Imitation in Social Cognition of Bottlenose Dolphins

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Abstract

Bottlenose dolphins (*Tursiops truncatus*) have been shown to be highly social and intelligent animals, as well as frequent and flexible mimics. Though little is known about the function of imitation in dolphins beyond observational learning, it seems to have a large role in the social world of humans. Can we say the same for dolphins? Does imitation affect how and with whom dolphins interact? Does how and with whom dolphins interact affect imitation? We aimed to answer these questions in our study of a captive bottlenose dolphin community. Using video footage, we scored all instances of body orientation changes done by the subjects, and classified the behaviors as imitative based on relative onset time. There were some social factors which did not play a significant role in the subjects' imitation preferences, namely, social rank and length of residency. There were other factors such as age and gender which appeared to mediate certain preferences, although not in a consistent pattern across subjects. Subjects did show an increased propensity to imitate kin, especially offspring imitating a parent. Pairs who demonstrated high rates of synchrony tended to have a reciprocal preference to imitate each other. Imitation patterns were not alway reciprocated, however, as we found that subjects with the highest rate of imitating others were the least likely to be imitated more in return.

Background

Behavioral psychologists have been aiming to define, explain, and understand the phenomenon of imitation for many decades, and continue to do so to this day. While the exact definition of imitation has slight variation across the field, those studying imitation generally agree that it involves the copying of one individual's behavior by another individual. Importantly, to be considered imitative, the copied behavior should not be explained by simpler explanations such as predisposition or due to some other motivation (Zentall, 2001). Beyond this general definition of imitation, however, there is much contest of how imitation occurs, who does it, and what function it serves.

While many have thought that imitation was unique to humans, the results of several experiments conducted to test the mimetic capabilities of dolphins show otherwise. Dolphins have shown the ability to imitate one another and imitate other animals, such as humans. They can even do so after a period of delay, with the model absent. Furthermore, they can imitate novel behaviors, although they do show higher success imitating familiar behaviors (Kuczaj & Yeater, 2006).

Herman (2002) trained two dolphins to respond to a "mimic" gesture by imitating a model dolphin's behavior after a delay period. Both dolphins performed above chance level. Herman also trained the pair to perform novel behaviors in synchrony. Video analysis revealed that this display was actually the result of one dolphin closely following the lead of the other dolphin, suggesting that the following dolphin may have been imitating the leading dolphin's chosen behavior. Finally, Herman trained the dolphins to respond to the “mimic” gesture by imitating the behaviors or postures of human models.

However, other studies using a “mimic” command have seen less successful, although interesting results. Bauer & Johnson (1994) attempted to train a pair of dolphins to imitate familiar and novel behaviors done by the other. While neither dolphin succeeded in imitating the novel behaviors, the subordinate individual of the pair performed considerably better than the dominant individual in imitating familiar behaviors. This led the authors to speculate that willingness to imitate may be mediated by social factors, such as social rank.

Outside of experimental paradigms, we also see evidence of spontaneous, naturally occurring imitation. Tayler and Saayman (1973) provide some of the most striking accounts. In one case, after seeing a human smoking a cigarette, a dolphin calf took milk from its mother, then returned to the window and released the milk from his mouth in a similar fashion to the human blowing smoke. Another dolphin replicated the body movements of a seal, which differ from the natural way in which a dolphin swims. While a seal propels itself through the water with its flippers, a dolphin would naturally propel itself using its tail, and would only use its flippers for steering.

Notable examples of spontaneous imitation of other dolphins come from literature on social learning in dolphins. Calves learn important survival skills, such as foraging behaviors, through imitating their mothers. Calves also often imitate the play behaviors of their peers, such as interaction with new objects. Tendency to imitate and be imitated, however, is selective. That is, younger calves are more likely to imitate their older peers, and “timid” calves are more likely to imitate their “bold” peers (Kuczaj & Yeater, 2006; Kuczaj, Yeater, & Highfill, 2012).

Synchrony may involve similar mechanisms and serve a related purpose to delayed imitation (Fellner, 2006; Kuczaj & Yeater, 2006). Immediately after birth, calves synchronize with their mothers and do so for 80% of their first few months of life, and may serve as an ontogenetic precursor to the ability to imitate after a delay (Fellner, 2006). Synchrony is also seen in adult dolphins. Swimming in unison and simultaneous behaviors such as surfacing or leaping are often seen in "closely associated individuals", and may serve to signal the dolphins' relationship (Pryor, 1991).

However, beyond its function in observational learning and development, few sources have examined why dolphins have the ability to imitate or what role it plays in their adult lives. Research on imitation in humans suggests that imitation has important social functions. Chartrand and Bargh (1999) found that subjects who were mimicked during an interaction tended to view the situation and the person doing the mimicking more favorably than subjects who had not been mimicked, and that imitation can lead to connections and fondness between those involved in instances of imitation.

Research on humans also shows us that the link between imitation and sociality does not seem to be unidirectional. That is, patterns of imitation do not just influence patterns of socialization; patterns of socialization influence patterns of imitation as well. Lakin, Chartrand, and Arkin (2008) found that those who have been excluded from a social situation imitate others more than those who have been included in the social situation, and these individuals also imitate those in the "in-group" more often than they imitate those in the "out-group". Lakin, Jefferis, Cheng, and Chartrand (2003) reflect the findings of these studies in their claim that today imitation plays less of a role in immediate survival situations, and instead functions more as a type of “social glue”. It can help individuals have smoother interactions, create social bonds, and develop a sense of belonging. Lakin & Chartrand (2003) show that individuals may even use imitation as a social tool in order to accomplish social goals such as building connections with others.

While there is not yet evidence for whether this is also the case in dolphins, the fact that dolphins not only are frequent mimics, but also have advanced cognitive capabilities and a highly complex social environment (Cantor & Whitehead, 2013; Connor & Mann, 2006) suggests that it is a worthy question to look into. Indeed, gaining insight into the factors which influence dolphins to imitate, and who is most likely to imitate or be imitated by others, will in turn inform our understanding of the minds of dolphins and social cognition in general (Kucjaz & Yeater, 2006).

Methods

Approach: We attempted to better understand the role of imitation in the social interaction of dolphins through an observational approach, using video data to watch and analyze the dolphins’ behaviors on a moment-to-moment basis. This approach is consistent with embodied, distributed models of studying cognition (see Anderson, 2007; Hutchins, 2006), based on the examination of visible behaviors. Through the microanalysis of changes in dolphins’ behaviors during their interactions with social others, we aimed to reveal contingencies between these shifts in behavior and the dolphins’ patterns of social interaction (Johnson, 2010).

Subjects: Our study focused on a community of seven bottlenose dolphins (*Tursiops truncatus*): three adults, ages 24 to 31; three subadults, ages 9 to 11; and one juvenile, age 7. The dolphins often associate with others in their age range, and each age group has its own social hierarchy, noted by the dolphins' trainers.

The adult group consists of a dominant female (T), a dominant male (C), and a subordinate female (L). The subadult group consists a dominant female (N), a mid-ranking male (M), and a subordinate female (S). The juvenile female (A) associates with both age groups. T is mother to N and A, while the rest of the dolphins are unrelated. The subjects have lived together for various amounts of time, with their order of arrival as follows: T, C, N, A, S, M, L (see Appendix A for exact arrival dates and residency durations).

