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

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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.

The Importance of Social Structure

Social structures and the patterning of social relationships are vital for the success of group living species. Social behaviors function to maximize benefits of group living while minimizing costs (Alexander, 1974; Silk, 2007). Social relationships shape the use of these behaviors, providing short-term benefits which increase fitness both indirectly and directly (Alexander, 1974; Cameron, Setsaas, & Linklater, 2009; Frère et al., 2010; Silk, 2007). By directly measuring relationships between individuals, social network analysis is a powerful tool for understanding how different features are related, the factors which shape or alter them, and how they impact the wellbeing of the animals which utilize them (Buchholz, 2007; Gowans, Würsig, & Karczmarski, 2008; Krause, Lusseau, & James, 2009; Whitehead & Gero, 2014).

Current Knowledge of Bottlenose Dolphin Social Structure

Bottlenose dolphins exhibit fission-fusion patterning of associations, such that individuals are often well connected and many contain hierarchical groupings of associates (Gowans et al., 2008; Lusseau, 2003; Rogers, Brunnick, Herzing, & Baldwin, 2004; Shane, Wells, & Wursig, 1986; Smolker, Richards, Connor, & Pepper, 1992; Wells, Scott, & Irvine, 1987). General trends for bottlenose dolphin social structure are consistent with slight variation observed between locations, likely due to differences in local ecology (Gowans et al., 2008; Möller, 2012; Moreno & Kuczaj, 2015). 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).

Social Structure Components

Although social structures are comprised of dyadic associations (Krause, Croft, & James, 2007), social structure research has focused on the overall structure while neglecting investigations into the components of dyadic relationships or the factors which shape them. Social structure research relies on the coefficient of association, which captures the proportion of time two animals spend together out of the proportion of time both animals are observed (Cairns & Schwager, 1987). While useful for mapping population wide patterns of associations, this method fails to account for different types of relationships which may exist between dyads due to differences in patterns of interactions those dyads have with one another. Recent research on chimpanzees (*Pan troglodytes*) (Fraser, Schino, & Aureli, 2008; Koski, Vries, Kraats, & Sterck, 2012), macaques (*Macaca fuscata yakui* and *Macaca sylvanus*) (Majolo, Ventura, & Schino, 2010; McFarland & Majolo, 2011), spider monkeys (*Ateles geoffroyi*) (Rebecchini, Schaffner, & Aureli, 2011), and ravens (*Corvus corax*) (Fraser & Bugnyar, 2010) has worked to group suites of 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 (Fraser & Bugnyar, 2010; Fraser et al., 2008; Hinde, 1976; Koski et al., 2012; Majolo et al., 2010; McFarland & Majolo, 2011), although some species specific patterns have also been demonstrated (Majolo et al., 2010; McFarland & Majolo, 2011; Rebecchini et al., 2011). 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). 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), which are consistent over time (Koski et al., 2012), provides promising support for the universality of the underlying framework for relationship components.

Personality May Influence Social Structure Components

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). This link has been demonstrated in humans (*Homo sapiens*) (e.g., Duck, 1973; Izard, 1960; Selfhout et al., 2010), great tits (*Parus major*, Aplin et al., 2013), and non-human primate species, including chimpanzees (Massen & Koski, 2014), capuchins (*Sapajus paella*, Morton, Weiss, Buchanan-Smith, & Lee, 2015), and rhesus monkeys (*Macaca mulatta*, Weinstein & Capitanio, 2008). Interestingly, the specific trait and association correlations differ between species. Extraversion predicts greater bonding in humans, great tit males, chimpanzees, and capuchins; Agreeableness predicts bonding in humans,

chimpanzees, capuchins, and rhesus monkeys; and Openness predicts bonding in humans, capuchins, and rhesus monkeys (Aplin et al., 2013; Massen & Koski, 2014; Morton et al., 2015; Selfhout et al., 2010; Weinstein & Capitanio, 2008). In contrast, barnacle geese (*Branta leucopsis*) 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).

Current 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 will illuminate differences and similarities between groups, informing us about evolution of social structure. Knowledge of which individuals form stronger or more positive bonds can improve animal welfare through informing housing decisions (Capitanio, Blozis, Snarr, Steward, & McCowan, 2015). Additionally, further understanding of factors which shape social structure and bottlenose dolphin wellbeing is advantageous for assessing and promoting aquatic ecosystem health (Buchholz, 2007; Wells et al., 2004; Wolf & Weissing, 2012). To further these aims, we 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.

