Preferential Association Among Kin Exhibited in a Population of Atlantic Spotted Dolphins (*Stenella frontalis*)

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While it is widely accepted that dolphins form associations with conspecifics based primarily on similarities in age class and reproductive status, perhaps equally important is the investigation into secondary influences such as kinship. Preferential association among kin is well-researched in numerous terrestrial species, but has only recently been investigated in cetaceans. This study brings another species into the body of work being formed on the influence of relatedness on cetacean relationships. The association indices of 26 individuals with known relatives in a population of Atlantic spotted dolphins, *Stenella frontalis*, were compiled from encounters in the Bahamas from 2002-2006. Analysis demonstrated that there is preferential association among kin in this population. Mean association indices were found to be significantly higher within families than between families, and there was a positive correlation between relatedness and coefficient of association. Also, the effects of social segregation based on sex and age class, which were evident in the sample population as a whole, were absent in kin dyads.

Coefficients of association, or COAs, have been used frequently in bottlenose dolphin studies (Gero, Bejder, Whitehead, Mann, & Connor, 2005; Rogers, Brunnick, Herzing, & Baldwin, 2004; Wells, Scott, & Irvine, 1987; Connor, Heithus, & Barre, 1999; Rossbach & Herzing, 1999) and also in studies of Atlantic spotted dolphins (Herzing & Brunnick, 1997). Analyses of individual patterns of association provide insight into the social structure of a population (Whitehead & Dufault, 1999; Hinde, 1976). Specifically, investigation into whether an individual is either associated with preferentially or actively avoided on the basis of its sex, relatedness, or dominance can be extremely informative.

Since 1985, a unique, non-invasive, and long-term assessment of the life history, communication, and behavior of a population of free-ranging, habituated Atlantic spotted dolphins (*Stenella frontalis*) has been conducted off Grand Bahama Island (Welsh, 2007; Herzing, 2005; Miles & Herzing, 2003; Herzing & Brunnick, 1997; Herzing & Johnson, 1997; Herzing, 1996). Like *Tursiops* species of dolphins, this population of spotted dolphins lives in a fission-fusion society in which group size, composition, and membership vary. However, strong and stable long-term bonds are often formed. It is known that close dolphin associations are formed between some individuals which are similar in age class and/ or reproductive status, and that mothers and calves form the strongest associations (Rogers et al., 2004; Herzing & Brunnick,

1997; Wells et al., 1987), but still unknown is whether relatedness has any role in the formation of preferential associations among juveniles and adults. Inclusive fitness theory, which proposes that individuals will cooperate with or aid genetic relatives to increase their own fitness (Hamilton, 1964), may be applicable to the association patterns of related dolphins.

Reciprocal altruism (Trivers, 1971) is, by definition, directed towards non-relatives and can arise only when there are many opportunities for reciprocation. Therefore, in societies of highly social animals, we can expect frequent associates to demonstrate altruistic behaviors towards one another (Goodall, 1986a; Connor & Norris, 1982). Inclusive fitness and reciprocal altruism are generally regarded as distinct mechanisms for the emergence of altruism. However, although reciprocal altruism is not necessarily based on kinship, the evolutionary conditions leading to altruism are the same as those for kin selection (Fletcher & Zwick, 2006; Goodall, 1986a; Connor & Norris, 1982). Mutual support among non-relatives can benefit the cooperating individuals indirectly by decreasing the reproductive success of a rival, but a more direct or obvious benefit can be seen when fitness is increased inclusively through the mechanism of kin selection.

Within every society, there are numerous selective pressures driving the formation of relationships. It is important to consider these pressures at every level: from how individuals recognize one another to how the population is ultimately affected by the relationships of its members. To begin with, preferential associations, and avoidance, can occur only when there is some form of recognition or familiarity. Recognition can be accomplished from chemical (Blaustein & O'Hara, 1986), visual, or vocal cues (Tyack, 1999; Caldwell, Caldwell, & Tyack, 1990; Caldwell, Caldwell, & Miller, 1973). Familiarity is developed socially from frequent or significant interactions with recognized conspecifics (Smith, Alberts, & Altmann, 2003). Goodall (1986a) states that among higher social mammals, the degree of familiarity is primarily *socially* based on close, prolonged associations. Spotted dolphins though, unlike these other social mammals, do not remain in family units throughout their lives. In fact, a significant decrease in association values between mothers and calves coincides with the birth of a sibling (Herzing & Brunnick, 1997).