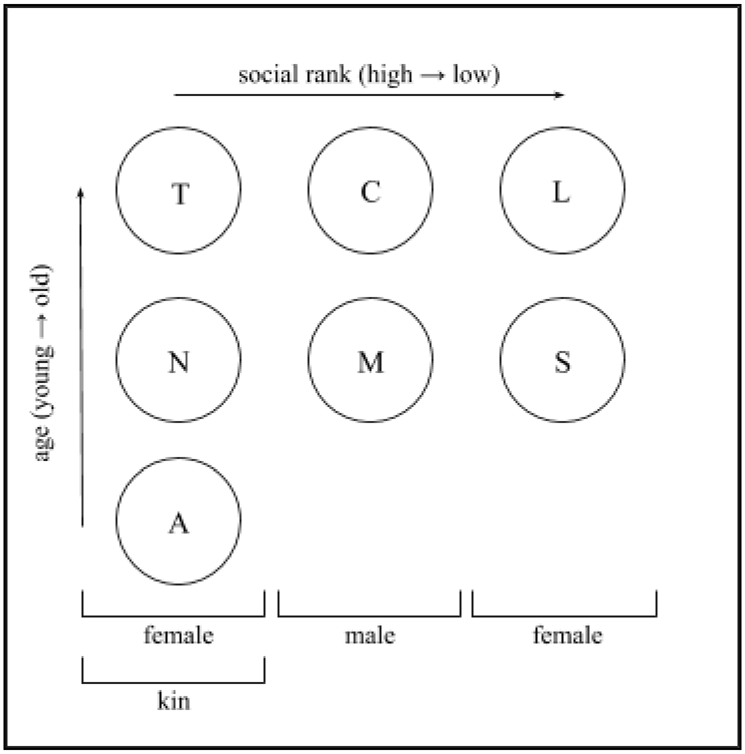

Figure 1

Social rank, age group, gender, and kin relationships of subjects

It is important to note that the social structure of this dolphin community differs from that of wild bottlenose dolphins. While the grouping of subadults and the frequent association of mother and offspring are seen in the wild, this community lacks the amount of, and tight coalitions formed by, males in wild dolphin populations (see Wells, 1991; Wiszniewski, Brown,

& Moller, 2012). Social interactions and relationships seen in our subjects thus may not fully represent those of all bottlenose dolphins.

Setting: The dolphins are located at the Brookfield Zoo in Chicago. They inhabit an enclosure with four connected tanks: one large main tank, two medium sized holding tanks, and one small tank connecting the two holding tanks. There are 13 cameras installed either underwater or above water throughout the tanks. These cameras record footage of the dolphins for seven hours per day. In our study, we have examined three hours of footage each from February 2, 3, and 4, 2013, totaling nine hours of scored footage. We chose these days because extensive data has already been taken on these video segments, including the time and identity of dolphins entering and exiting every tank, all vocalizations made in the tanks, and the partnering states of the dolphins, which will be of use during the analysis of our data. For the purposes of this project, we have only examined footage from the cameras installed in the main tank. We chose this tank because it has six cameras installed, the most of any tank, and the least amount of off- camera space.

For various reasons, we must be cautious in extending our findings to claims about bottlenose dolphins as a species or social cognition in general. Firstly, our video analysis only covers three days in the lives of these long-lived animals, and thus may not be representative of long-term tendencies in their social interactions. Secondly, we are analyzing the behavior of captive dolphins, which may not be a completely accurate representation of behaviors of all bottlenose dolphins.

Scored Behaviors: In the most broad sense, we looked for instances in which one dolphin imitates the behavior of another. However, because imitation itself can be difficult for observers to recognize, we instead chose a specific behavior for which we recorded all occurrences, and then later classified the behaviors as imitative or not not based on relative onset time. We decided to record the occurrences of changes in body orientation. This includes: *belly-upping*, in which the dolphin moves from its usual upright position to swimming upside down; *tilting*, in which the dolphin moves from its usual upright position to swimming sideways; and *returning* to the upright position (see Appendix B for illustrations of behaviors). Imitation was defined as the first individual to do one of these behaviors subsequent to another individual doing the same behavior, as long as the onset times of the two behaviors were within 30 seconds of one another.

Because changes in body orientation are common behaviors of dolphins, it is possible that behaviors we categorize as imitative may be driven by motives unrelated to imitation. Furthermore, this is not the only behavior that dolphins have been observed to spontaneously imitate (see Kuczaj & Yeater, 2006; Reiss & McCowan, 1993; Tayler & Saayman, 1973), and thus patterns of its occurrence will not fully represent the extent of the dolphins' imitation. Thus, we must be cautious in extrapolating our findings to the nature of imitation in general. However, we believe that looking at these body orientation changes is a wise starting point for examining imitation because it happens frequently, thus providing a large data set, and involves the revealing of the dolphins' white undersides, thus making the behavior highly salient to both the other dolphins in the tank and to the human observers.

Data Collection: Prior to data collection, the three interns involved in this project were first trained by interns with previous experience on identifying the seven individual dolphins based on size, color, and other physical markings. All three interns reached inter-rater reliability scores above 80% with their respective trainers on identifying dolphins. Two interns then developed data taking protocol, and after reaching inter-rater reliability above 80% with each other on coding behaviors and their respective timing. These interns then trained the third intern, who also reached inter-rater reliability above 80% with the interns who developed protocol.

The data collectors involved in this project scored every belly up, tilt, or return to upright that occurred in the selected six camera views of the 9 hours of video footage. The video analysis was done through the program ChronoVis, which allows the viewer to watch multiple camera views at once, and can show the video frames as separated by down to one tenth of a second. By watching this video data, we recorded:

1. Identity of dolphin doing the behavior
2. Which behavior was done
3. Onset time of the behavior

As there were two blind spots in the video footage, we also noted when animals went off-camera if the animal had a different body orientation upon returning to camera than it did when going off-camera. This was done in order to eliminate noise from the data in cases where it was impossible to know when a behavior was initiated, thus making it potentially ambiguous who the mimic and model were in instances of imitation occurring off-camera. See Appendix C for more detailed data taking protocol.

Results

All results were analyzed using a two-tailed z-score test for two population proportions of categorical data, with alpha level 0.05, against the null hypothesis that the tested populations did not differ on a given characteristic ($p1 - p2 = 0$). The set of behaviors done by one subject during the 9 hours of scored data constituted one population, with all behaviors within a population categorically classified as imitated or not imitated.

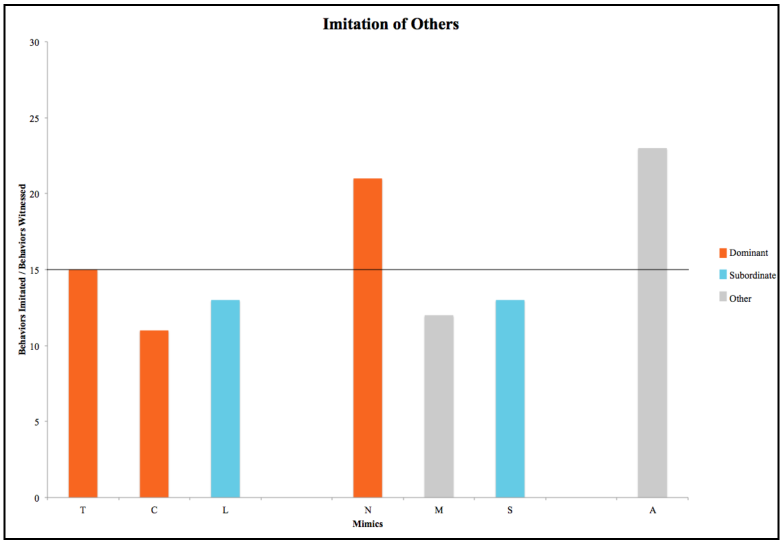

Figure 2

Imitation rates by subjects of all other subjects, organized by social group

Social Rank: Rank did not play a consistently significant role in the subjects' propensity to imitate or be imitated. In the adult group, there were no significant differences found between the rate of one subject imitating another subject, for any possible pairing of adult subjects. In the subadult group, the only significant result found was that the dominant female (N) was more likely to imitate the mid-ranked male (M) ($p1 = .25$) than M was to imitate N ($p2 = .14$), $z = 3.93$.

