Spring 5-2017

Does Personality Similarity in Bottlenose Dolphin Pairs Influence Dyadic Bond Characteristics?

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DOES PERSONALITY SIMILARITY IN BOTTLENOSE DOLPHIN PAIRS

INFLUENCE DYADIC BOND CHARACTERISTICS?

by

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

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May 2017

Published by the Graduate School

ABSTRACT

DOES PERSONALITY SIMILARITY IN BOTTLENOSE DOLPHIN PAIRS INFLUENCE DYADIC BOND CHARACTERISTICS?

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May 2017

Social structures are critical to the success of many species and have repercussions on health, well-being, and adaptation, yet little is known about the factors which shape these structures aside from ecology and life history strategies. Dyadic bonds are the basis of all social structures; however, mechanisms for formations of specific bonds or patterns in which individuals form which types of bonds have yet to be demonstrated. There is a variety of evidence indicating personality may be a factor in shaping bonds, but this relationship has not been explored with respect to bond components and is yet to be demonstrated in dolphins. This study utilizes a captive population in a naturalistic environment to test for correlation between similarity within the dyad along each personality factor and the strength of the dyad's bond characteristics. Personality was assessed using a Five Factor Model questionnaire. Dyadic bond strength and characteristic qualities were determined through an exploratory factor analysis to group behaviors recorded via underwater opportunistic focal-follow video. Discovered bond components differed from previous studies and were termed affiliative support, sociosexual, and conflict play. Individuals who differed in Extraversion and Neuroticism and were similar in Conscientiousness displayed greater levels of bonding. This study expands our understanding of the formation of bonds between individuals and the

evolution of social structure. Furthermore, it better equips us for making informed environmental policy decisions and improving captive animal care.

ACKNOWLEDGMENTS

I thank the members of the Marine Mammal Behavior and Cognition Lab of the University of Southern Mississippi and Mitch Brown for their unwavering support and immensely helpful discussions. I am incredibly grateful for the time and effort of Ali Taylor in coding 20% of video data for behavioral interaction reliability calculations. Teri Bolton has my eternal gratitude for her invaluable support in all aspects of data collection for this project, and I thank her and the rest of the animal training staff at RIMS for completing personality surveys for this project. Finally, I am enormously appreciative of the support and guidance of my committee, Dr. Stanley Kuczaj, Dr. Lauren Highfill, Dr. Donald Sacco, and Dr. Richard Mohn, without whom this project would never have flourished.

DEDICATION

I would like to dedicate this thesis to a few of the many amazing people in my life who have supported me and made this achievement possible. First, to my husband, Matthew, for being my continual emotional care and encouragement. You always listen to my excited ramblings when things go well and reassure me that there will be a solution when they don't. I'm so fortunate to have you join me while I follow my dreams. Second, to my parents, Robert and Linda. I am so grateful for your constant encouragement and assistance. Thank you, Mom, for reminding me that I can do anything I put my mind to, and Dad, for nurturing my interests by letting me drag you to anything science or animal related. Finally, to Stan, who believed in me, got excited by my research ideas, and helped me with the tools and opportunities to make them happen. Thank you for all you have taught me; I hope to carry your legacy forward and make you proud.

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CHAPTER I - INTRODUCTION

The Importance of Social Structure

Social structures and the patterning of social relationships are vital for the success of group living species. Group living brings with it many potential costs and benefits, including increased competition, higher likelihood of disease transmission, lower predation, and an increased ability to utilize extremely localized or difficult to obtain resources (Alexander, 1974; Silk, 2007). In response, many species have developed social behaviors, which function to maximize benefits while minimizing costs (Alexander, 1974). For example, the social behavior of grooming in primates minimizes the cost of increased parasitism via reciprocal parasite removal and has since taken on the additional social role of influencing and reinforcing relationships, providing further benefit to the behavior and ensuring its continued use (Alexander, 1974). Social relationships which provide short-term benefits such as these are assumed to increase fitness (Silk, 2007). Additionally, there is direct evidence of cases where factors such as group size, relatedness, and within group associations may impact offspring production and survival (Silk, 2007). For example, female calving success is related to the success of a female's associates and modulated by relatedness in bottlenose dolphins (Frère et al., 2010), social bonds between non-related females increases foal birth rates and survival in feral horses (Cameron, Setsaas, & Linklater, 2009), and research on primates indicates the nature of relationships, such as quality, grooming equality, strength, stability, may impact reproductive success (Silk, 2007). These increases in reproductive success would provide an advantage over non-social competitors and may be responsible for the

ecological dominance and wide dispersion of highly social organisms, despite comprising a relatively small number of species (Wilson, 1992).

By impacting the success of individuals and populations, social structure in turn shapes the evolutionary trajectory of clades. As a barrier to gene flow, social separation underlies genetic differentiation (Möller, Wiszniewski, Allen, & Beheregaray, 2007). Thus, certain social structures, through barriers to gene flow and the lowering of the effective sizes of populations, will amplify genetic drift (Storz, 1999). This can enhance fixation time or probability of fixation of beneficial mutations (Frean, Rainey, & Traulsen, 2013) and accelerate divergent evolution by increasing genetic differences between social groups (Storz, 1999) and promoting shifts towards new adaptive peaks (Wilson, 1992). Social structures can also work against these processes, which are dampened by exchange of individuals between groups via fission and fusion events, thus promoting behavioral polymorphism and heterozygosity (Wilson, 1992).