Studies of various animals, including dolphins, have shown familiarity to be more important than relatedness (Curry, 1988), lack of kin recognition in the absence of familiarity (Blaustein & O'Hara, 1986), and a lack of preferential behavior towards either maternal siblings (Mitani, Merriwether, & Zhang, 2000) or paternal siblings (Erhart, Coelho Jr., & Bramblett, 1997). For example, genetic analysis of bottlenose dolphins in Sarasota Bay, Florida demonstrated that strongly associating male pairs are not closely related (Owen, 2003).

Furthermore, there is uncertainty as to which animals even have the capacity to recognize paternal siblings at all. Mitani et al. (2000) for example, argue that this is likely prevented by internal fertilization in a promiscuous society. However, numerous studies have found that some animals can not only recognize paternal kin (Alberts, 1999), but preferentially associate with them as well (Smith et al., 2003; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001; Blaustein & O'Hara, 1986).

Still, many male alliances are known to be based on relatedness (bottlenose dolphins: Krützen et al., 2003; Parsons et al., 2003; lions: Girman,

Mills, Geffen, & Wayne, 1997; dogs: Grinnell, Packer, & Pusey, 1995; and chimpanzees: Goodall, 1986b). Krützen et al. (2003), for example, found that primary alliance (groups of two or three individuals) members of bottlenose dolphins (*T. aduncus*) in Shark Bay, Australia were significantly more closely related to one another and to their secondary alliance partners than randomly expected. It has also been shown that female baboons bias social behaviors towards both maternal and paternal half-sisters (Smith et al., 2003) and female striped dolphins tend to form groups with their kin (Gaspari, Azzellino, Airold, & Rus Hoelzel, 2007). Even tadpoles have been found to prefer to associate with full siblings to half siblings, maternal siblings to paternal siblings, and paternal siblings to half siblings (Blaustein & O'Hara, 1986).

A number of other factors contribute to the variability found in studies of affiliative bonds in highly social mammals, one of which is gene flow (Haig, 2000; Haig, 1999; Haig, 1997). Genetic flow in most dolphin communities is male-mediated (Krützen, Barre, Connor, Mann, & Sherwin, 2004; Wells et al., 1987) however, Parsons (2002) found unique evidence of female-mediated gene flow in the bottlenose dolphins in the Bahamas. Demographics also affect kin associations. For example, the options for choosing associates for individuals in a small, closed population are restricted so that they may be required to differentiate between paternal and maternal kin (Smith et al., 2003). Also, relatively long inter-birth intervals make it less likely that maternal siblings will become close affiliates, as they would be dissimilar in age and reproductive status (Goldberg & Wrangham, 1997). Additionally, kinship may have less influence on associations when there are more mature males than there are females or when there is a low level of genetic variance. In these cases, alliance formation is beneficial regardless of relatedness (Parsons et al., 2003).

For this project, COAs of Atlantic spotted dolphins were compiled from encounters in the Bahamas from 2002-2006. This study investigates the relevance of Hamilton's theory to this population of spotted dolphins by analyzing COAs of relatives and non-relatives. To address the issue of preferential association with kin in this population of spotted dolphins, the following questions were addressed: 1) Do dolphins have significantly stronger associations with kin than with non-kin?, 2) Are strong associates that differ greatly in age more likely to be related?, 3) Is age difference correlated with the strength of kin associations?

Method

This population of free-swimming Atlantic spotted dolphins, *Stenella frontalis*, has been the focus of scientific observation for over 20 years. Identities of individual dolphins are known, as are the maternal relationships of individuals born after 1985. Eighteen of the known mother-calf relationships have been genetically confirmed through mitochondrial sequencing and none have been refuted (Green, Herzing, & Baldwin, 2007).

This study is an analysis of data from annual surveys from May through early September of 2002-2006 conducted by the Wild Dolphin Project (WDP) on board the *RV Stenella*, an 18.9m power catamaran. *Ad lib* sampling (Altmann, 1974) was conducted daily from 0700 to 2000 hours. An observer was stationed on the bridge to visually survey the water surface for the presence of dolphins. When dolphins were sighted, the vessel was steered in the direction of the dolphins and brought to idle. A group was defined as all individuals moving in the same direction and generally involved in the same activity (Rogers et al., 2004; Shane, 1990). Individual dolphins were identified from underwater photographs and video documenting the morphologies of the dorsal fin, flukes, scars, and spotting patterns (Herzing & Brunnick, 1997).