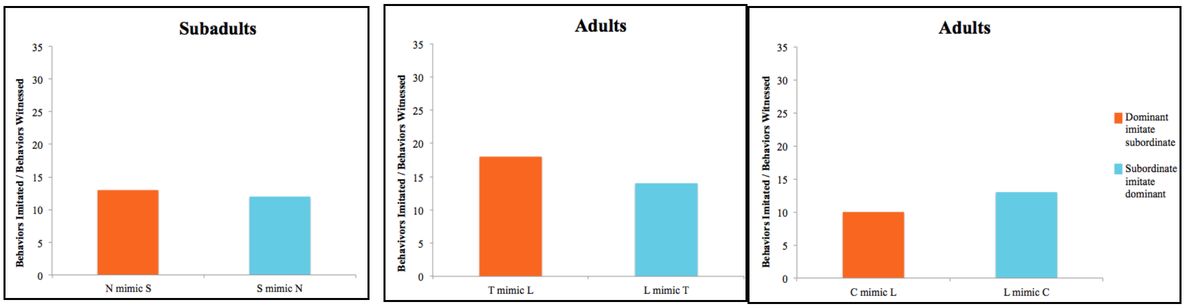

Figure 3

Pairwise comparisons of dominant and subordinate subjects in adult and subadult groups

Length of Residency: Recency of arrival to the tank also did not play a consistently significant role in the subjects' imitation preferences. The juvenile female (A) showed a significant tendency to imitate those who arrived in the tank before her (p1 = .25) compared to those who arrived in the tank after her (p2 = .21), z = 2.00. All other subjects showed no significant differences in their rates of imitating those who arrived in the tank before or after them.

Age and In-Group/Out-Group: There were various significant results found related to age and imitation preference. However, the patterns differed from subject to subject. The adult male (C) was significantly more likely to imitate those somewhat younger (p1 = .16) than either those in his own age group (p2 = .10), z = 4.80. C was also significantly more likely to imitate those somewhat younger (p1 = .16) than the much younger subject (p2 = .08), z = 5.42. However, the dominant adult female (T) was significantly more likely to imitate those in her age range (p1 = .16) than those slightly younger (p2 = .08), z = 2.30. She was also significantly more likely to imitate the much younger subject than those slightly younger (p1 = .17), z = 3.76.

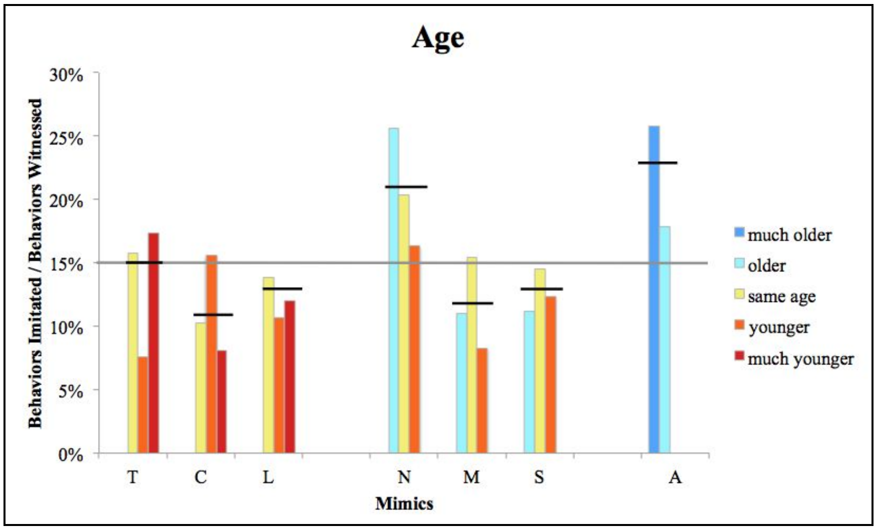

Figure 4

Imitation preferences for older, younger, and same age subjects

Other subjects showed significant tendencies to imitate an age group over only one other group, although these preferences also varied amongst subjects. The subadult male (M) was significantly more likely to imitate those in his age range (p1 = .15) than those younger (p2 = .08), z = 1.98. There was not a significant difference between either of these proportions and that of M's imitation of the adult subjects. The dominant subadult female (N) was significantly more likely to imitate those older than her (p1 = .26) than those younger (p2 = .16), z = 3.53. There was not a significant difference between either of these proportions and that of N's imitation of those in her age group. The juvenile female was significantly more likely to imitate those much older than her (p1 = .26) than those slightly older (p2 = .18), z = 3.62.

Kin: There were various significant results found related to kin relatedness and imitation preference. The dominant adult female (T), mother of the dominant subadult female (N) and juvenile (A), was significantly more likely to be imitated by a subject related to her (p1 = .30) than a subject unrelated to her (p2 = .12), z = 11.35. Pairwise, it was significantly more likely for A to imitate T (p1 = .32) than for T to imitate A (p2 = .17), z = 7.86. It was also significantly more likely for N to imitate T (p1 = .22) than for T to imitate N (p2 = .12), z = 2.59. There was no significant difference found between A's tendency to imitate N and N's tendency to imitate A.

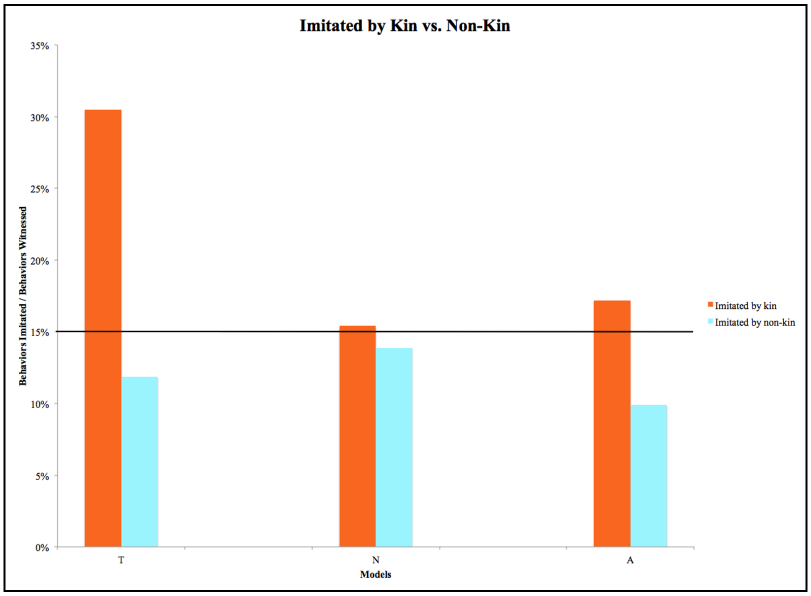

Figure 5

Imitation rates of family members by related and unrelated subjects

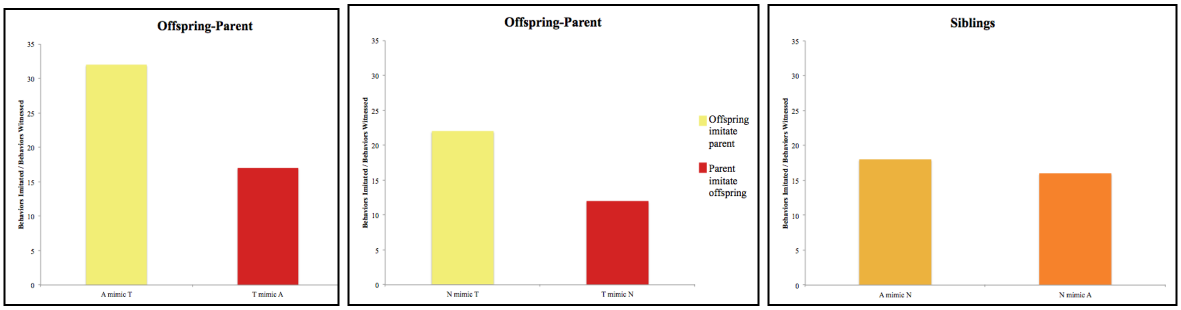

Figure 6

Pairwise comparisons of parent, offspring, and sibling-related subjects

A also showed a significant preference for imitating T (p1 = .32) over all other subjects: C (p2 = .17), z = 5.76; L (p2 = .25), z = 2.77; M (p2 = .18), z = 4.17; N (p2 = .18), z = 4.26; and S (p2 = .17), z = 3.92. She did not show a significant preference to imitate N over any of the other subjects. N was significantly more likely to imitate T (p1 = .22) than she was to imitate S (p2 = .12), but was not significantly more likely to imitate T over any other subject besides S, nor was she significantly more likely to imitate A over any subject. T, however, was significantly more likely to imitate A (p1 = .17) over all other subjects except L: C (p2 = .13), z = 2.04; M (p2 = .05), z = 4.78; N (p2 = .12), z = 2.06; and S (p2 = .04), z = 4.25. T also had a significant preference for imitating N (p1 = .12) over imitating M (p2 = .05), z = 2.78 and S (p2 = .04), z = 2.74, although she did not prefer N over C or L.