Social structures also make possible the rapid development of new behavioral repertoires, as social learning proceeds far more quickly than genetic change (Galef & Laland, 2005). Individuals glean information from those around them in a variety of ways, from stimulus enhancement to true imitation (Galef & Laland, 2005; Tomasello, Savage-Rumbaugh, & Kruger, 1993) and can copy selectively (Laland, 2004). Additionally, another animal engaging in a behavior or some altered aspect of the environment is required for an individual to gain social information (Coussi-Korbel & Fragaszy, 1995), thus the paths which information transmission follows will be constrained via social structure (Coussi-Korbel & Fragaszy, 1995; Krause, Lusseau, & James, 2009; Kurvers, Krause, Croft, Wilson, & Wolf, 2014). This has been

demonstrated by patch discovery in songbirds (Aplin, Farine, Morand-Ferron, & Sheldon, 2012) and transmission of various feeding behaviors in a variety of cetacean species (Allen, Weinrich, Hoppitt, & Rendell, 2013; Lopez & Lopez, 1985; Mann, Stanton, Patterson, Bienenstock, & Singh, 2012; Sargeant, Mann, Berggren, & Krützen, 2005). This selective pattern of information transmission is so strong that in some instances, such as social transmission of vocalization patterns resulting in the shaping of multi-level groups, it may even be indicative of culture (Cantor et al, 2015; Rendell & Whitehead, 2001). Thus, who an individual's associates are can have a great impact on which behaviors an individual learns and uses, how a behavior propagates through the population, and even how those behaviors reinforce or alter the original social structure, forming the basis of culture (Cantor et al., 2015).

Current Knowledge of Bottlenose Dolphin Social Structure

In order to investigate one possible driving force of social structure, this study focused on bottlenose dolphins, a gregarious aquatic mammal with a cosmopolitan distribution which is frequently found near shore. Due to these features, the bottlenose dolphin has been the subject of numerous studies on various aspects of social structure, providing an extensive background of literature. Bottlenose dolphins exhibit fission-fusion patterning of associations, such that individuals are often well connected and many contain hierarchical groupings of associates (Gowans, Würsig, & Karczmarski, 2008; Lusseau, 2003; Rogers, Brunnick, Herzing, & Baldwin, 2004; Shane, Wells, & Wursig, 1986; Smolker, Richards, Connor, & Pepper, 1992; Wells, Scott, & Irvine, 1987). Males typically have fewer, stronger bonds, and are well known for forming alliances, although the manifestation of this feature varies greatly between populations (Connor & Krützen,

2015; Connor, Watson-Capps, Sherwin, & Krützen, 2011; Foley, McGrath, Berrow, & Gerritsen, 2010; Lusseau, 2007; Lusseau et al., 2003; Owen, Wells, & Hofmann, 2002; Randić, Connor, Sherwin, & Krützen, 2012; Wells et al., 1987). Females typically have many loose bonds, sometimes display grouping by reproductive status, and in some populations are organized into clans (Félix, 1997; Möller & Harcourt, 2008; Rogers et al., 2004; Scott, Irvine, & Wells, 1990; Smolker et al., 1992; Wells et al., 1987; Wells, 1991; Wiszniewski, Allen, & Möller, 2009).

While general trends for bottlenose dolphin social structure are consistent, variation is observed between locations. Most research has focused on a handful of habitats which, despite all displaying some similar habitat features, exhibit variation in population social structure as well as connections between and within the sexes (Connor & Krützen, 2015; Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012; Félix, 1997; Foley et al., 2010; Lusseau, 2007; Owen, Wells, & Hofmann, 2002; Rogers et al., 2004; Wells et al., 1987). It is likely that populations inhabiting even more geographically diverse locations will display more social structure differences (Moreno & Kuczaj, 2015) as we know ecology plays a role in shaping social structure patterns for different species (Gowans et al., 2008), and will likely have impacts within species as well, particularly depending on whether the habitat is open water, coastal, or inshore (Möller, 2012).

Social Structure Components

Although social structures are comprised of dyadic associations (Krause, Croft, & James, 2007), social structure research in bottlenose dolphins, like research on other species, has focused on the overall structure while neglecting investigations into the

components of dyadic relationships or the factors which shape them. Additionally, much social structure research relies on a single measure of dyadic relationships, the coefficient of association. The coefficient of association relies on the proportion of time two animals spend together out of the proportion of time both animals are observed and can be adjusted to increase estimation accuracy in different sampling situations (Cairns & Schwager, 1987). This is very useful for mapping population-wide patterns of associations but fails to account for different types of relationships which may exist between dyads or the types of interactions those dyads have with one another.

In order to capture more detail about social relationships between individuals, we must describe various components of dyadic relationships in as accurate and detailed a manner as possible. To do so, we must first consider that a relationship is made up of a series of interactions over time, and is influenced by the content, quality, frequency, and patterning of the interactions (Hinde, 1976). Then we must devise a methodology to measure suites of interactions which impact the relationship similarly, thus indicating consistent components of relationships. Recent research on chimpanzees (Fraser, Schino, & Aureli, 2008; Koski, Vries, Kraats, & Sterck, 2012), macaques (Majolo, Ventura, & Schino, 2010; McFarland & Majolo, 2011), spider monkeys (Rebecchini, Schaffner, & Aureli, 2011), and ravens (Fraser & Bugnyar, 2010) has worked to do exactly that, though grouping multiple behaviors into components which capture different aspects of the overall relationship between individuals. All but one (Rebecchini et al., 2011) of these studies have confirmed the three relationship components proposed by theory: value, compatibility, and security. Value measures the benefits afforded by the relationship in terms of resource or opportunity gain, compatibility is indicative of

tolerance and affiliation between the two individuals, and security denotes the predictably and consistency of interactions over time (Cords & Aureli, 2000; Fraser & Bugnyar, 2010; Fraser et al., 2008). These components have also been demonstrated to be relatively consistent over time in chimpanzees (Koski et al., 2012). Finally, in addition to confirming theoretical components, some species-specific patterns have been found, such as the importance of asymmetry in macaque relationships (Majolo et al., 2010; McFarland & Majolo, 2011), and the component of risk in spider monkey relationships (Rebecchini et al., 2011).

Dolphins may or may not exhibit components similar to those found in other species. The findings of similar relationship components in species with different social systems and evolutionary backgrounds (Fraser & Bugnyar, 2010; Fraser et al., 2008; McFarland & Majolo, 2011; Rebecchini et al., 2011) provides promising support for the universality of the underlying framework for relationship components. However, due to species differences in physiology, habitat, and behavior, the interaction behaviors exhibited may lead to different results, either in the overall pattern or the details of components within the overall pattern, and thus may not be directly comparable with previous studies. Observed differences in components will most likely be due to presence or absence of specific behaviors and potential differences in use or significance of the same behaviors (McFarland & Majolo, 2011).

