, the average association coefficient increased to 0.16. Interestingly, the same dyads remained as those with the highest association coefficients (Han-Hector= 0.49; Dixon-Vin=0.43; Mickey-Vin=0.39).

The existence of preferred companionships within homosexual interactions was indicated by a significantly high standard deviation of the real association indices after 20,000 permutations (SD= 0.08347, M (random) = 0.04916, $p < 0.001$). The same pattern was found when the observers were included in the analysis (SD = 0.09029, M (random) = 0.05930, $p< 0.001$). The proportion of non-zero association coefficients in the random data was lower in comparison with the real data (Real=0.9359, M (random) = 0.9316, $p = 0.56$), which indicated no avoidance for partner selection within male-male interactions. A different pattern was found when observers were taken into consideration: (Real = 0.9872, M (random) = 0.9994, $p = 0.02$), indicating that some level of avoidance might be occurring in this colony.

Considering that two years within the study period, 2011 and 2012, held 68% of recorded interactions, two independent Mantel tests were completed to examine the null hypothesis of similar association measures within and between age classes. For both years within class associations were higher than between class associations (2011: $t = 2.3268$, $p = 0.9901$; 2012: $t = 2.539$, $p = 0.9944$). A separate pair of Mantel tests, which included observers, produced similar results (2011: $t = 3.2334$, $p = 0.9993$; 2012: $t = 4.4768$, $p \leq 1.00$).

In the context of homosexual interactions, association patterns of adult male bottlenose dolphins showed evidence of segregation according to age class. Adults preferentially associated with other adults, followed by subadults and juveniles. Calves were their less frequent associates. This pattern was constant across years, and whether observers were included in the analysis or not. Subadults also associated with those of the same age class more frequently; but, unlike adults, showed greater variability in their association patterns, since the position of second most frequent associate alternated between juveniles and adults across years and test conditions. Association between subadults and calves came last. Male calves preferentially associated with other calves. Juveniles were consistently calves' second most common associates. Subadults and adults, however, alternated in the third position according to sampling period and the inclusion/exclusion of observers. Lastly, juveniles exhibited the most fluid patterns of association. Measures of association between juveniles and subadults/calves were occasionally higher than between juveniles. Adults were almost exclusively the least frequent associates of juveniles.

Symmetry of Same-Sex Socio-Sexual Interactions

A total of 51 events were excluded because actors and recipients were not positively identified, due to reduced visibility. In this way, the number of records available for analysis was equal to 1821. An index of asymmetry was calculated for a total of 22 dyads, out of 78 possible, that were interacting for at least five sampling periods. Only five dyads exhibited an asymmetric pattern of interaction ($X^2 \geq 3.84$, $p < 0.05$). For two of those dyads, the individual assuming the role of actor more frequently was younger than the receiver, while the opposite was found for two other dyads. The remaining pair included two males of the same age, where role exchange was limited. For all asymmetrical dyads the dynamic of role exchange was constant during the study period. Appendix H includes calculated symmetry indices.

CHAPTER V

DISCUSSION

Homosexual interactions are common in bottlenose dolphins. Previous studies have suggested that these interactions tend to be symmetrical, with frequent role exchange for the actor and receiver positions. Although patterns of association have been assessed in different populations, and association preferences have been found in many cases, association measures are often generalized, and do not examine affiliative, agonistic and socio-sexual contexts separately. Overall, the results of the current study suggest that homosexual interactions in bottlenose dolphins do favor symmetry over asymmetry. Also, there is evidence for preferences of association, and only limited avoidance, between males of this population.

General Features of Same-Sex Socio-Sexual Interactions

Male-male socio-sexual bouts included a median of three individuals and lasted for an average of 53 seconds. The number of participants reported here is consistent with observations made for wild populations (Bagemihl, 1999; Connor & Krützen, 2015; Furuichi et al., 2014; Mann, 2006; Shimomaki, 2000). Some captive colonies, however, show a more limited resemblance to the patterns of socio-sexual interactions among males, as sexual proportions tend to be skewed in favor of females (Brown & Norris, 1956; Tavolga & Essapian, 1957; Tavolga, 1966). The average duration of homosexual interactions at RIMS was quite short, probably due to the intrinsic limitations of underwater data collection. Same-sex socio-sexual interactions observed near Ogasawara Islands had a minimum duration of 77 minutes, but extended for up to 160 minutes (Shimomaki, 2000). Similarly, homosexual bouts between three young males at Marine Studios lasted from a few minutes to several hours (Tavolga, 1966).

In the current study, juveniles were consistently the most frequent actors of male-male socio-sexual interactions, followed by subadults, calves and adults. Conversely, for this same population, Harvey (2015) recorded no instances of socio-sexual behavior between juvenile dyads and attributed most socio-sexual interactions to two adult males (Han and Hector) who directed mounts and gooses to younger animals (Harvey, 2015). However, her study analyzed a much more limited number of socio-sexual interactions, which explains some of the differences. The number of juveniles was fairly constant in both studies, which suggest that differences in data collection techniques might have contributed to the observed discrepancies.

With the exception of interference, all the behaviors recorded as part of same-sex socio-sexual interactions had been previously noted in the literature, for both captive and wild dolphins (Bagemihl, 1999; Bateson, 1974; Caldwell & Caldwell, 1977; Connor, Wells, et al., 2000; Furuichi et al., 2014; Harvey, 2015; Mann, 2006; McBride & Hebb, 1947; Norris & Dohl, 1980; Östman, 1991; Shimomaki, 2000; Tavolga & Essapian, 1957; Tavolga, 1966). At RIMS, interference occurred irrespective of the age class, suggesting that its function might be other than dominance assertion. Instead, this behavior might illustrate the occasional competitiveness of intra-sexual interactions.