Gender and Sexual Preference: We found several significant results regarding sex, gender, and imitation preferences. The juvenile female, A, significantly preferred to imitate other females (p1 = .26) over male subjects (p2 = .17), z = 2.23. All other subjects either preferred to imitate subjects of the opposite gender or showed no significant preference. A was also significantly more likely to be imitated by female subjects (p1 = .15) compared to imitated by male subjects (p2 = .08), z = 4.61. The dominant adult female, T, was also more likely to to be imitated by female subjects (p1 = .23) compared to imitated by male subjects (p2 = .10), z = 7.72, as was the subordinate adult female, L (p1 = .22, p2 = .10), z = 5.39. The subordinate female, S, was the only subject who was significantly imitated more by opposite gender subjects (p1 = .20) than by other female subjects (p2 = .10), z = 2.44.

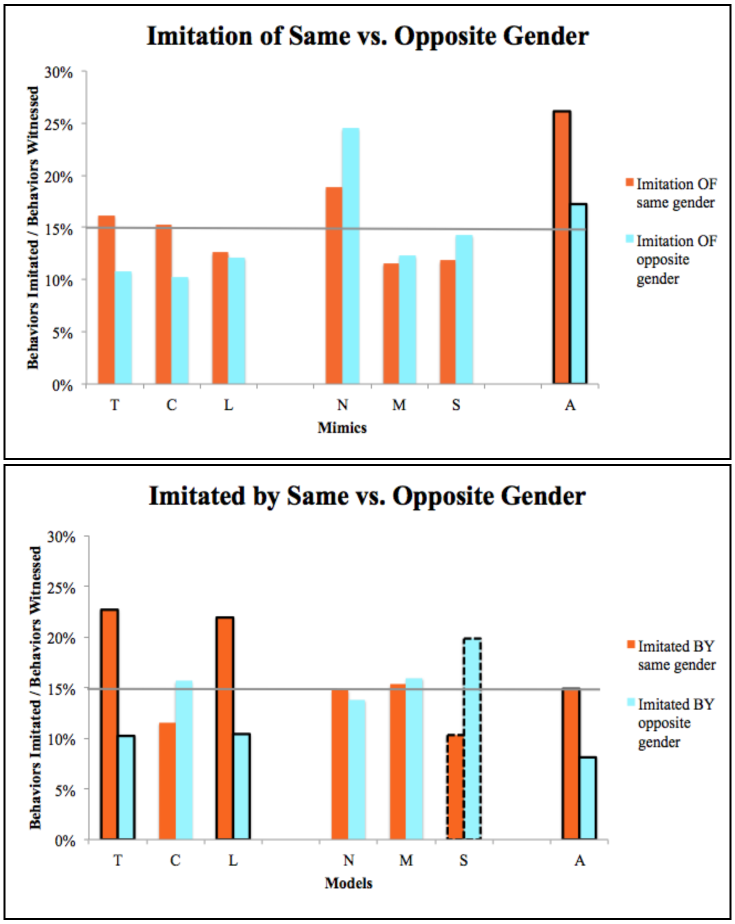

Figure 7

Imitation preferences for and by same and opposite gender subjects

There are also significant results when looking at which opposite gender subjects are preferred over others. The adult male (C) showed a significant preference to imitate S (p1 = .20) over A (p2 = .08), z = 5.50; L (p2 = .10), z = 3.64; N (p2 =.14), z = 2.14; and T (p2 = .10), z = 3.73. The subadult male (M) showed a significant preference to imitate S (p1 = .19) over A (p2 = .08), z = 5.50 and T (p2 = .09), z = 2.58. He also tended to imitate S over L and N, although not significantly. S did not show a significant preference for imitating any subject, although she did show a tendency to imitate M over any other subject. The other female subjects showed stronger tendencies to imitate other females compared to imitating male subjects.

Reciprocity and Synchrony: There appears to be a relationship between mutual imitation preference and simultaneous behaviors. Pairs of subjects who were mutually in each other's top 3 highest rates of imitating comprised 8 of the 11 pairs who showed above average rates of synchrony, with none of such pairs having below average rates of synchrony (M = .87).

Two pairs were mutually each other's first preference for imitating: M/S and L/N. M showed a significant preference to imitate S (p1 = .19) over A (p2 = .08), z = 5.50; T (p2 = .09), z = 2.58; and C (p2 = .12), z = 2.30. He also tended to imitate S over L and N, although not significantly. S did not show a significant preference for imitating any subject, although she did show a tendency to imitate M over any other subject. Likewise, M showed a significant tendency to synchronize with S (p1 = .038) over all other subjects: A (p2 = .003), z = 4.37; C (p2 = .011), z = 2.81; L (p2 = .007), z = 2.49; N (p2 = .015), z = 2.54; and T (p2 = 0.003), z = 3.43. S showed a significant tendency to synchronize with M (p1 = .038) over A (p2 = .011), z = 2.62;

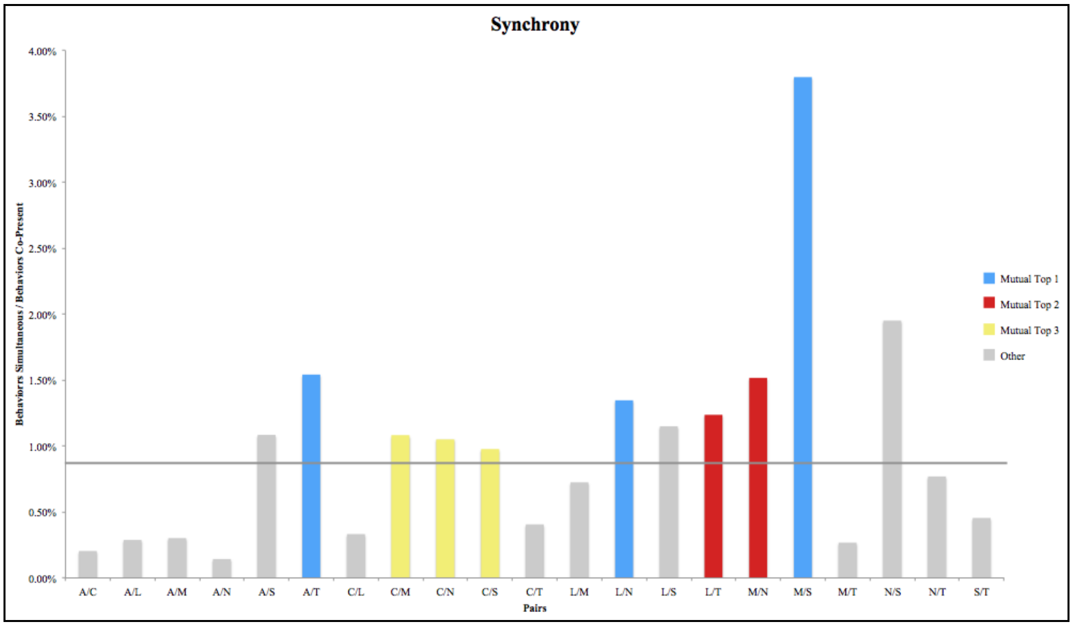

Figure 8

Rates of synchrony between all possible subject pairs

C (p2 = .010), z = 2.64; and T (p2 = 0.005), z = 2.50. She also tended to synchronize with M over the remaining two subjects, L and N, although not significantly.

