



Behavioral Asymmetries of Pectoral Fin Use During Social Interactions of Bottlenose Dolphins (*Tursiops truncatus*)

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The preference for utilizing certain appendages (handedness) has been explored in a variety of vertebrate species. Similar to primates, dolphins possess hemispheres that allow an individual to present behaviorally dominant features and appendages (i.e., pectoral fins) that are utilized both as social facilitators, as well as means to interact with objects. Thus, the possibility of handedness in a captive population of 27 bottlenose dolphins (*Tursiops truncatus*) was explored. Dolphins in a mother-offspring relationship made significantly more pectoral fin contacts than in the absence of this relationship. No significant difference was observed between maternal siblings and non-maternal siblings in overall pectoral fin contact. Handedness indexes were calculated for 26 individuals that initiated pectoral fin contact with both conspecifics and flora (i.e., seagrass) in their habitat. No significant differences were observed between the sexes in handedness indexes; however calves displayed a significant right-fin handedness compared to both sub-adults and adults. Both sub-adults and adults showed a left-fin handedness indexes, but no significant difference in the strength of this relationship among these two age classes was observed. Individual variation in handedness indexes was also noted. These results suggest that handedness may be present in Atlantic bottlenose dolphins with regards to social contact, and a larger and more diverse sample size may provide a better understanding in why handedness may change across development.

Lateralized behavior is classified by the use of a specific side or directional movement that is constant across behavioral contexts. Initially thought to be uniquely human (Corballis & Beale, 1983), these behavioral asymmetries have been demonstrated in a variety of different species and may be a characteristic of all vertebrates (e.g., Vallortigara, Chiandetti, & Sovrano, 2011; Versace & Vallortigara, 2015; Wells, 2003) with evidence for lateralization also being found in invertebrates (see Frasnelli, Vallortigara, & Rogers, 2012 for review). Examples of behavioral lateralization are broad; primates will more commonly use a specific hand for object manipulation (e.g., Chapelain, 2010), blue gourami (*Trichogaster trichopterus*) initially touch novel objects more often with their left fin (Bisazza, Lippolis, & Vallortigara, 2001), grey whales (*Eschrichtius robustus*) benthic forage more frequently with one side of their mouths (Woodward & Winn, 2006), dolphins exhibit asymmetries with listening response (Au, 1993; Au & Benoit-Bird, 2003), horses (*Equus ferus caballus*) tend to lead with a preferred foot (Murphy & Arkins, 2008), psittiformes and corvids tend to hold and manipulate food with a specific foot (Rogers, 2007), rodents and felines tend to reach towards objects with a preferred paw (e.g., Warren, 1980), and dogs show both an asymmetry with paw preferences (Berta, 2011) as well as tail-wagging when responding to varying stimuli (Quaranta, Siniscalchi, & Vallortigara, 2007). While hypotheses have been made as to the benefits of consistent behavioral lateralization, such as increasing brain efficiency to multitask (e.g., Rogers, Zucca, & Vallortigara, 2004), or increased social coordination (e.g., Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005), some evidence suggests that asymmetric populations also receive benefits from the lack of uniform lateralization (Ghirlanda, Frasnelli, & Vallortigara,

2009). However, no universal answers exist, though research also suggests individual advantages may be present.

Behavioral lateralization focuses on the motor coordination of external limbs where one hand or limb shows dominance or more usage, known as *handedness* (Hopkins et al., 2011). Handedness is suggested to be more a function of the brain, specifically cerebral asymmetries and dominance for function, rather than anatomical need (Corballis, 2003). Individuals showing strong preference, or unequal distribution of fine motor coordination between hands identifies people as being right-handed or left-handed (Dunham, 2012), is not reliant on the preference being used 100% of the time (Corballis, 2003), but rather a significantly greater proportion of utilizing a select side. At the population level, humans are suggested to be right hand biased (9:1 ratio), which is suggested to be stable across cultures, geographical locations (Uomini, 2009), and across evolution, as 88% of Neanderthal men are suggested to have been right-handed (Frayer et al., 2010). While there is inconsistency in individuals designated as being right or left handed, it is clear that hands serve different but equally important roles (Balter, 2009).