Personality May Influence Social Structure Components

In addition to categorizing the components of dyadic relationships, it is important to investigate factors which may influence the formation of these relationships and their features. Personality, the construct of stable individual differences in suites of behavioral

tendencies (Bell, 2007; Carere & Eens, 2005; Sih, Bell, Johnson, & Ziemba, 2004), has been predicted to influence the types of relationships which an individual dolphin is likely to have (Highfill & Kuczaj, 2007; Highfill & Kuczaj, 2010; Wilson, Krause, Dingemanse, & Krause, 2012). Thus, it may be a driving factor of bond formation and different types of dyadic relationships.

This link has been demonstrated in humans (e.g., Duck, 1973; Izard, 1960; Selfhout et al., 2010), great tits (Aplin et al., 2013), and non-human primate species, including chimpanzees (Massen & Koski, 2014), capuchins (Morton, Weiss, Buchanan-Smith, & Lee, 2015), and rhesus monkeys (Weinstein & Capitanio, 2008). Interestingly, the specific trait and association correlations differ between species. Humans preferentially form friendships with individuals similar in agreeableness, extraversion, and openness (Selfhout et al., 2010). Great tit males displayed assortative mixing along a proactive-reactive axis (Aplin et al., 2013). Chimpanzees engaged in higher levels of contact sitting, a behavior indicative of affinitive bonds, with individuals similar in sociability and boldness (Massen & Koski, 2014). In Capuchins, similar levels of neuroticism correlated with higher affiliative relationship scores, similar levels of sociability correlated with a larger difference between affiliative and agonistic scores, and, when non-dispositional factors such as age and rank were not controlled for, similar levels of openness correlated with lower agonistic scores (Morton et al., 2015). Finally, rhesus monkey yearlings preferentially associated with peers with similar equitability and adaptability (Weinstein & Capitanio, 2008). In contrast, barnacle geese displayed no effect of personality on foraging associations or mate choice (Kurvers et al., 2013). However, none of these studies contained relationship quality component information

beyond affiliative and agonistic components (Morton et al., 2015), and so do not match with the 3 components of value, compatibility, and security, which may also be influenced differently by individual differences such as personality (Cords & Aureli, 2000).

To understand how personality influences social structure, we must note that individually stable behavioral variation provides a source of individual variation on which multiple processes can act. For many species and habitats, behavioral types exhibit non-random distributions as a result of their behavioral differences. This can occur through influencing habitat use (Croft et al., 2009), location in the population structure, level of social interaction (Wolf & Krause, 2014), or situation choice (Sih et al., 2004). For example, more proactive animals may range over a larger area than reactive individuals or utilize areas which reactive individuals do not (Aplin et al., 2013), or reactive individuals may have greater success in areas where proactive individuals fare poorly (Capitanio, Mendoza, & Baroncelli, 1999). Thus, different individuals are better suited to different situations, and many trait suites represent trade-offs (Sih et al., 2004; Wolf, van Doorn, Leimar, & Weissing, 2007). This in turn influences who individuals can interact and form bonds with (Kurvers et al., 2014; Wilson et al., 2012), as a non-random distribution will result in non-random interactions between individuals with different behavioral types (Wolf & Weissing, 2012). Thus, individuals with different behavioral types will differ in the location, structure, and dynamics of the networks of which they are a part (Aplin et al., 2013; Croft et al., 2009; Wolf & Krause, 2014; Wolf & Weissing, 2012).

Non-random assortment provides an evolutionary benefit for frequency dependent strategies, such that clustering of types promotes cooperation and increases fitness of those with similar phenotypes (Kurvers et al., 2014), which often leads to behavioral trait assortment (Croft et al., 2009). We see the fitness benefit of pairing on the basis of at least one trait in the higher breeding success of great tits when both members of a mating pair lie on the same extreme of the boldness behavioral trait (Both, Dingemanse, Drent, & Tinbergen, 2005), and of Steller's jays when pair members displayed similarity across multiple traits, particularly after a severe winter (Gabriel & Black, 2012). These benefits may have selected for a personality influence on social bond formation. Thus, we have identifiable mechanisms and reasons for personality to be a shaping factor in social structures.

Present Study

This study aims to further our understanding of the connection between personality and social bonds in animals. While this relationship has already been demonstrated in some birds and primates, additional findings showing similar or different patterns in a new taxon could help illuminate differences and similarities between groups This can, in turn, inform us about evolution of social structure, both through phylogenetically related groups and ecological pressures in disparate taxa which may produce convergent evolution.

Benefits of this study also extend to more practical applications such as improving captive animal housing. Personality assessments are often stated to be useful in decisions about animal care and housing or that personality may be directly linked to animal health and well-being in captive settings, as seen in the Scottish wildcat (Gartner & Weiss,

2013), yet few studies propose how these assessments are useful. One suggestions is using personality to match individuals with roles for which they are most suited (Watters & Powell, 2012), another is to use personality to inform housing (Capitanio, Blozis, Snarr, Steward, & McCowan, 2015).

Behavioral studies, such as this, are also a powerful tool for conservation (Buchholz, 2007). Individual behavioral variation not only impacts transmission dynamics and social evolution within a species but also has effects further downstream on community structure and ecosystem processes, particularly through interactions between predator and prey communities (Buchholz, 2007; Wolf & Weissing, 2012). As dolphins are a high-level aquatic predator, cetacean health is often indicative of ecosystem health (Wells et al., 2004), and it would be logical to expect that behavioral variation and social relationships will have an impact on the ecosystem they inhabit. Thus, understanding social structure and the factors which shape it, such as personality, in dolphins is advantageous for understanding and conserving many aquatic systems.

For the current study, I examined the potential relationship between dolphin personality and dyadic bond characteristics. Anticipated results were that individuals with similar personalities would display bonds that were stronger and more valuable, compatible, and secure in nature than those with dissimilar personalities, particularly with regard to the traits of agreeableness, extraversion, and openness.