L showed a significant preference to imitate N (p1 = .17) over M (p2 = .09), z = 2.27 and S (p2 = .04), z = 3.48. She also tended to imitate N over the other subjects: A, C, and T, although not significantly. N mutually showed a significant preference to imitate L (p1 = .33) over A (p2 = .16), z = 4.06; S (p2 = .13), z = 4.18; and T (p2 = .22), z = 2.08. She also tended to imitate N over the other subjects: C and M, although not significantly. Likewise, L showed a significant tendency to synchronize with N (p1 = .014) over A (p2 = .003), z = 2.54 and C (p2 = .003), z = 1.99. She also showed a tendency to synchronize with N over the other subjects: M, S, and T, although not significantly. N showed a significant tendency to synchronize with L (p1 = .014) over A (p2 = .001), z = 2.46, and showed a tendency to imitate L over C and T, though not significantly. However, she did tend to synchronize with M and S over L, although not significantly.

A and T are not technically included in those who are each other's first preference for imitating, as L is T's first preference. However, T's tendency to imitate A (p1 = .17) is not significantly different from her tendency to imitate L (p2 = .18), z = -0.35. She also significantly prefers to imitate A over all other subjects: C (p2 = .13), z = 2.04; M (p2 = .05), z = 4.79; N (p2 = .12), z = 2.06; and S (p2 = .04), z = 4.25. A also shows a significant tendency to imitate T (p1 = .32) over all other subjects: C (p2 = .17), z = 5.76; L (p2 = .25), z = 2.77; M (p2 = .18), z = 4.17; N (p2 = .18), z = 4.26; and S (p2 = .17), z = 3.92. Likewise, T showed a significant tendency to synchronize with A (p1 = .015) over C (p2 = .004), z = 3.02 and M (p2 = .003), z = 1.97. She also tended to synchronize with A over the other subjects: L, N, and S, although not significantly. A showed a significant tendency to synchronize with T (p1 = .015) over C (p2 = .002), z = 4.54; L (p2 = .003), z = 3.95; M (p2 = .003), z = 2.51; and N (p2 = .001), z = 2.96. She also tended to synchronize with T over the remaining subject, S, though not significantly.

Personality: Given any other model, A was significantly more likely to imitate in general (p1 = .23) than C (p2 = .11), z = 13.15; L (p2 = .13), z = 10.18; M (p2 = .12), z = 9.00; S (p2 = .13), z = 7.19; and T (p2 = .15), z = 7.90. N also was significantly more likely to imitate other subjects on average (p1 = .21) compared to C (p2 = .11), z = 9.97; L (p2 = .13), z = 7.46; M (p2 = .12), z = 6.84; S (p2 = .13), z = 5.49; and T (p2 = .15), z = 5.26.

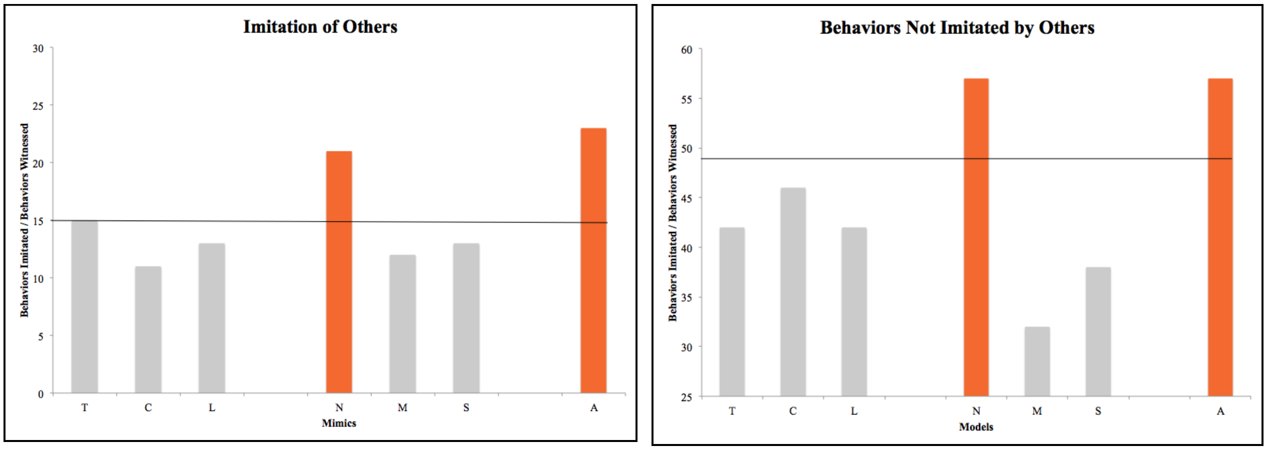

Figure 9

Imitation rates of subjects of all other subjects; rates of behaviors by subjects which are not imitated

A and N were also more likely to fail to be imitated compared to the other subjects. That is, when A does a behavior, it was significantly more likely for her to be the next one to repeat the behavior or for nobody to repeat the behavior (p1 = .57) compared to C (p2 = .46), z = 4.57; L (p2 = .42), z = 6.06; M (p2 = .32), z = 8.36; S (p2 = .38), z = 5.27; and T (p2 = .42), z = 6.68. Likewise, it is also significantly more likely for N to repeat her own behavior or have no one repeat the behavior (p1 = .57) than C (p2 = .46), z = 3.75; L (p2 = .42), z = 5.06; M (p2 = .32), z = 7.34; S (p2 = .38), z = 4.75; and T (p2 = .42), z = 5.34.

See Appendix D for all subjects' preferences to imimitate all other subjects.

Discussion

Social Rank: Contrary to our social rank hypothesis, rank was not a major factor in patterns of imitation seen in our subjects. We predicted that for any given pairing within each social group, the adults and the subadults, a subordinate dolphin would be more likely to imitate a dominant dolphin than a dominant dolphin would be to imitate a subordinate dolphin. This was not the case, as none of the possible pairings in the adult group significantly differed on who was more likely to imitate the other. In the subadult group, the dominant female was more likely to imitate the mid-ranked male than the mid-ranked male was to imitate the dominant female, and the other possible subadult pairings did not significantly differ on who was more likely to imitate the other. We also predicted that subordinate dolphins would have a higher propensity in general to imitate others than dominant dolphins would. This also was not the case. The dominant subadult female was actually the second-most frequent mimic of others, following the juvenile.

We therefore conclude that social hierarchy is not a straightforward predictor of our subjects' preferences for who to imitate, nor their propensity to imitate in general. This contradicts the suggestions that one's social status as "in-group" or "out-group" affects imitation preference and frequency (Lakin, Chartrand, & Arkin, 2008), and that willingness to imitate may be influenced by social rank (Bauer & Johnson, 1994). However, this may be largely due to the many other factors at play in our group of subjects, and the complex social lives of bottlenose dolphins in general. We will thus expand our discussion to other social factors which may help explain the imitation tendencies shown by our subject.

Length of Residency: It also does not appear that the amount of time subjects have lived in the tank plays a large role in who subjects tend to imitate, as only one subject showed a significant tendency to imitate those who arrived earlier, and all other subjects showed no preference for those who arrived earlier or later. It does seem that social rank and length of residency are roughly linked, as the dominant adults and the dominant subadult have been in the tank for the longest amounts of time, and the subordinate adult female and subordinate subadult female have been in the tank for the shortest amounts of time. Thus, it is sensible that length of residency is also not a major factor in dolphins' imitation tendencies.

Age and In-Group/Out-Group: Rather than equating "in-group" with high social rank and "out-group" with low social rank, when looking at in-group/out-group dynamics it may make more sense to examine one's tendency to imitate those within their own social group compared to those in other social groups. Our subjects tend to group themselves based on age. However, it does not seem that the role of age or in-group/out-group status plays a consistent role across subjects. Two subjects showed a propensity to imitate those in their own age group, two showed a propensity to imitate older subjects, one subject showed a propensity to imitate younger subjects, and the other two showed no significant preference for older, younger, or same age subjects.