Handedness is not a uniquely human trait as it has been documented in red kangaroos (*Macropus rufus*) and eastern gray kangaroos (*Macropus giganteus*; Giljov, Karenina, Ingram, & Malashichev, 2015), and wild chimpanzees (*Pan troglodytes*; Lonsdorf & Hopkins, 2005) and orangutans (*Pongo sp.*) have displayed left-handedness (e.g., Hopkins, 1995; Hopkins et al., 2011), with the opposite trend observed in captive chimpanzees (Hopkins, Wesley, Izard, Hook, & Schapiro, 2004). However, results vary across the types of task and may be influenced by rearing history, as an assessment of great apes, including chimpanzees, bonobos (*Pan paniscus*), orangutans, and gorillas (*Gorilla gorilla*) found a right hand bias for a reaching task (Meguerditchian et al., 2015). Characteristics such as being highly gregarious, large brained, and slow developing, similar to primates and humans, suggest that cetaceans are sentinel species to gain insight into the nature of lateralization (Karenina, Giljov, Glazov, & Malashichev, 2013).

Investigations of behavioral lateralization in marine mammals allows for a greater understanding of the asymmetrical functioning of their cognitive abilities (Sakai, Hishii, Takeda, & Kohshima, 2006). Visual and/or swimming pattern lateralization are the most common empirical investigations with dolphins (e.g., Marino & Stowe 1997a; Thieltges et al., 2011; Yaman et al., 2003; Yeater et al., 2014). However, studies of pectoral fin contact and assumptions to what it represents are on the rise.

Although cetaceans possess finger-like bones within their pectoral fins, the use of these appendages differs from terrestrial counterparts. Rather than the appendages being utilized for object modification or prey manipulation, the primary communicative purpose of the pectoral fins appears to be for play and socialization. Tactile interactions and exchanges are suggested to serve three functions among cetaceans (introductions, contact for hygienic reasons, or transferring information), but more so provides a pivotal function in garnishing social behavior (e.g., Dudzinski, 1998; Dudzinski, Gregg, Ribic, & Kuczaj, 2009). Pectoral touch has been likened to allogrooming in primates and is suggested to increase level of association among conspecifics (e.g., Defran & Pryor, 1980; Dudzinski et al., 2009; Seyfarth & Cheney, 2007). The behavior is suggested to be socially driven (e.g., Dudzinski, et al., 2009), occurs frequently during socio-sexual encounters (e.g., Nelson & Lien, 1994; Sakai, et al., 2006), facilitates or strengthens bonds (e.g., Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Morisaka, 2009), and is often documented during social learning events (e.g., Kaplan & Connor, 2007; Mann & Smuts, 1999).

Variations with pectoral contact have been documented between sexes in Atlantic spotted dolphins (*Stenella frontalis*); although males were more likely to initiate tactile interactions, females utilized pectoral

touch for tactile interactions more frequently (Kaplan & Connor, 2007). Furthermore, Atlantic white-sided dolphins (*Lagenorhynchus acutus*) in managed care revealed that females were over five times more likely to initiate pectoral fin contact than males (Nelson & Lien, 1994). Pectoral contact is also suggested to increase in frequency following aggressive encounters in bottlenose dolphins (*Tursiops truncatus*; Morisaka, 2009; Tamaki, Morisaka, & Taki, 2006). Behavioral asymmetries were observed with Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) with pectoral fin touch (left side bias) from the initiators to the recipient's body on the population level and no side bias for object carrying behavior (Sakai et al., 2006). Left pectoral fin behavioral asymmetries were also observed in a group of captive Commerson's dolphins (*Cephalorhynchus commersonii*), although brain lateralization was considered, these findings may be due to the serrated leading edge of the left pectoral fin, which is thought to enhance tactile stimulation (Johnson & Moewe, 1999).

Age may also play a function of behavioral lateralization. Mutual pectoral contact, petting and rubbing, between mothers and calves enhances the bond among conspecifics and is important for socialization and building alliances (e.g., Mann & Smuts, 1999). Spatial lateralization has been identified in beluga (*Delphinapterus leucas*) calves, with a stronger bias to right side swimming (Karenina et al., 2013). Humpback whales (*Megaptera novaeangliae*) show a strong right side bias as older adults (90%), but the lateralization is weaker in calves and sub-adults, suggesting the maturation of lateralization may extend beyond sexual maturity (Canning et al., 2011).