Mounting has consistently been reported as the most common type of male-male socio-sexual behavior executed by bottlenose dolphins (Bagemihl, 1999; Connor, Read et al., 2000; Furuichi et al., 2014; Harvey, 2015; Mann, 2006). The current study supports this conclusion, as mounting represented over 60% of observed interactions. Goosing, observed in 20% of homosexual encounters, is listed by many authors as the second most common behavior. This claim was again supported by observations made at RIMS. Socio-sexual petting, often regarded as a more affiliative behavior, was observed on 13% of observed interactions. Previous studies may have underestimated the frequency of socio-sexual petting, as reported values were lower compared to those reported here, which is not surprising considering how brief this interaction is (Mann, 2006).

In Shark Bay, males directed a higher proportion of mounting to other males, while females were the most common recipients of gooses. This pattern led researchers to suggest that goosing stimulated female receptivity (Connor, Read et al., 2000; Furuichi et al., 2014). A similar argument can be made for goosing and socio-sexual petting at RIMS. Both behaviors were seen previous to, or in association with, mounting; possibly stimulating the recipients of sexual interactions as a sort of “foreplay.” Other authors have reported that affiliative behaviors such as synchronous swimming and rubbing often precede, or follow, homosexual interactions among bottlenose dolphins and finless porpoises (Bagemihl, 1999; Shimomaki, 2000; Xian, Wang, Dong, Hao, & Wang, 2010).

Within male homosexual interactions, the sexual nature of the events is usually inferred by the observation of erections, which are often interpreted as a sign of arousal (Bagemihl, 1999; Tavolga & Essapian, 1957; Vasey, 1995). Previous studies have probably underestimated the proportion of males with an erection, mainly because interactions are brief, and detection can be obstructed when the actor’s penis is pressed against another individual (Furuichi et al., 2014; Mann, 2006). Also, males seem to display erections in many contexts, including social excitement, aggression, dominance assertion, play, and epimeletic behavior (Caldwell & Caldwell, 1977; Dudzinski et al., 2003; Herzing & Johnson, 1997; Herzing, 1996; Kuczaj et al., 2015; McBride & Hebb, 1947; Östman, 1991). At RIMS, actors displayed an erection 74% of times, while recipients did so only for 15% of observed bouts. While it can be argued that recipients were equally aroused, some of the erections can be related to the longer bouts where role exchange was frequent. It is possible that a recipient was observed with an erection simply because he was the actor in a previous event.

Patterns of Association

Association coefficients calculated for a captive colony at RIMS, based solely on the association patterns occurring during male-male sexual interactions, were consistent with previous studies, where most dyads shared low-level associations and only a few pairs engaged in high-level associations (Bräger et al., 1994; Connor & Krützen, 2015; Félix, 1997; García-Vital et al., 2015; Harvey, 2015; Quintana-Rizzo & Wells, 2001; Rogers, Brunnick, Herzing, & Baldwin, 2004; Smolker et al., 1992; Wells et al., 1987). The prevalence of low measures of association in bottlenose dolphins are often interpreted as a result of the fission-fusion structure, in which aggregations tend to be short-lived (Connor et al., 2001; Connor, Wells, et al., 2000). In the context of homosexual behavior, this pattern suggests that for most individuals, associations undergoing during this type of behaviors are transitory.

Harvey (2015) studied the nature of social relationships for this captive colony. According to her findings, Han and Hector also had the highest coefficient of association for a male-male dyad. The second and third highest association indices between males corresponded to two juvenile (Anthony - Ken) and two adult (Han - Ritchie) dyads (Harvey, 2015). Both pairs generated considerably smaller coefficients in the current study, suggesting that their relationship might depend on affiliative and/or aggressive interactions instead of socio-sexual ones. However, alternative explanations, such as differences in the data collection method, might also be promoting the differences discussed above.

Segregation by sex, age class, and reproductive status seems to be typical for bottlenose dolphins (Félix, 1997; García-Vital et al., 2015; Harvey, 2015; Irvine, Scott, Wells, & Kaufmann, 1981; Shimomaki, 2000; Smolker et al., 1992; Wells et al., 1987). For the current study, association measures within age classes were indeed higher than between age classes. Juveniles, however, exhibited a more fluid pattern of association, often displaying strongest measures of association with subadults and calves. Juveniles might be at a critical point of their social development, where it is advantageous to test the suitability of social partners within their social group, irrespective of their age class (Félix, 1997; Irvine et al., 1981; Scott, Mann, & Watson-Capps, 2005; Wells et al., 1987).

The Permutation analysis confirmed the existence of preferred associations within the RIMS colony. Evidence suggests that the association patterns occurring within homosexual displays vary considerably, with some dyads rarely interacting while others engage in same-sex socio-sexual behaviors frequently. Employing photo-identification methods, association preferences have been found in other locations around the world, and are often interpreted as a feature of the complex social structure of bottlenose dolphins (Bagemihl, 1999; Connor et al., 2001; Connor, Wells, et al., 2000; Connor & Krützen, 2015; Dagg, 1984; García-Vital et al., 2015; Rogers et al., 2004). Furthermore, there was only evidence of avoidance in partner selection when observers were included in the analysis. Considering that data was obtained opportunistically, and video analysis limited to clips that included socio-sexual interactions, an examination of the patterns of association during affiliative and aggressive interactions, employing systematic focal follows, is highly desirable to ensure that the indications of avoidance in partner selection within the RIMS colony are not the result of implicit bias of the sampling methods.

Long-term associations between males have been reported in several locations, including Shark Bay (Australia) and the Little Bahama Bank (Bahamas) (Connor & Krützen, 2015; Rogers et al., 2004). This kind of strong male-male bond is believed to have a cooperative basis to herd females (Connor & Krützen, 2015). Nonetheless, the consistent observation of male bonds in non-herding contexts implies that such relationships have a cooperative basis that extends to other contexts beside reproduction (Connor et al., 1992). A long-term examination of the stability of association preferences suggested here, as well as an assessment of paternity among bottlenose dolphins born in the facility, is necessary before any conclusions can be drawn about the impact of association preferences on mating success.