CHAPTER II - METHODS

Subjects

This study utilized the captive population at the Roatan Institute of Marine Science (RIMS) which is part of Anthony's key resort in Roatan, Honduras. This population has been shown to be similar to wild populations in regard to both the age and sex distribution of the population, and interactions between individuals (Dudzinski et al., 2012; Dudzinski, Gregg, Paulos, & Kuczaj, 2010). The population is housed in a natural enclosure which is approximately 300 m2 in area and ranges in depth from the shoreline to just over 8 meters (Dudzinski et al., 2010). The sea floor reflects the natural habitat, with sea-grass beds, sand, and coral. All members of the population are fed a regular diet of fish and receive regular human interaction. As a result, they are habituated to humans and filming possesses a minimal potential for disturbance.

Table 1

Number of Dolphins in each Age Class by Sex

Age Class	*Male*	*Female*
Adult (11 years and older)	4	7
Sub-adult (8 to 10 years)	1	1
Juvenile (4 to 7 years)	0	0
Calf (up to 4 years)	3	4

There were a total of 20 individuals, consisting of males and females of various ages (Table 1), included in the current study. Overall, there were 190 dyads used to characterized dyadic interactions and relationships. All individuals were identifiable via

unique features, and temporary identifiers such as rake marks were recorded and used to assist in identification.

Data Collection and Analysis

Dyadic Bond Characteristics

Video data were gathered by S. Kuczaj using a high-definition underwater video camera in 2014 from March 7th to March 15th and from May 12th to May 21st. Sampling consisted of opportunistic focal follows, and occurred daily while all individuals were in the main enclosure. Only videos containing a minimum of 15 seconds were included for analysis in order to focus on samples which were long enough to include information relevant to the study. Total video duration of the subset selected for analysis was 12 hours, 46 minutes and 45 seconds, which is above the 10-hour minimum shown to provide an accurate picture of calf associations (Gibson & Mann, 2009).

Behavioral coding of video samples was used to describe bond characteristics. Association coefficients to indicate bond strength were calculated from instantaneous samples taken every 15 seconds. Individuals were considered associated if they were located in the same group, defined as individuals within one adult body length (approximately 3 m) of one another using the chain rule. The half-weight ratio index (HWI) was used for the association coefficient as it is the most accurate index for situations where members of a pair are more likely to be sampled when together than apart (Cairns & Schwager, 1987), and is most applicable to the video samples used, as only a portion of the enclosure is in view of the video camera at a time, even in good visibility. The association index was included as a separate measure instead of being

incorporated with other bond characteristics due to its difference in nature from interaction measures and its widespread use in the literature.

Additional bond characteristics were assigned based on the nature of the interactions observed between individuals. To categorize these features, all observed interaction behaviors were recorded. Observed interaction behaviors (Appendix A) were similar to those in previously used comprehensive dolphin ethograms and bond characteristic studies (Dudzinski, 1996; Fraser & Bugnyar, 2010; Fraser et al., 2008). Duration of each behavior was recorded. Directionality of each interaction was recorded whenever possible, and non-directional behaviors were recorded as occurring in both directions. Only interactions and associations for which all individuals were identified were retained for further analysis. Reliability was assessed through coding of 20% of the data by an independent observer who is familiar with the population.

To group the observed interactions into factors indicative of relationship quality components, exploratory factor analysis, a method for uncovering the underlying structure of multiple variables, was used. Unlike the previous studies which used principal component extraction and verimax rotation (Fraser & Bugnyar, 2010; Fraser et al., 2008), this study employed principle axis factoring for variable extraction with oblimin rotation and kaiser normalization. This method is suited to finding variance shared among groups of factors rather than determining the major components which make up the total observed variability (Meyers, Gamst, & Guarino, 2013). Thus, it was a better fit for determining suites of observable interactions indicative of the underlying construct of relationship components. Finally, the values of the identified components

were determined for each pair based on the interactions observed between members of the dyad.

Personality Similarity

Personality was determined using a questionnaire (Appendix B) given to the trainers at RIMS familiar with the study subjects. Ratings of personality have been demonstrated to be consistent with observational and experimental personality assessments (Carter, Marshall, Heinsohn, & Cowlishaw, 2011; Highfill, Hanbury, Kristiansen, Kuczaj, & Watson, 2010; Horback, Miller, & Kuczaj, 2013), and show high levels of reliability and predictive validity (Gosling & Vazire, 2002). This questionnaire follows previous studies applying the human five-factor model of personality to animals (Highfill & Kuczaj, 2007; Highfill, 2013; Horback et al., 2013; Kuczaj, Highfill, & Byerly, 2012; Kuczaj & Kristiansen, 2013). Using the five human factor model has the benefit of being a well-established and well-developed model already in use which has already been applied successfully to multiple species, including dolphins, and can thus be used for interspecies comparisons (Highfill & Kuczaj , 2007; Horback et al., 2013; Kuczaj & Kristiansen, 2013). The disadvantage is that it was developed for use on humans and thus will likely retain anthropogenic biases and the associated limitations, so it may not be most accurate or best fitting model (Highfill & Kuczaj , 2007).

Each personality factor was assessed using three questions rated using a seven-point Likert scale. The three questions were selected as the most informative of the six questions per factor from the questionnaire used by Highfill & Kuczaj (2007) to assess dolphin personality. Questionnaires were provided in both English and Spanish to minimize language barriers to participation. Raters were asked to not discuss the

questionnaires with one another and complete the assessments independently. Responses were gathered from two raters for each dolphin and tested for inter-observer agreement. Personality factors which did not achieve inter-observer agreement were removed from the analysis. Values for each trait were determined by averaging the responses provided by both observers for each trait. Then, for each dyad, similarity on each trait was determined using the absolute value of the difference score.

Relating Dyadic Bond Characteristics and Personality Similarity

Finally, a structural equation model was run to test for correlation between the similarity of personality traits of the individuals in the dyad and the dyadic strength and relationship quality components. The model employed HWI strength and the dyadic characteristics derived from the exploratory factor analysis as indicators of a latent variable named "bonding" which encompasses the idea of how well the dyad is bonded. Measures of similarity for each personality trait were incorporated as predictor variables to determine if they influence the bonding latent variable.