Social exchanges through tactile interactions, more specifically pectoral fins, have been studied in detail in both wild and captive cetacean populations. How these signals are utilized, based upon the sender, in respect to handedness and laterality is not well understood among Atlantic bottlenose dolphins. In this study, a large and diverse population of bottlenose dolphins was studied over the course of three years in an effort to document sex, age, and individual handedness among the population.

Method

Subjects and Study Site

Twenty-seven Atlantic bottlenose dolphins were housed at the Roatan Institute of Marine Sciences (RIMS), located on Bailey's Key in Roatan, Honduras (see Table 1 for population demographics and Appendix A for maternal relatedness). Age class was determined based on reproductive criteria in Eskelinen, Winship, and Borger-Turner (2015). The natural ocean water lagoons, approximately 8,000m² range in depths from beach wash to 9.5m. The behaviors of this population have been compared to wild dolphins and demonstrate consistent similarities (Dudzinski et al., 2010; Dudzinski et al., 2012; Dudzinski et al., 2009; Greene, Melillo-Sweeting, & Dudzinski, 2011).

Data Collection and Analysis

Underwater video footage (26.02 hrs.) was collected over the course of three years (2010-2012) using a Nauticam M16 with Amphibico hydrophone adapter. Dolphins were identified in the footage based on distinct dorsal fin, flukes, rake marks at the time of collection, sex, size, and individual characteristics. Videos were coded utilizing an all-occurrence sampling methodology (Altmann, 1974) to account for all instances of pectoral fin use. Only instances in which both the initiating and receiving dolphins were positively identified ($N = 445$) were utilized for analyses.

An individual making contact with another conspecific, regardless of behavioral context, determined pectoral fin contact. Thus, incidental contacts were not recorded. Most instances of pectoral fin contact occur when an individual clearly takes its pectoral fin and engages it on a part of another individual without other forces influencing the contact for a minimum of 1 s. Dolphins participating in pectoral fin contact were categorized as either the initiator or receiver. The initiator made first contact with the pectoral fin and the receiver was the dolphin or object that was touched by the initiator. Of the 27 dolphins, only one female (Carmella) was recorded as being the receiver and never the initiator.

Pectoral contact behavior events exhibited by the focal subjects (initiator and recipient) were recorded for demographics for all subject involved, initiator handedness, as well as localized body part. The contact was recorded based on the starting point of the interaction. For comparative analysis, pectoral fin interactions with naturally occurring flora in the lagoon were also recorded.

Table 1
Demographics of the RIMS Dolphins

Name	Sex	Age Class
Cortez	M	Calf
Mickey	M	Calf
Vin	M	Calf
Luna	F	Calf
Pigeon	F	Calf
Polly	F	Calf
Tilly	F	Calf
Anthony	M	Sub-Adult
Dixon	M	Sub-Adult
Ken	M	Sub-Adult
Mr. French	M	Sub-Adult
Ritchie	M	Sub-Adult
Bailey	F	Sub-Adult
Fiona	F	Sub-Adult
Margarita	F	Sub-Adult
Bill	M	Adult
Han Solo	M	Adult
Hector	M	Adult
Paya	M	Adult
Ronnie	M	Adult
Alita	F	Adult
Carmella	F	Adult
Cedena	F	Adult
Gracie	F	Adult
Maury	F	Adult
Mika	F	Adult
Mrs. Beasley	F	Adult

Note. Age class determined by biological definitions provided by Eskelinen et al. (2015).

Data Analyses

Handedness index (HI) analysis (Figure 1) was conducted at the population and individual level to assess laterality bias (Hopkins, 1995). These values were calculated for each individual based on initiated interactions with other conspecifics in the lagoon, as well as interactions with local flora and fauna (e.g., sea grass).

$$HI = \frac{R - L}{R + L}$$

Figure 1. Accepted equation for handedness (Hopkins, 1995); R = number of times right pectoral fin was used, L = number of times the left pectoral fin was used.

Values are interpreted on a positive and negative scale, where right-pectoral fin biases are reflected in positive values and negative values show a greater tendency for left-pectoral fin bias.