Symmetry of Same-Sex Socio-Sexual Interactions

Symmetry indexes, calculated for 22 of 78 possible dyads, indicated that socio-sexual interactions among male bottlenose dolphins at the RIMS are predominantly symmetric, supporting the results of previous studies (Bagemihl, 1999; Harvey, 2015; Mann, 2006; Shimomaki, 2000). Mann (2006) reported that most male-male interactions among calves were symmetrical, with regular role exchange between pairs in terms of actor/recipient roles. Similarly, Shimomaki (2000) observed role exchange, approximately every 2-3 minutes, in all homosexual bouts recorded near Ogasawara Islands. The same author stated that at the Suma Aquarium, asymmetry was found for only one of four dyads (Shimomaki, 2000).

However, asymmetry within socio-sexual interactions is not uncommon. In Shark Bay over 40% of dyads that included a calf, and engaged in socio-sexual interactions, were considered asymmetrical (Mann, 2006). Östman (1991) reported that homosexual interactions between two subadult males at Marine World were almost exclusively asymmetrical with very limited role exchange (Östman, 1991).

Asymmetry was also found in the homosexual behavior between two males at the Kolmården Wildlife Park in Sweden. The youngest male (Sting) directed socio-sexual interactions towards the oldest male (Pichi). The opposite was not recorded (Birgersson, 2011). According to Harvey (2015), symmetry appeared to be limited for adult male dyads, as socio-sexual events initiated by one of two adult males (Han or Hector) had the same three males as recipients, with no indication of role exchange (Harvey, 2015). In a captive colony of bottlenose dolphins at Marine Studios, two of the animals, Algie and Frank, tended to be somewhat dominant over the third dolphin, Floyd. Occasionally, some instances of role exchange were observed (Tavolga, 1966). Lastly, Herzing and Johnson (1997) reported that reciprocal mounting was never observed during socio-sexual interactions between bottlenose and spotted dolphins in Bahamian waters. Typically, interactions involved young spotted dolphins assuming a passive posture, while bottlenose dolphins rubbed their genitals against them (Herzing & Johnson, 1997).

Even if socio-sexual relationships are symmetrical, there is evidence of occasional resistance to assume the recipient role on socio-sexual interactions. For instance, Shimomaki (2000) noted that recipients of male homosexual interactions would sometimes hide their genital area from the other males (Shimomaki, 2000). Similarly, Mann (2006) indicated that receivers of mounts would engage in energetic behaviors, including tail slaps and belly ups, to avoid interactions. Although avoidance was mostly observed during mounting attempts, gooses and push-ups to the genital area could also be performed in a forceful manner (Connor & Smolker, 1996; Mann, 2006). Observations made at RIMS support this claim. Recipients occasionally went belly up, close to the water surface, or brought their ventral area in contact with the sandy bottom, to difficult access to their genital slit. This occurred mostly during mounting but also during gooses, socio-sexual pettings, and push-ups.

A common notion for asymmetries in socio-sexual behavior is that the phenomenon is related to dominance assertion, with older individuals being dominant over younger ones (Birgersson, 2011; Connor et al., 1992; Tavolga, 1966). Nonetheless, there are numerous observations of younger animals mounting older conspecifics (Bagemihl, 1999; Furuichi et al., 2014; Mann, 2006; Xian et al., 2010). For two asymmetric dyads at RIMS, the individual who adopted the actor role more frequently was younger (Vin vs. Ken and Dixon vs. Ritchie). The opposite pattern was found for two different pairs (Dixon vs. Cortez and Ritchie vs. Ronnie) with younger animals acting as recipients more often than the opposite. The remaining dyad, formed by two male calves (Vin and Mickey), which transitioned together to juveniles during the study period, had one male (Vin) consistently fulfilling the active role in homosexual interactions. A similar pattern was observed in Shark Bay where one male calf (COO) had six symmetrical relationships and no asymmetrical ones, while others (SMO and SRY) had more asymmetrical bonds than symmetrical (Mann, 2006). Individual differences in personality traits and differences in social and hormonal development might play a role, but more research is needed.

The Role of Homosexual Behaviors

Several hypotheses have been proposed to explain the occurrence and maintenance of homosexual interactions. Some of these, including dominance assertion, tension reduction, reconciliation, practice for future mating, and formation of social bonds are related to ultimate factors. In contrast, alternative explanations that include high mutation rates, pleiotropic effects, sexual hormones, sensory processing bias, and maternal effects rely on proximate factors (see Bagemihl, 1999; Bailey & Zuk, 2009; Vasey & Sommer, 2006 for a review).

While Östman (1991) reported that sexual interactions between two male bottlenose dolphins were a component of dominance assertion (Östman, 1991), Mann (2006) pointed out that whether mountees were subordinate to mounters was unknown for the Shark Bay population (Mann, 2006). At RIMS, a preliminary assessment of the dominance hierarchy was made after consulting with trainers and staff members. When this ranking was compared to the results of the asymmetry analysis carried out in the current study, an interesting pattern emerged. Three of the asymmetric dyads support the presumption that dominant animals adopt an active role within same-sex socio-sexual interactions. The two remaining pairs, however, showed the opposite trend, with lower ranking (and younger) animals assuming the actor role more often than their higher-ranking (and older) conspecifics.

Furthermore, individual differences were obvious when analyzing the frequencies in which each individual assumed the role of actor and recipient. Two of the older males, Han and Hector, were almost exclusively the actors in homosexual behaviors with younger males. However, other older males, ranked high in the dominance hierarchy, exhibited similar frequencies for the actor and recipient roles or were observed as recipients of same-sex socio-sexual interactions more often than expected. A similar pattern was found for younger individuals, where two juvenile males (Dixon and Vin) took on the actor role more often when interacting with both younger and older males. Therefore, it seems that the likelihood of adopting the actor or recipient roles within homosexual interactions depends on other factors beside the age class or the dominance status of the animals.