Sex was determined by direct underwater observation of the genital area, erections, or observational confirmations of pregnancy. Age classes were determined using the ontogenetic classification of the pan tropical spotted dolphin, *Stenella attenuata*, which correlates spotting patterns with age (adjusted for *Stenella frontalis* by Herzing, 1997; from Perrin, 1970). There is individual variation in the duration of the age classes, but *S. frontalis* generally follow the pattern of two-tone (0-3yrs), speckled (4-9yrs), mottled (10-16yrs), and fused (17+yrs).

In over 3600 survey hours there were 261 encounters with spotted dolphins, with the average encounter time lasting 56.8 minutes (SE = 44) and 76.34 minutes (SE = 50) for spotted-only and mixed species encounters, respectively. On average, 85% of the individuals in each encounter were identified (median = 94%, quartile range = 25%). Unidentified animals were not used in the analyses. The sighting criteria for calculating COAs of cetaceans in past studies have ranged from two (Slooten, Dawson, & Whitehead, 1993) or three (Rogers et al., 2004) sightings per individual to 10 (Quintana-Rizzo & Wells, 2001) to 30 (Gero et al., 2005) sightings per individual. Ninety-three individuals in this population were used in this study based on the criteria that each was seen at least four times between 2002 and 2006, and was born before 2002. The 93 individuals (Table 1) that met the criteria made up 81% of non-calf individuals identified since 2002. Calves were not included in this analysis due to the influence a calf's strong dependence on its mother potentially has on its associations with other individuals.

Table 1
Sex and age class composition

	Male	Female	Unknown	Total
Speckled	9	13	2	24
Mottled	10	15	0	25
Fused	20	24	0	44
Total	39	52	2	93

Study Site

The primary study area is centered north of West End, Grand Bahama Island, on the western edge of Little Bahama Bank. The entire study site is approximately 480 km^2, spanning 60km north to south, from 27°22' N to West End (26°29' N), and 8 km east to west. Little Bahama Bank (LBB) is an unprotected, shallow (6-16m) sand bank with patches of turtle grass, rock, and reef on the sandy bottom. The western border of the study area is a steep drop-off of over 500m in the Gulf Stream.

Data Analysis

COAs ranging from 0.00 (two dolphins never seen together) to 1.00 (two dolphins always seen together) were determined for each dolphin in the study using a half-weight index (HWI):

$$\text{Half-weight index} = N_{ab} / [N_{ab} + 1/2(N_a + N_b)],$$

where N_{ab} is the number of encounters where both individuals were present, N_a is the number of encounters that included dolphin a but not b, and N_b is the number of encounters that included dolphin b but not a. The half-weight index accounts for bias from pairs being more likely to be scored when separate than when together (Cairns & Schwager, 1987). HWIs were calculated and analyzed using Socprog version 2.3 (Whitehead, 2006) in Matlab® version 7.1 (The Mathworks, Inc., 2006). These programs were also used to determine the level of social differentiation, generate and compare randomly permuted data, and to run and analyze results from Mantel tests, principal coordinates analysis, and matrix correlations. All other statistical analyses were performed by SPSS 15.0.

To test the null hypothesis that individuals were associating randomly, a statistical comparison of randomized association matrices generated by Socprog to the observed association matrices was accomplished with a modification of the Manly/Bejder permutation test (Whitehead, Bejder, & Ottensmeyer, 2005; Whitehead & Dufault, 1999; Bejder, Fletcher, & Bräger, 1998; Manly, 1995). Mantel tests were then performed within and between age and sex

classes on all individuals to provide a baseline for comparison with association patterns of only kin dyads. Observed association matrices were randomized 20,000 times with 100 flips per permutation within daily sampling periods.

Kinship Associations - whole study group

Of the 93 dolphins in this study, there were 23 individuals with known relatives that were also in the study sample from ten matrilineal lines, or families. These individuals comprised 17 sibling pairs and five aunt/uncle-nephew pairs. To test for a correlation between relatedness level and association value, the observed association matrix was compared to a relatedness matrix with a Mantel test. The relatedness matrix was made by assigning a value of 0.00 to dyads not known to be related, a 0.25 to the 17 known sibships, and a 0.125 to the five known aunt/uncle-nephew dyads. These coefficients of relatedness represent the approximate proportion of genes shared by the relatives (Alcock, 1998). The values used here were based on the conservative assumption that all of the sibling pairs in this study were half-siblings. Next, analyses were restricted to mottled-speckled pairs. Mottled-speckled dyads should theoretically show weaker associations, as they are farther apart in age than dyads of individuals in the same age class. Since the more than half (55%) of kin dyads are mottled-speckled, the association index distribution of non-maternally related mottled-speckled pairs was compared to the association index distribution of maternally related mottled-speckled pairs.