Method

Subjects

This study utilized the captive population at the Roatan Institute for Marine Sciences (RIMS) which is part of Anthony's Key Resort in Roatan, Honduras. This population is 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 m^2 in area and ranges in depth from the shore line to just over 8 meters (Dudzinski et al., 2010). The sea floor reflects the natural habitat, with sea-grass beds, sand, and coral. All dolphins are fed a regular diet of Atlantic herring (*Clupea harengus*), Capelin (*Mallotus villosus*), and Atlantic mackerel (*Scomber scrombrus*) with supplementary vitamins; individual diet composition is determined by individual needs, preferences, and veterinary recommendations. Individuals are habituated to humans, and no aspect of data collection interfered with regular feeding, care, training, or other husbandry practices.

There were 20 individuals, consisting of males and females of various ages (Table 1), included in the current study. Overall, there were 190 dyads used to characterize 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.

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

Data Collection and Analysis

Dyadic bond characteristics.

Data collection. 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 s 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 hr, 46 min and 45 s, which is above the 10 hr minimum shown to provide an accurate picture of calf associations (Gibson & Mann, 2009).

Video coding. 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 s. 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 (Table 2) 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.

Statistical analysis. 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 varimax 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. Data appropriateness was determined using the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and Bartlett's test of sphericity (Meyers, Gamst, & Guarino, 2013). Finally, the values of the identified components were determined for each pair based on the interactions observed between members of the dyad.

Personality factors.

Data collection. Personality was determined using a questionnaire (supplemental material) 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). As a well-established and well developed model utilized with multiple species, it has demonstrated validity and is highly useful for interspecies comparisons

Table 2

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

(Highfill & Kuczaj, 2007; Horback et al., 2013; Kuczaj & Kristiansen, 2013). However, as it was developed for use on humans it will likely retain anthropogenic biases and the associated limitations, so it may not be most accurate or best fitting model (Highfill & Kuczaj, 2007).

Statistical analysis. 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.

Statistical analysis. 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. Fit was determined using the comparative fit index (CFI), Tucker-Lewis index (TLI), and root mean square error of approximation (RMSEA) (Meyers, Gamst, & Guarino, 2013).

Results

Dyadic Bond Characteristics

Reliability with an independent observer on 20% of video data was achieved for both association, 95.97%, $p < 0.001$, mantel Z-test, and interaction, 88.18%, Cohen's Kappa = 0.544, coding. As most disagreements in interaction coding 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, (KMO = 0.703; Bartlett's test of sphericity, $p < 0.001$) yielded three component dimensions of relationships (Table 3) as determined from the scree plot and factor loadings. The first factor was termed Affiliative Support due to the inclusion of affiliative, tolerant, synchronous, and supportive behavior. The second component consisted of behaviors which are all associated with sociosexual contexts, thus, this factor was termed Sociosexual. The third component consisted of behaviors which 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 3
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

Note. 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 $RMSEA = 0.103$. 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.
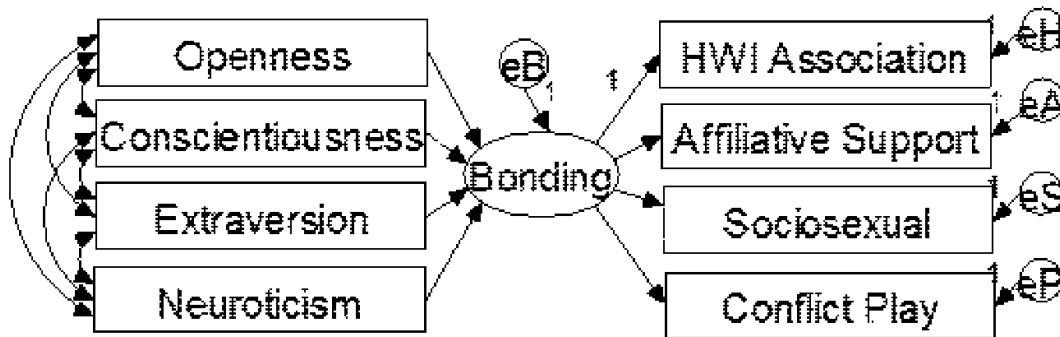
Figure 1. **Path Diagram for Structural Equation Model.**

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 in methodology, as this study only included discrete behavioral events, and thus 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 (Botero Acosta, 2015; Mann, 2006). However, the other unique factor, Conflict Play, is particularly interesting. This factor included both 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), and also 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). 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, though not 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, Mendoza, & Baroncelli, 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, so Openness may simply be unimportant to dolphin bond formation due to the much greater importance of other factors. Future research may be able to elucidate how personalities of individuals impact the different aspects of interindividual bonds. Additionally, it is currently unknown whether these relationships are stable or change though an animal's lifetime, thus future studies should also investigate whether age class impacts the influence of personality similarity on dyadic bonding.

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 the dyad down. This would be benefit the dyad, as high Neuroticism negatively impacts human relationships (Greenfield, Gunthert, & Forand, 2014; Roberts, et al., 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.

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 the similar behavior of grooming equitability in chimpanzees suggests a connection may exist (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.

Acknowledgments

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