Because many of the subjects did show a significant preference, it may be that age and in-group/out-group status are factors in one's preference to imitate. The tendency by some subjects to imitate those older than them may be related to claims that younger dolphins are more likely to imitate their older peers, especially with play behaviors (Kuczaj & Yeater, 2006; Kuczaj, Yeater, & Highfill, 2012). While this was specifically regarding dolphin calves, perhaps this tendency is carried on later in life as well, especially given the highly social and playful nature of dolphins into adulthood.

The tendency by other subjects to imitate those within their age range, and thus their own social group, may be in accordance with suggestions that individuals involved in imitation tend to have better connections with one another (Chartrand & Bargh, 1999) and that imitation facilitates group cohesion (Lakin, Jefferis, Cheng, & Chartrand, 2003), which may indicate an increased propensity to imitate those in one's own social group. Ultimately, however, due to the conflation of age and organization of social groups in our subjects, we are unable to determine if the effects found are due mainly to age, to in-group/out-group dynamics, or to a combination of both.

Kin: The kin relationship of three subjects seems to drive certain patterns to imitate and be imitated seen in these individuals. However, it does not appear to play the same role for each member of the family. Perhaps the most evident pattern in the entirety of our results is that the overwhelming majority of imitation of the mother subject is done by her two daughters, compared to the other, unrelated subjects. However, there is not a significant difference in imitation of either of the daughters by related subjects compared to unrelated subjects. Furthermore, both daughters had much higher tendencies to imitate their mother compared to the mother imitating the daughters, or to either daughter imitating the other. This indicates that propensity to imitate one's parent may be a larger factor than propensity to imitate kin in general. These results may be related to findings that dolphin calves often imitate their mothers during development (Kuczaj & Yeater, 2006; Kuczaj, Yeater, & Highfill, 2012), although neither of the daughter subjects are calves. However, the lack of other juveniles in this community, the relatively small number of individuals in general, or the fact that they live in a small enclosure compared to wild communities may lead the mother-juvenile pair to maintain closer ties later in life than would be seen in wild dolphins.

Some support for this speculation shows up in the relative tendencies between the subadult daughter and the juvenile daughter to imitate their mother compared to their imitation of other subjects. The mother was the juvenile's first preference to imitate, and she imitated her mother significantly more than she did over any other subject. On the other hand, the mother was the subadult daughter's third preference to imitate, and only imitated her significantly more than she imitated one other subject. This may be due to the fact that the subadult daughter has peers who are close in age, and spends the most time associating with this group. On the other hand, the juvenile does not have any same age peers, and spends much of her time associating with her mother, and thus does not have the opportunity to imitate peers, as discussed in Kuczaj & Yeater (2006) and Kuczaj, Yeater, & Highfill (2012).

Gender and Sexual Preference: Imitation preferences may also be mediated by gender and other sexual factors, especially in the subadult subjects. The only subject who significantly preferred to imitate same gender subjects compared to opposite gender subjects was the juvenile, who is also the only subject who has not yet reached sexual maturity. The juvenile was also significantly more likely to be imitated by same gender subjects compared to opposite gender subjects, as were both adult females. This may be a reflection of an increased focus on potential sexual interactions or partners during adolescence.

Only one subject, a subadult female, was imitated significantly more by opposite gender subjects compared to same gender subjects. This may be due to this subject's sexual history with both male subjects. This subject was the first preference to imitate by both male subjects, although this was only a mutual preference with the subadult male, while the female showed a low preference to imitate the adult male. Indeed, it seems that patterns of sexual involvement are related to patterns of imitation, as subjects who have been sexually involved show tendencies to imitate one another. Furthermore, it seems that subjects who are both sexually available and more prone to focusing on sexual interactions see greater rates of imitation by and of opposite gender subjects.

It is possible that these effects are influenced by the potentially sexual nature of the behaviors we scored for this project, rather than the role of imitation itself. While there is no evidence for the use of body orientation changes in social interactions of bottlenose dolphins, literature on spinner dolphins (*Stenella longirostris)* indicates that this purposeful display of the underside may be used to invite or request genital contact. However, it also may be used to invite or request other social interactions which are not sexual in nature (Norris, Wursig, Wells, & Wursig, 1994).

Reciprocity and Synchrony: It appears that there may be a relationship between reciprocated imitation and synchrony. While we have not analyzed tendencies to reciprocate individual instances of imitation, it at least seems that individuals who reciprocate a preference for imitating each other in general have relatively high rates of synchrony with one another. All pairs who were mutually in each other's top 3 preferred imitation partners also had above average rates of synchrony, and made up the majority of pairs who had above average rates of synchrony. The pair with the noticeably highest rate of synchrony were also mutually each other's top 1 preferred imitation partners, while the two other pairs who were each other's top preferences showed relatively high rates of imitating each other as well.

Our findings that synchrony and imitation preferences may be linked supports ideas that synchrony and imitation involve similar mechanisms and serve similar functions (Fellner, 2006; Kuczaj & Yeater, 2006). However, it is difficult from our study to determine whether synchrony drives imitation preferences, imitation drives synchronizing preferences, or if both are due to another factor. One source of confusion in interpreting these results is that one of the pairs who mutually preferred to imitate each other don't spend a great deal of time together. However, the other two pairs, including the one showing the relatively outstanding rate of synchrony, do spend a noticeable amount of time together, which indicates that imitation and synchrony may influence or be influenced by how closely affiliated those involved are. This supports ideas that synchrony between dolphins can serve as a signal of the participants' unity to each other and to observers (Pryor, 1991), and that imitation can lead to "increased rapport" and "interpersonal closeness" (Chartrand & Bargh, 1999).

Personality: Imitation preferences, however, are not always reciprocated. Two subjects stood out as most likely to imitate others in general. These same subjects also stood out as having the lowest rate of having their behaviors be imitated by others. That is, they seemed to have poor "success" at being imitated compared to other subjects. If we consider high propensity to imitate as a marker of "boldness", and low propensity to imitate as a marker of "timidness", then our results directly contradict Kuczaj, Yeater, & Highfill's (2012) finding that timid dolphins tend to imitate bold dolphins. This may be due to the fact that this discussion specifically pertained to dolphin calves in observational learning situations, and that the findings cannot be extended to older dolphins or social situations not involving observational learning.

Another possibility is that there is a limit to how "bold" an individual can be and still appear a desirable model to others. Support for this idea comes from literature on biological markets. Following the model proposed by Noe, van Schaik, and van Hooff (1991), power imbalances between individuals in a social system can arise due to discrepancies in the value of social resources held by the individuals. It may be the case that imitation is a "currency" in the market of bottlenose dolphins, and that at a certain point, imitating others too much causes the individual to appear less desirable, and thus not be imitated by others in return.

It is also possible that the causality is in the opposite direction. Research on humans shows that failure to form connections with others can lead an individual to imitate more in their next attempt at interacting with another in order to increase the likelihood of social connection on the second try (Lakin & Chartrand, 2003). If the failure to be imitated is taken as a form of failing to form social connections with others, then perhaps the subjects who have low success at being imitated feel driven to imitate others more frequently as a result.

General Discussion: Ultimately, bottlenose dolphins are highly intelligent animals with complex social lives, so it should not come as a surprise that their behaviors and interactions are not driven by a single factor such as social rank. While we hypothesized that rank would be a major mediating factor in the subjects' imitation preferences and tendencies, we found that it did not play a significant role, nor did various other factors such as length of residency or age. However, kin relatedness did seem to drive imitation factors, especially in offspring imitating a parent. Gender seemed to play some role in imitation preferences, as some tended to imitate and be imitated by potential sexual partners, while others tended to to prefer and be preferred by same-sex subjects. All pairs with a mutual preference to imitate one another also tended to have relatively high rates of synchrony. Interestingly, however, imitation was not always reciprocated, as the subjects who imitated others most frequently also had the highest rates of behaviors not imitated by others. With many of these factors, however, it is not clear whether their social patterns are the driving force for the observed imitation patterns, if the imitation patterns mediate social interactions and relationships, or a combination of both.