CHAPTER III – RESULTS

Dyadic Bond Characteristics

Reliability with an independent observer on 20% of video data was achieved for both association and interaction coding. Association coding had 95.97% agreement with $p < 0.001$ using a mantel z-test. Interaction coding had 88.18% agreement with a Cohen's kappa of 0.544 indicating moderate agreement. However, as most disagreements were due to differences in decision to include or exclude the behavior, not in the categorization of the behavior or identification of actor or recipient, agreement is more robust than the kappa indicates. Additionally, the primary coder (KRM) was more conservative, and only her data were used for analysis.

Exploratory factor analysis performed on interaction behaviors yielded 3 component dimensions of relationships (Table 2) as determined from the scree plot and factor loadings. The first component consisted of conflict support, group swim, open mouth, pair swim, pair swim with contact, pectoral rub, petting, synchronous breath, touch, and conflict support. Due to the inclusion of affiliative, tolerant, synchronous, and supportive behavior, this factor was termed affiliative support. The second component consisted of body rub, flee, group social ball, herd, other tactile, and sex. As these behaviors are all associated with sociosexual contexts, this factor was termed sociosexual. The third component consisted of exchange, head to head hit, open mouth, take object, and touch. These behaviors encompass both play and conflict interactions, thus this factor was termed conflict play.

The same factors were also obtained when the EFA was run without mother-calf pairs, indicating the presence of mother-calf interactions did not skew the results of the

analysis. However, slight differences in behavior loadings were obtained. In these results, open mouth was removed because it loaded evenly on all factors, mouthing was retained on the affiliative/support factor, and conflict support and other tactile did not load and were removed.

Table 2

Pattern Matrix With Factor Loadings from Exploratory Factor Analysis

	Component		
	1 – Affiliative Support	2 – Sociosexual	3 – Conflict Play
Body Rub		.537	
Conflict Support	.289		
Exchange			.312
Flee		.377	
Group Social Ball		.785	
Group Swim	.545		
Head to Head			.577
Herd		.301	
Hit			.348
Open Mouth	.316		.501
Other Tactile		.312	
Pair Swim	.969		
Pair Swim with Contact	.779		
Pectoral Rub	.622		
Petting	.628		
Sex		.789	
Synchronous Breath	.336		
Take Object			.683
Touch	.491		.564

EFA utilized principle axis factoring for variable extraction with oblimin rotation and kaiser normalization. Number of factors were indicated by the scree plot. Loadings above 0.25 displayed. Behaviors which did not load are not displayed.

Personality Factors

Pearson correlation coefficients determined that four of the five personality factors had interrater reliability between two raters with Pearson correlation coefficients ranging from r = 0.53 to r = 0.77. The factor of Agreeableness was found to not be

reliable between raters with a Pearson correlation coefficient of r = 0.14 and was thus removed from further analyses.

Relating Dyadic Bond Characteristics and Personality Similarity

The structural equation model between personality similarity and bond components with a latent variable for bonding (Figure 1) was a valid fit with TLI = 0.874, CFI = 0.937, and RMSEA = 0.103 (90% CI = 0.069, 0.140). All bond characteristics were indicative of the latent variable of bonding at $p < 0.001$ (HWI association strength $\beta = 0.909$; Affiliative support $\beta = 0.856$; Conflict play $\beta = 0.746$; and Sociosexual $\beta = 0.379$). Three personality traits significantly predicted bonding; they were extraversion ($\beta = -0.240$, $p = 0.006$), conscientiousness ($\beta = 0.159$, $p = 0.040$), and neuroticism ($\beta = -0.145$, $p = 0.049$). Openness to experience ($\beta = -0.153$, $p = 0.074$) did not significantly predict bonding.

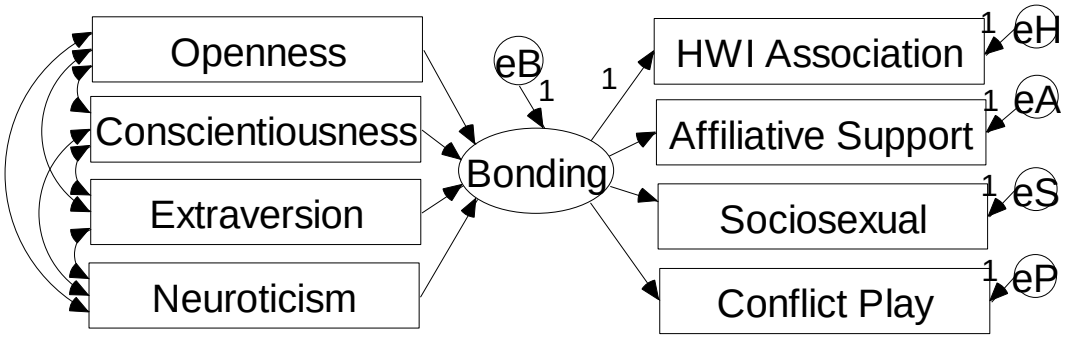

Figure 1. Path Diagram for Structural Equation Model.

CHAPTER IV – DISCUSSION

Dyadic Bond Characteristics

The facets of dyadic interactions which resulted from the exploratory factor analysis were logical, though they did not replicate the findings of previous research on relationship components conducted in other taxa. Only one factor, affiliative support, closely resembles previously described relationship factors. The other two factors, sociosexual and conflict play, were novel, and their presence may be due to the difference in behavioral coding scheme, inherent differences in dolphins from other species studied, or unique behavioral patterns in this population. Additionally, the previously found factor of security was not evident in the factor results. This is likely due to the differences from previous studies in behaviors measured. This study only included discrete behavioral events, and as such, did not specifically measure temporal change or reciprocity, the two main facets of security.