Nonparametric statistics (Mann Whitney U and Kruskal Wallace) were used to assess mean number of contacts between relationship categories (mother-offspring, maternal siblings), initiator age class and sex. Handedness indexes were calculated for each individual across the three years of data collection, and nonparametric statistics were used to analyze these values within the parameters of age class and sex.

Results

Pectoral Fin Contacts

The mother-offspring relationship resulted in significantly more pectoral fin contacts than non-mother-offspring relationships, $U = 5211.00$, $Z = -4.08$, $p < 0.001$. Both males, $U = 881.00$, $Z = -3.15$, $p < 0.01$, and females, $U = 1464.55$, $Z = -2.72$, $p < 0.01$, initiated significantly more pectoral fin contacts when the mother-offspring relationship was present (Figure 2). The number of contacts when comparing males and female initiators within this population subset did not result in a significant difference, $U = 256.00$, $Z = -0.74$, $p = 0.460$.

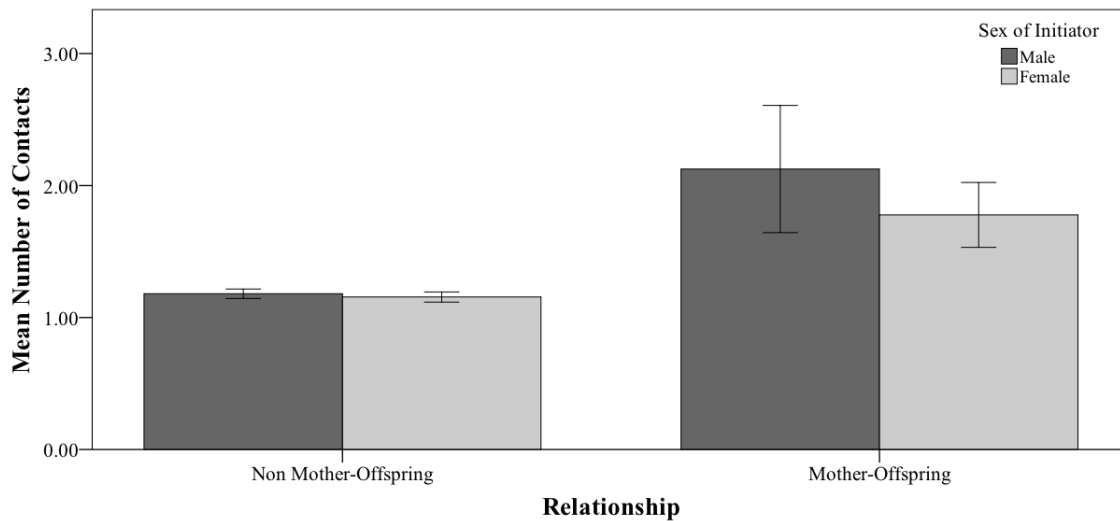


Figure 2. Dolphins within the mother-offspring relationship initiated significantly more pectoral fin contacts ($p < 0.001$) and both males and females initiated significantly more contacts in this relationship compared to dolphins that were not in the mother-offspring relationship ($p < 0.01$).

Maternal siblings and non-maternal siblings did not differ in number of pectoral fin contacts, $U = 2931.00$, $Z = -0.61$, $p = 0.541$.

The mean number of contacts differed among age classes, $H = 14.28$, $p = 0.001$ (Figure 3). Calves initiated significantly more pectoral contacts than adults, $U = 5022.00$, $Z = -2.85$, $p < 0.01$, and sub-adults, $U = 3779.50$, $Z = -3.354$, $p = 0.001$, but no significant difference was found between adults and sub-adults, $U = 5646.50$, $Z = -0.77$, $p = 0.442$.



Figure 3. Calves initiated significantly more pectoral fin contacts than sub-adults ($p < 0.001$) and adults ($p < 0.01$). No significant difference was observed in the utilization of particular fins.