Future Directions

While this study has revealed some social factors which seem to play a role on how often and with whom dolphins imitate, additional research on the subject will help us further understand the role of imitation in the social lives of these complex animals. Because the current data is only on 9 of the existing 21 hours of available footage, we will first continue scoring behaviors for the remaining 12 hours. More than doubling our populations of behaviors to analyze may strengthen the patterns we have already found, or reveal new patterns which were not evident in the current data.

We also plan to examine the relationship between imitation and partnering, by comparing our findings with those of a concurrent study in our lab on partner states of the subjects. By looking at patterns in both data sets, we can analyze whether the patterns of one data are predictive of patterns in the other. We may look to see whether individuals involved in an instance of imitation are more likely to be partners before the imitation instance. That is, whether imitation is more likely to occur between partners than between non-partners. We may also look to see whether individuals involved in an imitation instance are significantly more likely to be partners after the imitation instance. That is, whether imitation leads to subsequent partnering relationships.

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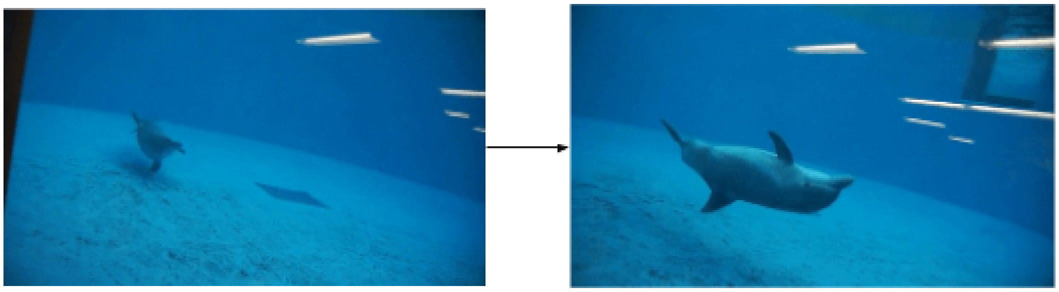
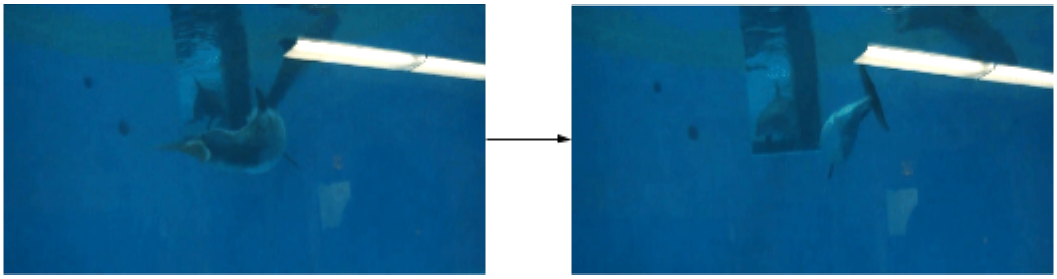
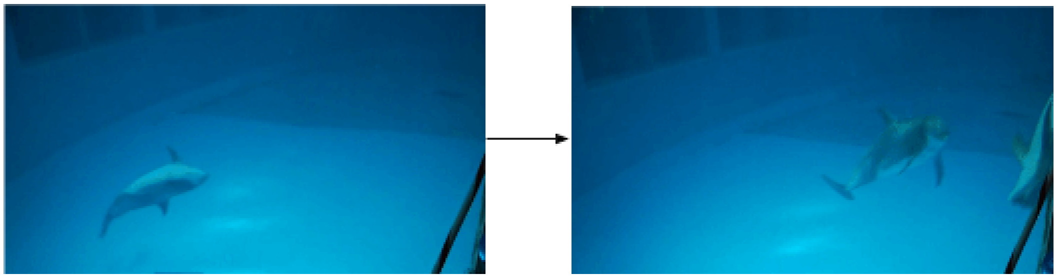
Appendix A

Arrival dates and residency durations of subjects at Brookfield Zoo

Subject	**Arrival Date**	**Residency Duration at Time of Video Recording**
Tapeko (T)	1999	14 years
Chinook (C)	2000	13 years
Noelani (N)	2003 (born in tank)	10 years
Allison (A)	2005 (born in tank)	7 years
Tatum (M)	April 2010	3 years
Spree (S)	September 2010	2.5 years
Allie (L)	2012	6 months

Table 2

Illustrations of scored behaviors

Belly Up	
Tilt	
Upright	

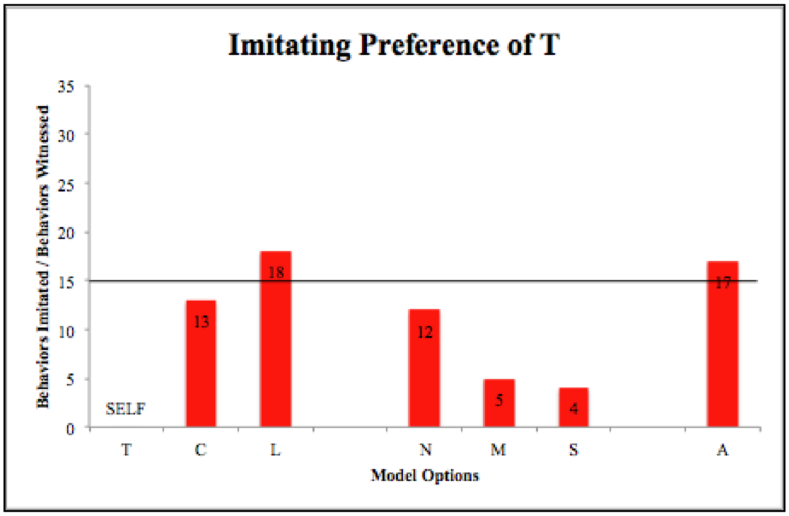
Appendix C

Protocol for data collection

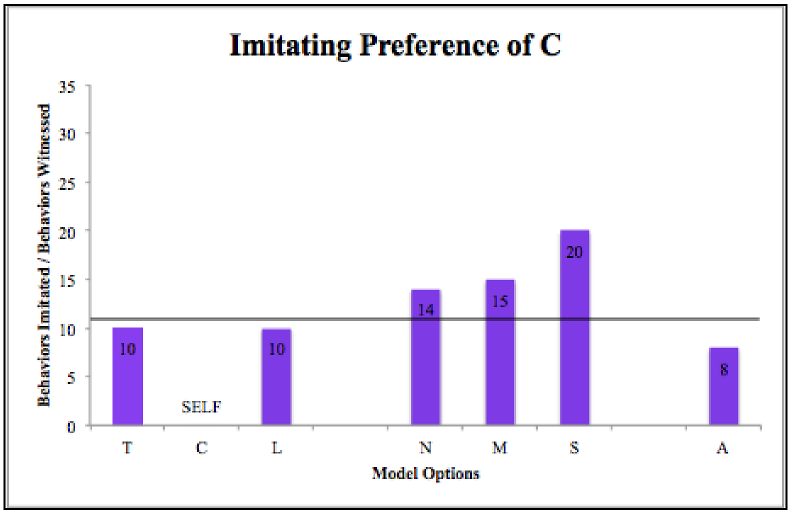
Behavior	**Code**	**Description**
Belly Up	B	- Definition: dolphin's body is rotated over 135° from normal, upright swimming - No required minimum or maximum duration of behavior - Scored at onset time, precise to the second
Tilt	H	- Definition: dolphin's body is rotated between 45° and 135° from normal, upright swimming - Tilts occurring at the beginning or end of a belly up must last for more than 3 seconds in order to be scored as a separate behavior from the belly up - Tilts occurring independently from a belly up have no required minimum or maximum duration - Scored at onset time, precise to the second
Upright	R	- Definition: return to normal, upright swimming after other behavior - Scored at offset of previous behavior, precise to the second
Flash	F	- Definition: special case of the above behaviors in which onset (belly up or tilt) and offset (upright) occur within the same second
Unseen	U	- Definition: dolphin goes off camera, and is doing a different behavior than its behavior upon reappearing - Scored starting from the last second during which any body part indicating body orientation is visible, until but not including the second indicating its new behavior upon reappearing