The factor of affiliative support most closely resembles that of compatibility found in previous research (Fraser & Bugnyar, 2010; Fraser et al., 2008; Majolo et al., 2010; McFarland & Majolo, 2011). However, the behavior of conflict support also weakly loads onto this factor, despite previous research grouping it with the value factor. This difference may be due to the lack of additional value behaviors which would group with conflict support into a stand-alone factor in conjunction with the possible value behavior "exchange" grouping with play behaviors. Interestingly, the behaviors touch and open mouth loaded on both affiliative support and conflict play, likely because the behaviors may convey different information based on context and other associated behaviors (Kaplan & Connor, 2007; Kuczaj & Frick, 2015).

Of the two factors unique to this study, sociosexual was unsurprising given the great amount of sexual behavior engaged in by this population and dolphins in general (Mann, 2006). However, the other unique factor, Conflict Play, is particularly interesting. This factor included behaviors which were positive play behaviors which may improve the compatibility or value of a relationship, such as exchange (Fedorowicz, Beard, & Connor, 2003; Greene, Melillo-Sweeting, & Dudzinski, 2011; Paulos, Trone, & Kuczaj, 2010), with behaviors which have been observed in aggressive or conflict contexts, such as hit and head to head (Lusseau, 2007; Tamaki, Morisaka, & Taki, 2006; Yamamoto et al., 2015). Which demonstrates that pairs which engage in positive play behaviors also engage in conflict behaviors. This may be due to reconciliation (Weaver, 2003; Yamamoto et al., 2015), or behaviors typically considered to constitute conflict may not actually be serving an agonistic function. Additionally, these behaviors almost exclusively occurred in pairs where one or both animals were immature. Thus, they may be behaviors specific to interactions which include an immature animal or these behaviors may not carry the same implications for a dyadic bond when occurring in an interaction with an immature individual as they would if they occurred between adults.

Personality Factors

Lack of reliability for the personality factor of agreeableness is consistent with previous findings which indicate interobserver agreement is lowest for agreeableness in both animals and humans (Gosling, 2001). Reliability on the other 4 factors was good, demonstrating they were an accurate depiction of the personality of the study subjects (Gosling, 2001; Highfill & Kuczaj, 2007).

The biggest limitations in assessing personality of the dolphins in this study were the number of questionnaires obtained per animal and the number of questions presented on the survey. Additional questionnaires per animal and additional questions on the survey could have allowed us to limit the analyses to highly reliable raters and items, thus removing error effects from rater disagreement. This was not done due to the number of animals involved in the study and to avoid undue burden on the raters. Additionally, selecting responses based on agreement may have artificially removed sources of variation and resulted in personality assessments which were not reflective of the animals.

Relating Dyadic Bond Characteristics and Personality Similarity

The structural equation model demonstrated personality similarity is implicated in the strength of dyadic bond facets. Interestingly, the personality factors did not influence relationship components in the manner predicted. Extraversion, Conscientiousness, and Neuroticism similarity were found to be significant predictors of dyadic bonding, despite predictions from human and animal literature that openness and agreeableness would also play important roles in bond quality (Aplin et al., 2013; Capitanio et al., 1999; Duck, 1973; Izard, 1960; Massen & Koski, 2014; Morton et al., 2015; Selfhout et al., 2010; Weinstein & Capitanio, 2008). Agreeableness was not found to be a significant predictor due to the inability to include this trait in the overall model of the present study as the ratings were not reliable. The insignificance of openness similarity as a predictive factor indicates this facet is unimportant to dolphins when shaping interactions and relationships. This may mimic the low influence of openness on friendship satisfaction in humans (Wilson, Harris, & Vazire, 2015). However, while relationship satisfaction and

bonding levels are connected (Medvene, Teal, & Slavich, 2000), they are not the same thing, so openness may simply be unimportant to dolphin bond formation due to the much greater importance of other factors. Additionally, future research may be able to elucidate how personalities of individuals impact the different aspects of interindividual bonds.

Previous studies found more positive bonds when individuals were more similar, in direct contrast to the present findings of greater levels of bonding between individuals with greater trait disparity for two of the three significant traits. For extraversion, the factor with the greatest influence on bonding, this may be due to a connection with dominance (Mehrabian, 1996). Difference in dominance is likely to be especially important for male relationships, as a difference may minimize interindividual conflict (Highfill & Kuczaj, 2007) and increase complementarity of the pair. This phenomenon may or may not apply to female or mixed-sex bonds as well, suggesting future research into the effects of sex on extraversion difference impacting bonding.

For neuroticism, differences between dyad members in the trait may reduce the chances of both individuals being high, thus keeping total neuroticism in they dyad down. This would be benefit the dyad, as high neuroticism negatively impacts human relationships (Greenfield, Gunthert, & Forand, 2014; Roberts, Kuncel, Nathan, Shiner, Caspi, & Goldberg, 2007; Wilson et al., 2015). Investigating the effects of total neuroticism levels of the dyad may shed light onto the validity of this proposed mechanism. Future studies should also investigate whether age class impacts the influence of personality similarity on dyadic bonding as it is currently unknown whether these relationships are stable or change through an animal's lifetime.

Only conscientiousness, correlated with higher levels of bonding when similar between the two dyad members. This pattern was unanticipated, though studies on human relationships do indicate a role for conscientiousness in interindividual bonds. Conscientiousness has not yet been demonstrated to play a role in animal relationships, though similar behaviors suggest a connection may exist. In chimpanzees, one related behavior, grooming equitability, is more similar between friends than non-friends for non-kin, while another, exploration-persistence, had no bearing on bonding (Massen & Koski, 2014). In humans, conscientiousness of an individual is associated with greater friendship satisfaction (Wilson et al., 2015), number of reciprocal friends, friendship quality, and peer acceptance in adolescents (Jensen-Campbell & Malcolm, 2007), and negatively correlated with divorce (Roberts et al., 2007). Among pairs of individuals, differing levels of conscientiousness in romantic partners is correlated with lower relationship satisfaction, intimacy, and commitment (Barelds & Barelds-Dijkstra, 2007) while similar levels of conscientiousness among roommates is associated with higher relationship quality (Kurtz & Sherker, 2003). Conscientiousness is also thought to play a greater role in bond maintenance than bond formation (Selfhout et al., 2010), thus future studies should examine whether conscientiousness differentially impacts bond formation and maintenance in dolphins.