Handedness Indexes

Handedness indexes for the population were stable and did not vary significantly across the three years of data collection, Friedman Test: $\chi^2 = 1.02$, $p = 0.602$. There were no significant differences between the sexes in the handedness indexes, $U = 74.50$, $Z = -0.516$, $p = 0.614$, or within each sex when age class was considered: males, $H = 2.35$, $p = 0.309$, females, $H = 4.07$, $p = 0.131$. Handedness indexes varied significantly among age classes, $H = 5.97$, $p = 0.050$ (Figure 4). Calves displayed a significant difference in handedness indexes compared to both sub-adults, $U = 9.00$, $Z = -2.24$, $p < 0.05$, and adults, $U = 15.50$, $Z = -2.09$, $p < 0.05$. No significant difference was present between sub-adults and adults, $U = 42.00$, $Z = -0.17$, $p = 0.904$.

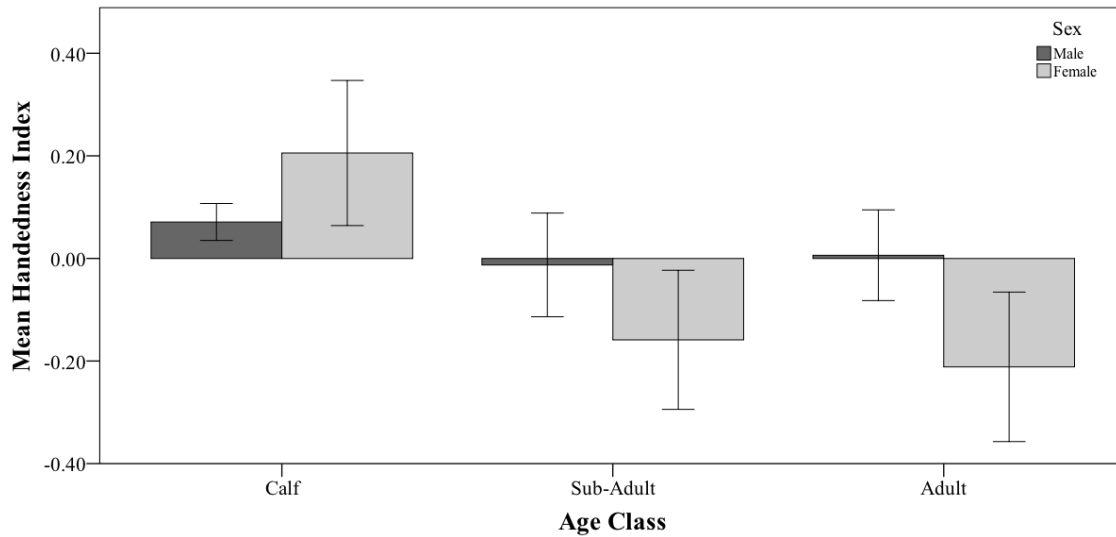


Figure 4. Calves displayed significantly different handedness indexes compared to sub-adults ($p < 0.05$) and adults ($p < 0.05$). No difference was observed between adults and sub-adults ($p > 0.05$).

Large variations across individuals were seen in the calculated handedness indexes, $M = -0.02$, $SE = 0.05$; see Figure 5. Carmella was not noted to initiate pectoral fin contacts in this data set, thus her index was not calculated.