Appendix D

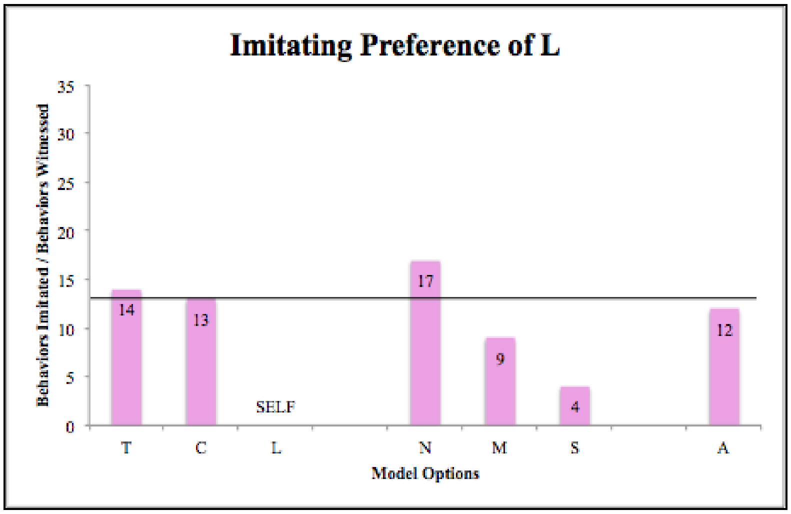
Imitation tendencies of all subjects



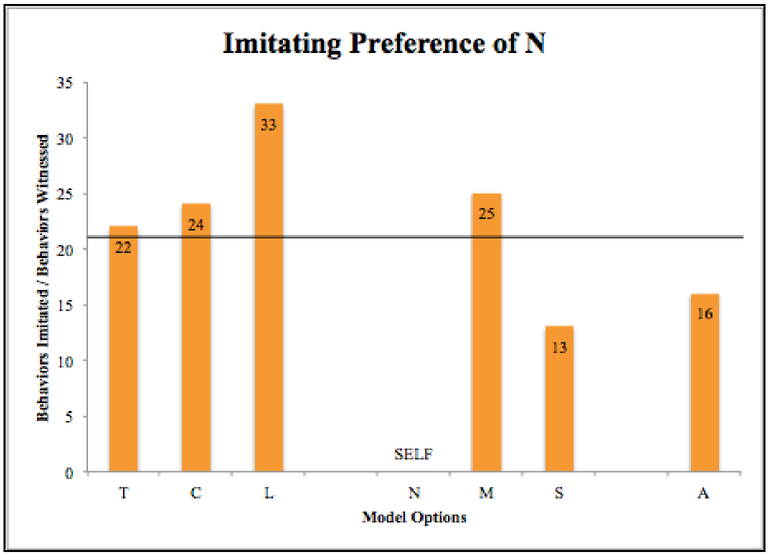
Imitating Preference of T



Imitating Preference of C



Imitating Preference of L


Imitating Preference of N
Behaviors Imitated / Behaviors Witnessed
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30
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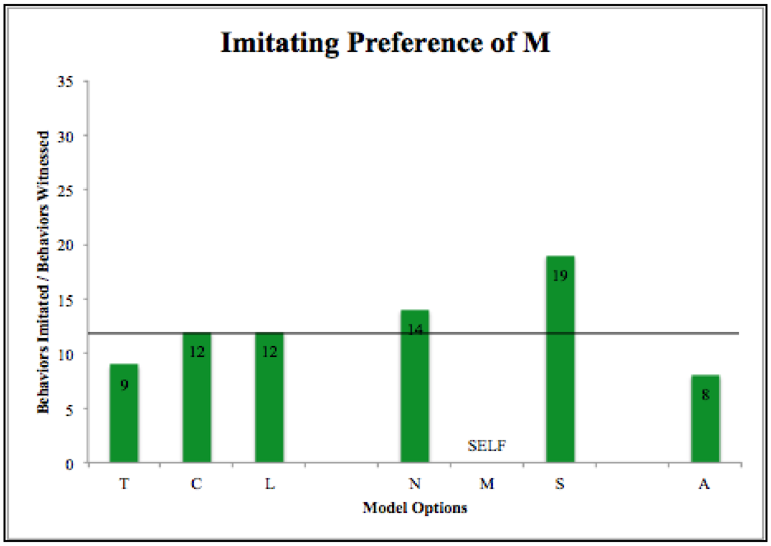
Model Options


Imitating Preference of M
Behaviors Imitated / Behaviors Witnessed
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25
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14
SELF
19
8
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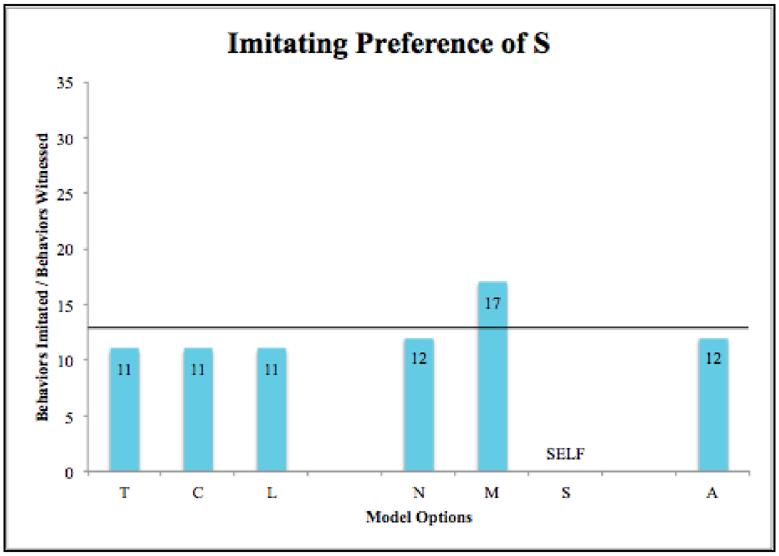
Model Options


Imitating Preference of S
Behaviors Imitated / Behaviors Witnessed
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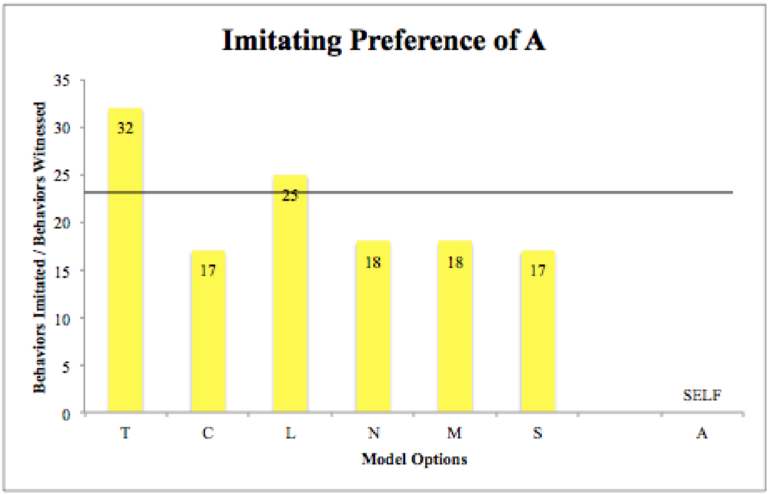
Model Options


Imitating Preference of A
Behaviors Imitated / Behaviors Witnessed
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17
SELF
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Model Options