According to Bagemihl (1999), a limitation of looking at homosexual interactions from the perspective of dominance is that only mounting lends itself to such interpretation (Bagemihl, 1999). Most male dyads at RIMS shared a symmetric relationship regarding their participation within homosexual interactions. As pointed out by several authors, evidence of symmetry conflicts with this hypothesis, as interactions should occur in a unidirectional mode if it strictly followed the social rank (Bagemihl, 1999; Levan, Fedina, & Lewis, 2009).

The tension reduction hypothesis predicts that rates of socio-sexual interactions will be higher if resources such as prey and/or receptive females can be monopolized (Furuichi et al., 2014; Manson, Perry, & Parish, 1997; Perry, 1998). The applicability of this hypothesis is limited at RIMS, since dolphins are provisioned on a daily basis, so that food items cannot be monopolized. However, access to receptive females could be a resource controlled by a few males in the colony. Additional research, including a paternity analysis, is needed before any conclusion can be made regarding this hypothesis.

Key predictions for the reconciliation hypothesis include joint occurrence of sexual and agonistic interactions, increased rates of homosexual events after aggressive encounters, and increased rates of sexual contact between related individuals (Bagemihl, 1999; Vasey, 2004). Opportunistic footage recorded at RIMS is predominantly composed of short video clips where it was not possible to evaluate the occurrence of socio-sexual interactions during pre and post conflict periods. Most same-sex socio-sexual events were not aggressive in nature. Individuals often interacted in a “relaxed” manner with no obvious sign of intended aggression. Furthermore, information about genetic relatedness is not available to test if related individuals employ homosexual behaviors to repair social relationships after conflict. According to Holobinko and Waring (2010), sexual behaviors between bottlenose dolphins rarely occurred in the context of reconciliation in a captive colony at the Brookfield Zoo (Holobinko & Waring, 2010).

Same-sex socio-sexual behavior is often referred as a way for younger animals to practice heterosexual courtship and mating (Bagemihl, 1999). Within homosexual interactions, bottlenose dolphins appear to “mimic” the structure of herding groups, with at least two males taking turns to act on a third individual (Mann, 2006; Shimomaki, 2000). This pattern was consistent with homosexual bouts observed in the current study. However, a major issue with the practice hypothesis is that same-sex socio-sexual interactions are often not restricted to young animals, which are presumed to be the ones in need of practice (Bagemihl, 1999). While young animals are typically responsible for the highest frequencies, homosexual interactions are not uncommon among older males (Mann, 2006; Shimomaki, 2000). At RIMS, a total of 12.4% of all mounting events were classified as attempts. These incomplete interactions were observed from males of all age classes and dominance statuses, not only by young (and presumably inexperienced) males. Under the practice hypothesis, the efficacy of mounts would increase with age, as the animals gain more experience. However, younger animals (calves and juveniles) actually had the highest ratio of completed mounts when compared with their older conspecifics, which does not offer much support to this hypothesis.

Lastly, the social bonding hypothesis states that social bonds and alliances between males are formed and maintained through participation in same-sex socio-sexual interactions (Bagemihl, 1999; Bailey & Zuk, 2009; Furuichi et al., 2014; Mann, 2006; Smuts & Watanabe, 1990; Vasey, 2004). The advantage of this hypothesis is that it seems equally likely for young and older males to employ homosexual contact to develop and maintain cooperative relationships with other males (Smuts & Watanabe, 1990). For example, adult males were detected as observers more often than younger animals. Although it is possible that by observing young males’ performance during homosexual interactions, older males might be selecting the best potential partner(s), this pattern can also be explained if we consider that younger males were the most frequent actors, and since they preferentially associated with conspecifics of the same age, that leaves older males to be the most frequent observers.

An important prediction is that same-sex socio-sexual interactions are more common among kin or individuals that associate closely (Harvey, 2015; Shimomaki, 2000). Although there is no available assessment of the degree of genetic relatedness among individuals at RIMS, the patterns of association and symmetry found here provide some support for this hypothesis. For example, the male dyad (Han and Hector) with the highest coefficient of association in the Harvey study (2015) was commonly seen as part of homosexual bouts in the current study. Interestingly, while they often interacted with younger males with which they shared lower measures of association, only one interaction occurred between them.

In contrast, younger dyads (Dixon-Vin and Mickey-Vin), that shared lower association measures in the Harvey study, were involved in many interactions together for the current study. Considering that Harvey (2015) restricted her analysis to data collected in 2010, it would be interesting to know if, as predicted, association measures between these two dyads increased in the following years as suggested in the current study. Overall, male-male socio-sexual interactions at RIMS favored symmetry over asymmetry. This also provides support for the social bonding hypothesis, as frequent role exchange might be the mechanism through which males establish trust and build social relationships with other males (Mann, 2006).

None of the hypotheses discussed above can satisfactorily explain the occurrence and maintenance of homosexual interactions in bottlenose dolphins by itself. As with other cases of non-conceptive behavior, it seems that male-male sexual contact serves multiple purposes. Additional data is needed in order to evaluate the relevance of most hypotheses. So far, the information available on frequencies of homosexual interactions according to age class, patterns of association, and symmetry suggests that one of the main roles for same-sex socio-sexual interactions in bottlenose dolphins is to facilitate the formation and maintenance of social bonds which are thought to be crucial for reproductive success and survival.