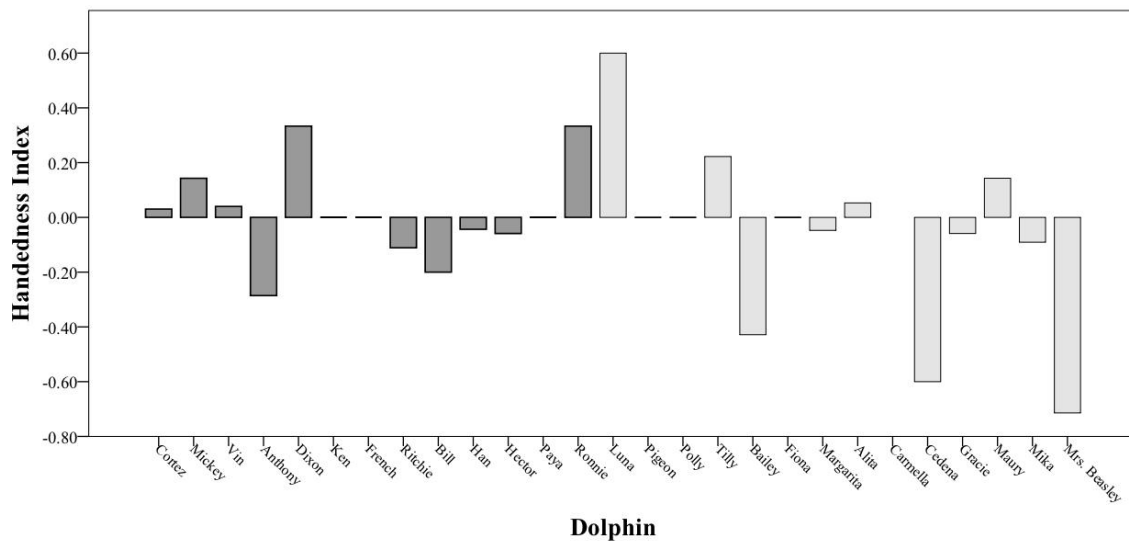


Figure 5. Individual Handedness index (HI) values for all dolphins in the population ordered by age class and sex. Dark grey bars indicate males and light grey bars indicate females.

Discussion

The results of this study indicated little support for a significant handedness trend at the population level for this grouping of Atlantic bottlenose dolphins. Although humans generally display right-handed bias on a population level (Uomini, 2009), some individuals show no preference or bias. As reported in primate literature (e.g., Meguerditchian et al., 2015), there was variability across individuals in the handedness index. The handedness indexes reported in these subjects were generally very small and less than values that have been reported in chimpanzees (e.g., Hopkins & Pearson, 2000; Hopkins et al., 2004; Llorente et al., 2011). Some individual HI's were larger, thus handedness in cetaceans could be trait that is predominantly dependent on individual variations in behavior and genetics. Manatees displayed a lateralization on the individual level when recorded performing particular behaviors (Tyler-Julian, Chapman, Frances, & Bauer, 2016), so it is possible that dolphins may show such distinctive inclinations. Thus, it is possible that dolphins may show preferences that could relate to dominance, age class, sex, prior reinforcement history, or environmental influences.

Cetacean pectoral fin contact is an important communicative behavior, and is known to maintain relationships between individuals (e.g., Dudzinski et al., 2010; Dudzinski, Danaher-Garcia, & Gregg, 2013; Morisaka, 2009; Sakai et al., 2006; Tamaki, et al., 2006). Thus, the increased contact between mothers and calves compared to those that are not related in this manner is not surprising, and is consistent with other reports (e.g., Dudzinski et al., 2010; Mann & Smuts, 1999). Maternal siblings did not show a significant difference in pectoral fin contact, suggesting that behavioral influences, potentially from the mother, may have an affect on handedness (e.g., Tang & Verstynen, 2002). Paternal relationships could not be assessed due to lack of DNA analyses within this population; however, it is possible that full siblings could display different relationships than unrelated individuals based on genetic and behavioral differences. Also, the potential to explore paternal roles in development (Eskelinen, Borger-Turner, & Kuczaj, 2017) could be better assessed with this information.

While the initiating pectoral fin contact of calves was predominantly performed by their right pectoral fin, the relationship changed with the older age classes, culminating in a left pectoral fin bias in both sub-adults and adults. This relationship appeared to be driven by females with no large changes observed across males (Figure 4); the significance was only found when all data was collapsed and did not hold true when sexes were analyzed individually. Factors such as pattern swimming (e.g., Marino & Stowe, 1997a; 1997b; Stafne & Manger, 2004) may influence the usage of particular fins (e.g., calves always swimming on the inside of the mother), such stereotyped swimming was not observed during data collection. The enclosure size, diverse and natural topography allows the dolphins to more easily engage in typical social behaviors (Dudzinski et al., 2010; Greene et al., 2011). Thus, a larger sample size may be able to better assess the trend of pectoral fin asymmetries across age classes and between sexes.

Although individual indexes across the three-year sampling period did not reveal differences, it is important to note that during this time all subjects also remained in the same age class. Thus, individual handedness is unknown to remain stable over time, similar to paw preferences in rats (Tang & Verstynen, 2002), but more so behavioral asymmetries may be subject to environmental influences during early developmental stages. A longer sampling period might be able to ascertain when, and if, these preferences change over time.