Conclusions

Personality assessments are touted for their utility in informing positive housing situations for captive animals by predicting pairing success, as demonstrated in Rhesus monkeys (Capitanio et al., 2015). Similarly, this study can inform facilities on improving cetacean housing situations by predicting which animals may form positive relationships

and do well in shared housing, and which animals may have negative relationships and need to be separated for the well-being of both individuals. Since these findings demonstrate bottlenose dolphins have greater levels of bonding with individuals who are dissimilar to them in extraversion and neuroticism and similar in conscientiousness, they suggest dolphins will be most able to form positive social bonds in housing situations containing individuals with a mix of personalities.

As social structures are ecologically salient and assessing change in network structure can show anthropogenic effects (Ansmann, Parra, Chilvers, & Lanyon, 2012; Wey, Blumstein, Shen, & Jordán, 2008) or be utilized for wildlife mortality assessments (Whitehead & Gero, 2014), further knowledge of driving forces behind social structures can inform conservation policy. Similar to what will most benefit captive dolphins, these findings suggest wild populations will do best with a mix of personalities, which is further supported by the impacts of personality population dynamics, evolution, and ecology (Wolf & Weissing, 2012). Additionally, they advocate for vigilance in avoiding disturbances which may disproportionately impact one personality type over another, as this may cause disruptions in the social system and may indirectly impact large portions of the population.

Finally, despite the limitations of survey and video data collection, this study clearly provides additional support for individual personality as a major impact on the interactions and associations animals have with one another. By further linking two fields of study which examine critical aspects of animals' lives, we gain a better understanding of the mechanisms behind social relationship formation and can make more informed decisions regarding captive animal care and wildlife conservation efforts. Thus, these

findings highlight an important relationship which warrants further study, particularly into the components and mechanisms of this relationship, as well as the impact of demographic factors such as sex and age.

APPENDIX A – Interaction Behaviors

Table A1.

Behaviors Included in Interaction Coding and their Operational Definitions

Behavior	*Definition*
Approach	Dolphin quickly swims toward another
Flee	Dolphin moves quickly away from another dolphin
Open Mouth	Dolphin directs jaws held apart at another dolphin
Mouthing	Dolphin contacts or manipulates a part of another dolphin within its mouth
Bite	Dolphin applies force on another dolphin with its teeth
Rake	Dolphin drags teeth along another dolphin with force
Jaw Clap	Dolphin snaps jaws shut in a forceful manner directed at another dolphin
Body Rub	Dolphin moves its body along another dolphin in a back and forth motion
Pectoral Rub	Dolphin rubs a pectoral fin along another dolphin
Petting	Two dolphins rub their pectoral fins together
Touch	Dolphin very briefly contacts another dolphin
Maintained contact	Extended contact between individuals which is not part of a pair swim with contact. Similar to a touch, but longer
Push	Dolphin applies force to another so as to move the recipient
Head to Head	Dolphins contact one another with their melons
Brush Past	Dolphin quickly and forcefully swims past another while in contact
Other Tactile	Dolphin is in contact with another in a manner not included in another category
Pair Swim	Two dolphins swim together within one body length in a synchronous manner
Pair Swim With Contact	Dolphins engage in a pair swim while maintaining contact with one another
Group Swim	More than two dolphins swim together synchronously within one body length
Follow	A dolphin swims after another while maintaining distance between them
Group Social Ball	Three or more dolphins swim rapidly around each other and appear to be “wrestling” – such that it is extremely difficult to identify the individual behaviors each dolphin is engaging in
Sexual	Dolphins are engaging in contact with genitals
Chase	Dolphin rapidly and persistently pursues another
Herd	Dolphin is behind another dolphin and is directing the other dolphin’s movement

Hit	Dolphin quickly and forcibly contacts another using a body part such as a rostrum or fluke
Hold	Dolphin positions itself against another dolphin to keep it in a location
Synchronous Breath	Two or more dolphins surfacing to breathe at the same time
Exchange	Dolphin gives an object to another
Take Object	Dolphin forcefully removes object from the possession of another
Conflict Support	When dolphin A is engaged in an aggressive interaction (involving chase, hit, bite, rake, or jaw clap), dolphin B joins the interaction by directing aggressive behaviors towards the other party to assist dolphin A

APPENDIX B – Personality Survey

Dolphin Name: _____ Date: _____

Rater's Name: ___ _____ Years with Animal: _____

How confident are you in rating this animal?

Very Confident	Somewhat Confident	Slightly Confident	Neutral	Slightly Unsure	Somewhat Unsure	Very Unsure

Please circle the dimension which best describes the target animal.

1. Curious: Appears to be interested in new situations or objects.

Very Curious	Somewhat Curious	Slightly Curious	Neutral	Slightly Uninterested	Somewhat Uninterested	Very Uninterested

2. Demanding: Requires much effort or attention from other dolphins and/or humans.

Very Demanding	Somewhat Demanding	Slightly Demanding	Neutral	Slightly Undemanding	Somewhat Undemanding	Very Undemanding

3. Alert, Vigilant: Ready, attentive, watchful, appears to pay attention to surroundings.

Very Alert	Somewhat Alert	Slightly Alert	Neutral	Slightly Oblivious	Somewhat Oblivious	Very Oblivious

4. Aggressive: Threatens or causes harm, high frequency of raking, biting or hitting other animals and/or humans.

Very Aggressive	Somewhat Aggressive	Slightly Aggressive	Neutral	Slightly Unaggressive	Somewhat Unaggressive	Very Unaggressive

5. Affiliative, companionable: Agreeable and sociable. Appears to like the company of others. Seeks out social contact with another animal or person.

Very Affiliative	Somewhat Affiliative	Slightly Affiliative	Neutral	Slightly Solitary	Somewhat Solitary	Very Solitary

6. Creative, imaginative: Approaches situations and addresses problems in novel, creative ways. (E.g. finds various ways to play with a toy)

Very Creative	Somewhat Creative	Slightly Creative	Neutral	Slightly Uncreative	Somewhat Uncreative	Very Uncreative

7. Friendly, gentle: Friendly, amicable, and congenial toward other animals and humans. Responds to others in an easy, kind, manner.