APPENDIX A

AGE CLASS DETAILS OF RIMS MALE DOLPHINS

ID	Age Class 2010	Age Class 2011	Age Class 2012	Age Class 2013
Anthony	Juvenile	Juvenile	Subadult	Subadult
Bill	Subadult	Subadult	Adult	Adult
Champion	--	--	--	Calf
Cortez	Calf	Calf	Calf	Juvenile
Dixon	Juvenile	Juvenile	Juvenile	Subadult
French	Juvenile	Subadult	Subadult	Subadult
Han	Adult	Adult	Adult	Adult
Hector	Adult	Adult	Adult	Adult
Ken	Juvenile	Subadult	Subadult	Subadult
Lenca	--	--	--	Calf
Mickey	Calf	Calf	Juvenile	Juvenile
Paya	Adult	Adult	Adult	Adult
Ritchie	Adult	Adult	Adult	Adult
Ronnie	Subadult	Subadult	Subadult	Adult
Vin	Calf	Calf	Juvenile	Juvenile

APPENDIX B

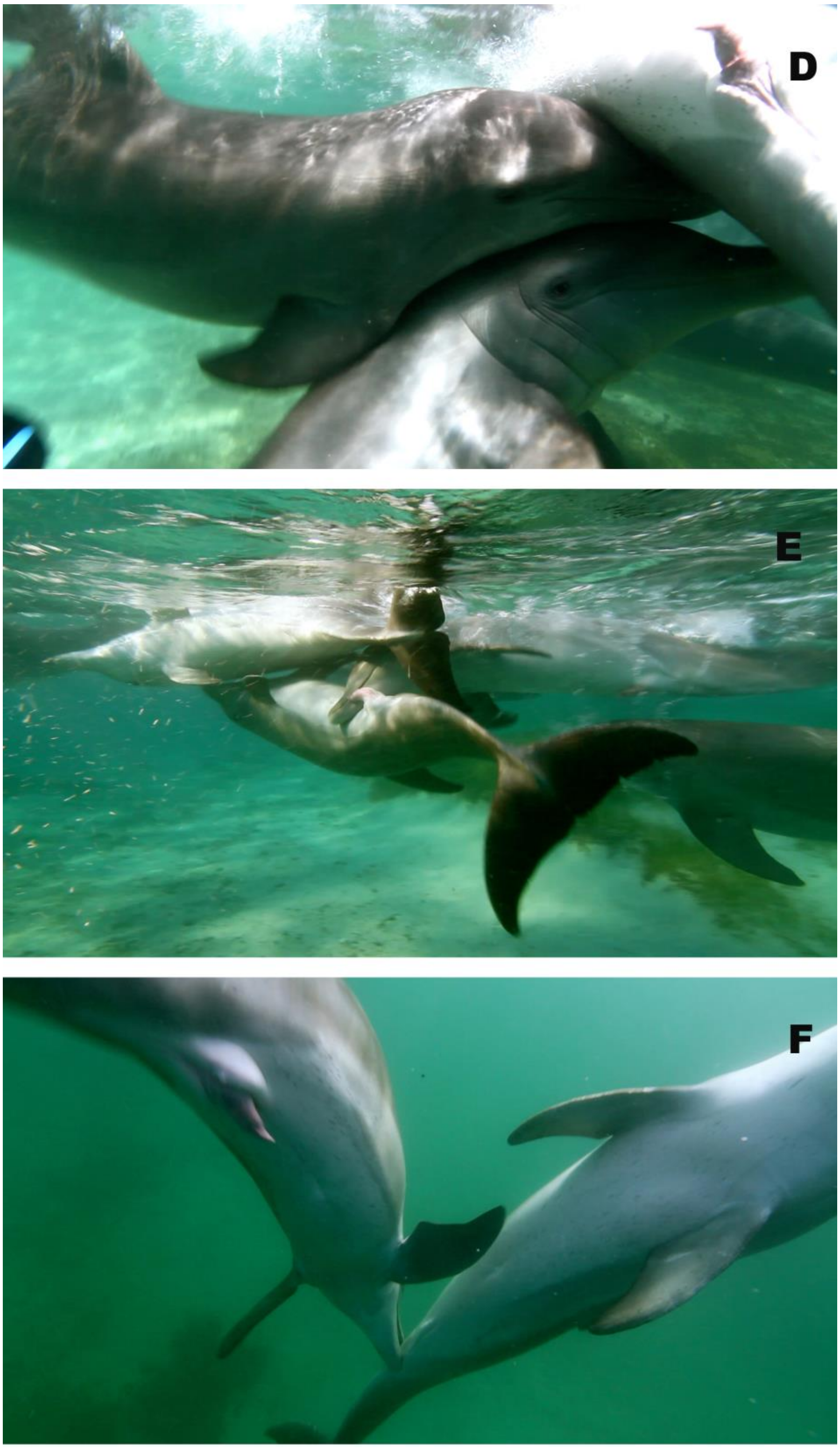
BEHAVIORAL DEFINITIONS

Code	Name	Description
MOU	Mounting	Actor attempts to mount by orienting its genital region to recipient's genital region
SSP	Socio-sexual petting	Actor touches the genital area of the recipient with its pectoral fins
GOO	Goosing	Actor inspects the genital area of the recipient with its rostrum
PSU	Push-up	Actor pushes the genital area of the recipient with its head or rostrum
INT	Interference	Actor gets in between two dolphins preventing an interaction from occurring
MTH	Mouthing	Actor has its mouth around the genital area of the recipient but it is not biting down

Note. Definitions and codes adapted from (Mann, 2006)

APPENDIX C

SAME-SEX SOCIO-SEXUAL BEHAVIORS



Same-sex socio-sexual behaviors: A) Mounting; B) Goosing; C) Socio-sexual petting; D) Push-ups; E) Interference; F) Mouthing.