While non-human primate handedness is frequently tested during particular tasks (e.g., Hopkins et al., 2004, Hopkins et al., 2011; Llorente et al., 2011), recently other methodologies have been employed to

investigate lateralization during social contexts (e.g., Quaresmini, Forrester, Spiezio, & Vallortigara, 2014) or while the primates interact with animate or inanimate objects (e.g., Forrester, Leavens, Quaresmini, & Vallortigara, 2011; Forrester, Quaresmini, Leavens, Spiezio, & Vallortigara, 2012). Similarly to the latter methodologies, this study focused on observations collected during social interactions in which pectoral fin interactions were documented. Dolphins do not use pectoral fins for object manipulation, rather only to carry or engage in social contact. Thus, a task requiring them to utilize their pectoral fins would likely not be salient to cetaceans, as they will generally investigate and manipulate objects using their rostrums. Other variables, such as swimming direction in front of the camera, could influence which side the subjects may be located. Bottlenose dolphins are known to display individual personalities (e.g., boldness; Highfill & Kuczaj, 2007; Kuczaj, Highfill, & Byerly, 2012), thus more timid animals might prefer to be farther from the camera, thus influencing the current findings.

Stan Kuczaj found the likelihood of individual differences within bottlenose dolphins a fascinating and worthwhile topic of exploration. Through the assessment of dolphin personality, “creativity”, and problem solving, individual variation within this species appears frequently. Stan also wholeheartedly encouraged others to explore the behavioral idiosyncrasies in these animals on a population and individual level, including undergraduate students, which led to this project’s beginnings. This study should further encourage researchers to explore handedness preferences across cetacean species and within populations. While the sample size utilized for this study was small, the results suggest that handedness may play a role in the social behaviors of this population of bottlenose dolphins, and further analyses of interaction context, as well as interaction between age classes may reveal further differences.

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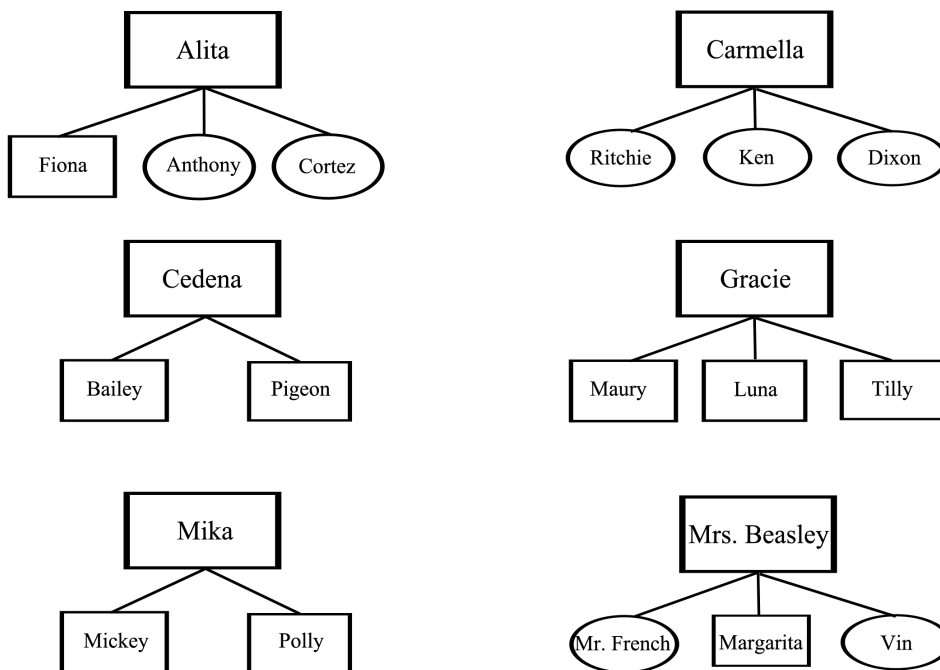
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Appendix A

Maternal Family Tree



The maternal family trees of the RIMS population from 2010-2012. Females are recorded in rectangular boxes and males in oval boxes. Subjects are ordered from oldest (left) to youngest (right).

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