Very Friendly	Somewhat Friendly	Slightly Friendly	Neutral	Slightly Unfriendly	Somewhat Unfriendly	Very Unfriendly

8. Undependable, unreliable: Not easily relied or depended on. Not a "go-to" animal.

Very Undependable	Somewhat Undependable	Slightly Undependable	Neutral	Slightly Dependable	Somewhat Dependable	Very Dependable

9. Relaxed, calm: Assured or at ease. Not tense or highly sensitive.

Very Relaxed	Somewhat Relaxed	Slightly Relaxed	Neutral	Slightly Tense	Somewhat Tense	Very Tense

10. Careful, cautious: Animal exhibits caution in its actions.

Very Careful	Somewhat Careful	Slightly Careful	Neutral	Slightly Careless	Somewhat Careless	Very Careless

11. Active, Energetic: Moves around a lot. Locomotion can include swimming normally, swimming quickly, surface behavior, diving, playing, active exploration, etc.

Very Active	Somewhat Active	Slightly Active	Neutral	Slightly Inactive	Somewhat Inactive	Very Inactive

12. Timid: Hesitant, apprehensive, and tentative.

Very Timid	Somewhat Timid	Slightly Timid	Neutral	Slightly Bold	Somewhat Bold	Very Bold

13. Tolerant and easy-going: Inclined to be relaxed and tolerant.

Very Tolerant	Somewhat Tolerant	Slightly Tolerant	Neutral	Slightly Irritable	Somewhat Irritable	Very Irritable

14. Playful: Engages in play behavior.

Very Playful	Somewhat Playful	Slightly Playful	Neutral	Slightly Unplayful	Somewhat Unplayful	Very Unplayful

15. Not exploratory or inquisitive: Does not seek out nor investigate novel situations or objects.

Very Unexploratory	Somewhat Unexploratory	Slightly Unexploratory	Neutral	Slightly Exploratory	Somewhat Exploratory	Very Exploratory

APPENDIX C – IACUC Approval Letter

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

APPENDIX D – IRB Approval Letter

INSTITUTIONAL REVIEW BOARD
118 College Drive #5147 | Hattiesburg, MS 39406-0001
Phone: 601.266.5997 | Fax: 601.266.4377 | www.usm.edu/research/institutional.review.board

NOTICE OF COMMITTEE ACTION

The project has been reviewed by The University of Southern Mississippi Institutional Review Board in accordance with Federal Drug Administration regulations (21 CFR 26, 111), Department of Health and Human Services (45 CFR Part 46), and university guidelines to ensure adherence to the following criteria:

- The risks to subjects are minimized.
- The risks to subjects are reasonable in relation to the anticipated benefits.
- The selection of subjects is equitable.
- Informed consent is adequate and appropriately documented.
- Where appropriate, the research plan makes adequate provisions for monitoring the data collected to ensure the safety of the subjects.
- Where appropriate, there are adequate provisions to protect the privacy of subjects and to maintain the confidentiality of all data.
- Appropriate additional safeguards have been included to protect vulnerable subjects.
- Any unanticipated, serious, or continuing problems encountered regarding risks to subjects must be reported immediately, but not later than 10 days following the event. This should be reported to the IRB Office via the "Adverse Effect Report Form".
- If approved, the maximum period of approval is limited to twelve months.
  Projects that exceed this period must submit an application for renewal or continuation.

PROTOCOL NUMBER: 16020402
PROJECT TITLE: Does Personality Similarity in Bottlenose Dolphin Pairs Influence Dyadic Bond Characteristics?
PROJECT TYPE: New Project
RESEARCHER(S): Kelsey Moreno
COLLEGE/DIVISION: College of Education and Psychology
DEPARTMENT: Psychology
FUNDING AGENCY/SPONSOR: N/A
IRB COMMITTEE ACTION: Expedited Review Approval
PERIOD OF APPROVAL: 02/11/2016 to 02/10/2017
Lawrence A. Hosman, Ph.D.
Institutional Review Board

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI.

INSTITUTIONAL REVIEW BOARD
118 College Drive #5147 | Hattiesburg, MS 39406-0001
Phone: 601.266.5997 | Fax: 601.266.4377 | www.usm.edu/research/institutional.review.board

NOTICE OF COMMITTEE ACTION

The project has been reviewed by The University of Southern Mississippi Institutional Review Board in accordance with Federal Drug Administration regulations (21 CFR 26, 111), Department of Health and Human Services (45 CFR Part 46), and university guidelines to ensure adherence to the following criteria:

- The risks to subjects are minimized.
- The risks to subjects are reasonable in relation to the anticipated benefits.
- The selection of subjects is equitable.
- Informed consent is adequate and appropriately documented.
- Where appropriate, the research plan makes adequate provisions for monitoring the data collected to ensure the safety of the subjects.
- Where appropriate, there are adequate provisions to protect the privacy of subjects and to maintain the confidentiality of all data.
- Appropriate additional safeguards have been included to protect vulnerable subjects.
- Any unanticipated, serious, or continuing problems encountered regarding risks to subjects must be reported immediately, but not later than 10 days following the event. This should be reported to the IRB Office via the "Adverse Effect Report Form".
- If approved, the maximum period of approval is limited to twelve months.
  Projects that exceed this period must submit an application for renewal or continuation.

PROTOCOL NUMBER: CH16020402
PROJECT TITLE: Does Personality Similarity in Bottlenose Dolphin Pairs Influence Dyadic Bond Characteristics?
PROJECT TYPE: Change to a Previously Approved Project
RESEARCHER(S): Kelsey Moreno
COLLEGE/DIVISION: College of Education and Psychology
DEPARTMENT: Psychology
FUNDING AGENCY/SPONSOR: N/A
IRB COMMITTEE ACTION: Expedited Review Approval
PERIOD OF APPROVAL: 06/09/2016 to 06/08/2017
Lawrence A. Hosman, Ph.D.
Institutional Review Board

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