APPENDIX D

ASSOCIATION COEFFICIENTS BASED ON SAME-SEX SOCIO-SEXUAL INTERACTIONS

Dyad	COA	SE
Anthony-Bill	0.05	0.03
Anthony-Cortez	0.08	0.04
Anthony-Dixon	0.05	0.02
Anthony-French	0.19	0.05
Anthony-Han	0.02	0.02
Anthony-Hector	0.02	0.02
Anthony-Ken	0.26	0.05
Anthony-Mickey	0.04	0.02
Anthony-Paya	0.10	0.04
Anthony-Ritchie	0.04	0.03
Anthony-Ronnie	0.16	0.05
Anthony-Vin	0.09	0.03
Bill-Cortez	0.02	0.02
Bill-Dixon	0.04	0.02
Bill-French	0.13	0.05
Bill-Han	0.08	0.05
Bill-Hector	0.08	0.04
Bill-Ken	0.07	0.03
Bill-Mickey	0.12	0.04
Bill-Paya	0.09	0.05
Bill-Ritchie	0.06	0.03
Bill-Ronnie	0.02	0.02
Bill-Vin	0.06	0.02
Cortez-Dixon	0.11	0.03
Cortez-French	0.03	0.02
Cortez-Han	0.06	0.04
Cortez-Hector	0.03	0.03
Cortez-Ken	0.04	0.02
Cortez-Mickey	0.06	0.03
Cortez-Paya	0.00	0.00
Cortez-Ritchie	0.02	0.02
Cortez-Ronnie	0.04	0.02
Cortez-Vin	0.11	0.03
Dixon-French	0.04	0.02
Dixon-Han	0.01	0.01
Dixon-Hector	0.01	0.01
Dixon-Ken	0.24	0.04
Dixon-Mickey	0.21	0.04

Dixon-Paya	0.01	0.01
Dixon-Ritchie	0.14	0.04
Dixon-Ronnie	0.08	0.03
Dixon-Vin	0.36	0.04
French-Han	0.02	0.02
French-Hector	0.08	0.04
French-Ken	0.16	0.04
French-Mickey	0.03	0.02
French-Paya	0.06	0.04
French-Ritchie	0.10	0.04
French-Ronnie	0.20	0.05
French-Vin	0.04	0.02
Han-Hector	0.39	0.10
Han-Ken	0.00	0.00
Han-Mickey	0.00	0.00
Han-Paya	0.04	0.04
Han-Ritchie	0.08	0.04
Han-Ronnie	0.02	0.02
Han-Vin	0.03	0.02
Hector-Ken	0.05	0.03
Hector-Mickey	0.03	0.02
Hector-Paya	0.04	0.04
Hector-Ritchie	0.05	0.03
Hector-Ronnie	0.00	0.00
Hector-Vin	0.01	0.01
Ken-Mickey	0.04	0.02
Ken-Paya	0.03	0.02
Ken-Ritchie	0.07	0.03
Ken-Ronnie	0.08	0.03
Ken-Vin	0.16	0.03
Mickey-Paya	0.03	0.02
Mickey-Ritchie	0.04	0.02
Mickey-Ronnie	0.05	0.02
Mickey-Vin	0.37	0.05
Paya-Ritchie	0.00	0.00
Paya-Ronnie	0.24	0.07
Paya-Vin	0.01	0.01
Ritchie-Ronnie	0.11	0.04
Ritchie-Vin	0.06	0.02
Ronnie-Vin	0.05	0.02

APPENDIX E

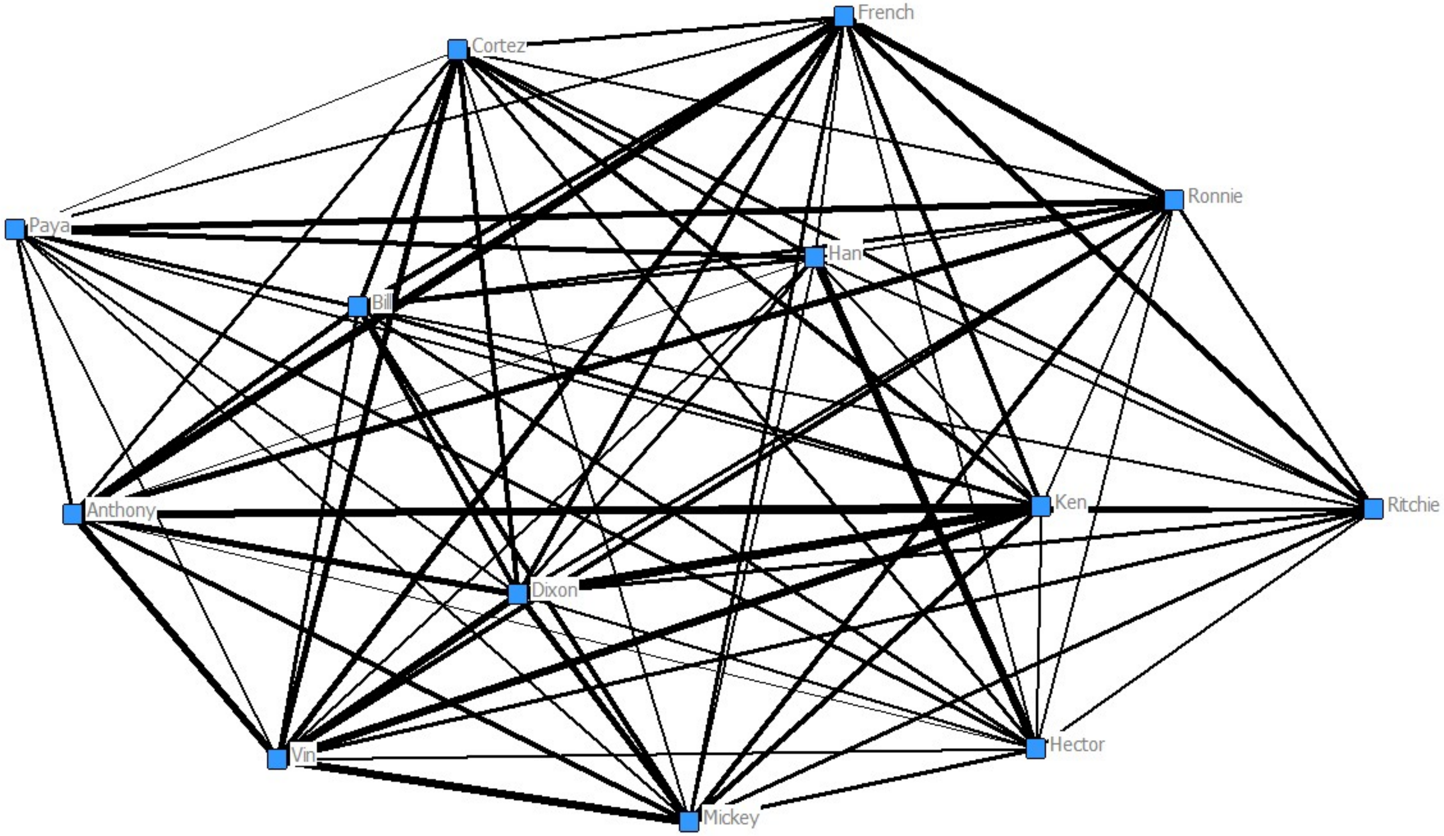
ASSOCIATION COEFFICIENTS BASED ON SAME-SEX SOCIO-SEXUAL INTERACTIONS INCLUDING OBSERVERS

Dyad	COA	SE
Anthony-Bill	0.18	0.04
Anthony-Cortez	0.10	0.03
Anthony-Dixon	0.17	0.03
Anthony-French	0.28	0.05
Anthony-Han	0.09	0.03
Anthony-Hector	0.12	0.04
Anthony-Ken	0.35	0.05
Anthony-Mickey	0.12	0.03
Anthony-Paya	0.17	0.04
Anthony-Ritchie	0.14	0.04
Anthony-Ronnie	0.24	0.04
Anthony-Vin	0.18	0.03
Bill-Cortez	0.04	0.02
Bill-Dixon	0.19	0.04
Bill-French	0.21	0.05
Bill-Han	0.22	0.05
Bill-Hector	0.21	0.05
Bill-Ken	0.14	0.03
Bill-Mickey	0.12	0.03
Bill-Paya	0.20	0.06
Bill-Ritchie	0.27	0.05
Bill-Ronnie	0.28	0.05
Bill-Vin	0.13	0.03
Cortez-Dixon	0.15	0.03
Cortez-French	0.03	0.02
Cortez-Han	0.03	0.02
Cortez-Hector	0.09	0.04
Cortez-Ken	0.03	0.02
Cortez-Mickey	0.10	0.03
Cortez-Paya	0.00	0.00
Cortez-Ritchie	0.01	0.01
Cortez-Ronnie	0.04	0.02
Cortez-Vin	0.14	0.03
Dixon-French	0.13	0.03
Dixon-Han	0.10	0.03
Dixon-Hector	0.08	0.03
Dixon-Ken	0.26	0.04
Dixon-Mickey	0.24	0.04

Dixon-Paya	0.07	0.02
Dixon-Ritchie	0.21	0.04
Dixon-Ronnie	0.21	0.04
Dixon-Vin	0.43	0.04
French-Han	0.13	0.04
French-Hector	0.12	0.04
French-Ken	0.22	0.04
French-Mickey	0.12	0.03
French-Paya	0.12	0.04
French-Ritchie	0.21	0.05
French-Ronnie	0.28	0.05
French-Vin	0.13	0.03
Han-Hector	0.49	0.08
Han-Ken	0.06	0.02
Han-Mickey	0.12	0.04
Han-Paya	0.17	0.05
Han-Ritchie	0.27	0.06
Han-Ronnie	0.21	0.05
Han-Vin	0.12	0.03
Hector-Ken	0.09	0.03
Hector-Mickey	0.11	0.03
Hector-Paya	0.17	0.06
Hector-Ritchie	0.19	0.05
Hector-Ronnie	0.13	0.04
Hector-Vin	0.07	0.02
Ken-Mickey	0.10	0.03
Ken-Paya	0.13	0.04
Ken-Ritchie	0.14	0.03
Ken-Ronnie	0.17	0.04
Ken-Vin	0.21	0.03
Mickey-Paya	0.08	0.03
Mickey-Ritchie	0.07	0.03
Mickey-Ronnie	0.11	0.03
Mickey-Vin	0.39	0.05
Paya-Ritchie	0.14	0.05
Paya-Ronnie	0.21	0.05
Paya-Vin	0.06	0.02
Ritchie-Ronnie	0.25	0.05
Ritchie-Vin	0.09	0.03
Ronnie-Vin	0.17	0.03

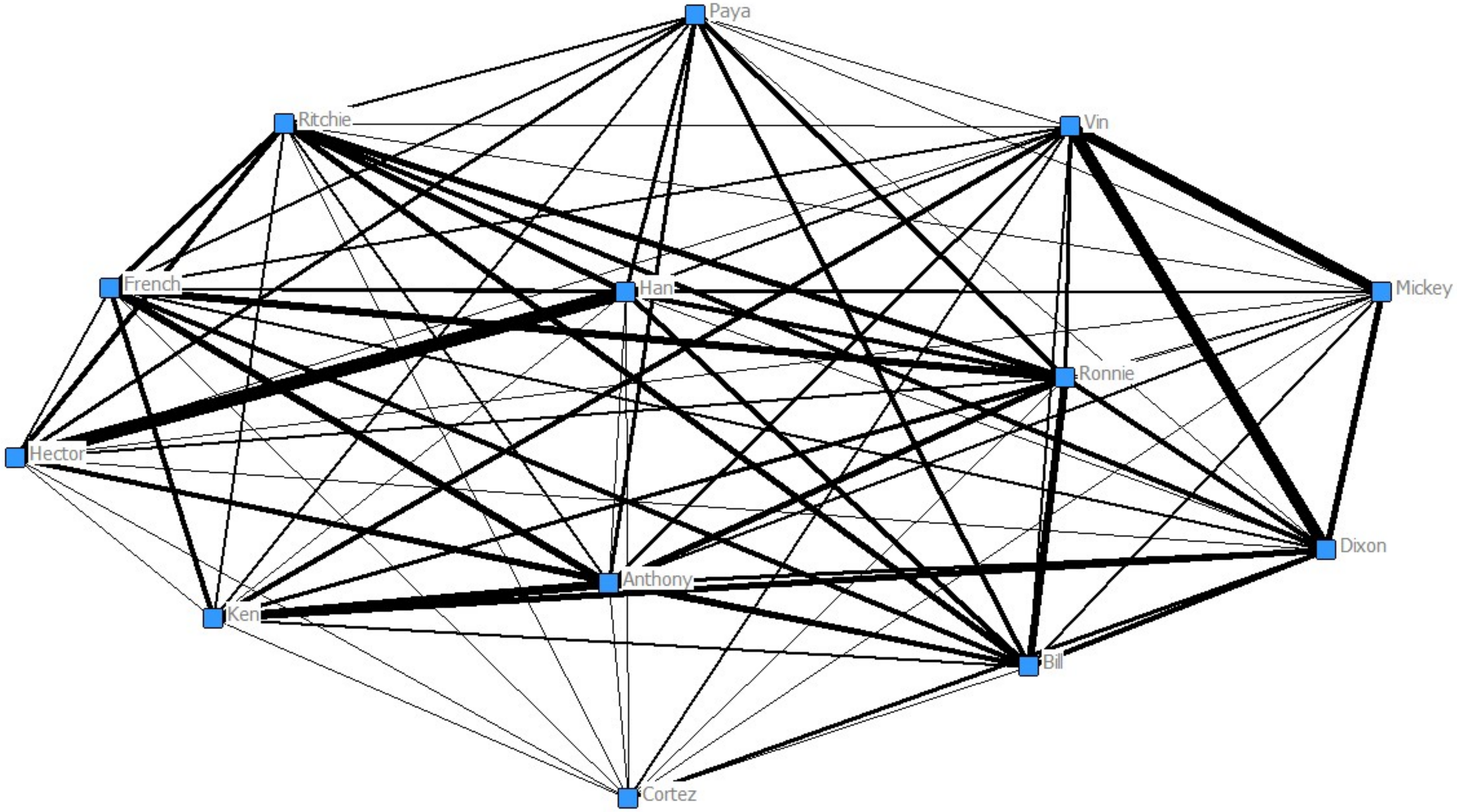
APPENDIX F

SOCIOGRAM



APPENDIX G

SOCIOGRAM INCLUDING OBSERVERS



APPENDIX H

SYMMETRY INDEX BASED ON SAME-SEX SOCIO-SEXUAL INTERACTIONS

Dyad	α_{AB}	X^2	Standard Error
Anthony-French	-0.45	2.27	0.27
Anthony-Ken	0.23	1.19	0.21
Anthony-Ronnie	0.20	0.40	0.88
Anthony-Vin	-0.71	3.57	0.26
Bill-Ken	0.20	0.20	0.44
Bill-Mickey	0.33	0.67	0.38
Cortez-Dixon	-0.78	**5.44***	0.21
Cortez-Vin	-0.11	0.11	0.17
Dixon-Cortez	0.78	**5.44***	0.21
Dixon-Ken	0.24	1.19	0.21
Dixon-Mickey	0.47	3.27	0.23
Dixon-Ritchie	0.73	**8.07***	0.18
Dixon-Ronnie	0.50	2.00	0.31
Dixon-Vin	-0.36	3.24	0.19
French-Anthony	0.45	2.27	0.27
French-Ken	-0.54	3.77	0.23
French-Ronnie	0.20	0.40	0.31
French-Vin	0.20	0.20	0.44
Ken-Anthony	-0.23	1.19	0.21
Ken Bill	-0.20	0.20	0.44
Ken-Dixon	-0.24	1.19	0.21
Ken-French	0.54	3.77	0.23
Ken-Ronnie	0.14	0.20	0.37
Ken-Vin	-0.80	**12.80***	0.13
Mickey Bill	-0.33	0.67	0.38
Mickey-Dixon	-0.47	3.27	0.23
Mickey-Vin	-0.70	**13.37***	0.14
Paya-Ronnie	0.33	0.67	0.38
Ritchie-Dixon	-0.73	**8.07***	0.18
Ritchie-Ronnie	1.00	**6.00***	0.00
Ronnie-Anthony	-0.20	0.40	0.88
Ronnie-Dixon	-0.50	2.00	0.31
Ronnie-French	-0.20	0.40	0.31
Ronnie-Ken	-0.14	0.20	0.37
Ronnie-Paya	-0.33	0.67	0.38
Ronnie-Ritchie	-1.00	**6.00***	0.00
Ronnie-Vin	-0.33	0.67	0.38
Vin-Anthony	0.71	3.57	0.26

Vin-Cortez	0.11	0.11	0.17
Vin-Dixon	0.36	3.24	0.19
Vin-French	-0.20	0.20	0.44
Vin-Ken	0.80	**12.80***	0.13
Vin-Mickey	0.70	**13.37***	0.14
Vin-Ronnie	0.33	0.67	0.38

Note. X^2 *(1 d.f) = 3.87,* significant at $p < 0.05$. Significant values are bolded.

APPENDIX I

IACUC APPROVAL

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
118 College Drive #5116 | Hattiesburg, MS 39406-0001
Phone: 601.266.4063 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: **14100901**
PROJECT TITLE: **"Bottlenose dolphin (Tursiops truncates underwater behavior"**
PROPOSED PROJECT DATES: **10/2014-9/2017**
PROJECT TYPE: **New**
PRINCIPAL INVESTIGATOR(S): **Stan Kuczaj**
DEPARTMENT: **Psychology**
FUNDING AGENCY/SPONSOR: na
IACUC COMMITTEE ACTION: **Full Committee Approval**
PROTOCOL EXPIRATON DATE: **September 30, 2017**

____
Frank Moore, Ph.D.
IACUC Chair

_____October 9, 2014_____________
Date

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