Kinship Associations - restricted to individuals that have known relatives

Only individuals with known relatives were used for this portion of the analysis. The data set was restricted in this way to ensure that individuals associating with known kin exhibited the same general association patterns as the whole population, such as gender and age segregation. A Mantel test was then used to compare the HWIs of relatives between and within families.

Results

The null hypothesis of no preferred or avoided associations was rejected ($CV_{observed} = 1.11$, $CV_{random} = 1.02$, $p < 0.01$). The mean HWI of the dyads formed by the 93 individuals was 0.12 (SE = 0.13). Association indices were significantly higher in same-sex associations than in mixed-sex associations ($t = 7.89$, $p < 0.01$, matrix correlation = 0.15). They were also significantly higher within age class than between ($t = 3.8333$, $p < 0.01$, matrix correlation = 0.08, Table 2). As mentioned earlier, mother-calf associations are the strongest associations and, therefore, the mean HWIs reported here are relatively low since those dyads were not included in the analyses.

Table 2
Mean HWIs show segregation based on sex and age class

	Same-sex	Mixed-Sex	Same Age Class	Different Age Class
Mean (SE)	0.14 (0.04)	0.10 (0.04)	0.13(0.04)	0.11 (0.04)
Max (SE)	0.54 (0.17)	0.39 (0.13)	0.48 (0.14)	0.51 (0.15)

Kinship Associations - whole study group

Association indices were significantly higher within families than between families ($t = 2.74$, $p < 0.01$, matrix correlation = 0.15, Table 3). The mean within-family index (0.23, SE = 0.11) was much higher than the value of the between family index (0.14, SE = 0.07). When the data set was restricted to

mottled-speckled dyads, thirteen of the 592 possible dyads were kin. Where the majority of non-maternally related mottled-speckled dyads (n = 580 dyads) were below the population average of 0.12, the majority (58.3%) of the related mottled-speckled dyads (n = 12 dyads) were high, at above 0.25.

Table 3
Mean HWIs within and between families

	Mean (SE)	Max (SE)
Within	0.23 (0.10)	0.26 (0.12)
Between	0.14 (0.07)	0.42 (0.15)
Overall	0.15 (0.06)	0.44 (0.13)

Kinship Associations - restricted to individuals that have known relatives

There was a significant positive relationship between the association matrix and the relatedness matrix according to the Mantel correlation test. With 10,000 permutations, the mean association was 0.12 for non-relatives (n = 4257 dyads), 0.24 for aunt/uncle-nephew pairs (n = 5 dyads), and 0.22 for sibships (n = 16 dyads). The overall mean association was 0.12 (Mantel z-test, p < 0.01, matrix correlation = 0.06). There was no significant correlation between the number of years separating the siblings and their association indices (n = 17 dyads, r = 0.24, p = 0.18). The same held true for all kin dyads (n = 22 dyads, r = 0.14, p = 0.27). Results from analysis of same-sex and mixed-sex associations of kin with non-relatives were consistent with results from the rest of the sample population. However, in kin dyad associations, there was no difference between same-sex and mixed-sex associations (Mann-Whitney U, U = 45, p = 0.77). This set included thirteen same-sex dyads, though only one was male-male. Considering only female-female associations versus mixed-sex, the mean of the same-sex associations of kin dyads (0.19) was lower than the mixed-sex associations (0.23, SE = 0.13, Table 4).

Table 4
Sex class segregation in non-kin dyads vs kin dyads

Mean HWIs within and between sex		
Class	Non-kin	Kin
Male-Female	0.13 (0.06)	0.23 (0.13)
Male-Male	0.14 (0.15)	0.39*
Female-Female	0.16 (0.08)	0.19 (0.14)
Within	0.15 (0.07)	0.22 (0.13)
Between	0.13 (0.06)	0.23 (0.13)
Overall	0.14 (0.06)	0.23 (0.13)

*one dyad only

There was also deviation from the population trends in within age-class and between-age class association of kin dyads. Their average between-class associations were lower than their average within-class associations with non-relatives, but the opposite was seen for associations of kin dyads. In that

case, the between-class associations were actually higher than the within-class associations, although not significantly (Mann-Whitney U, U = 29.5, p = 0.73, Table 5).

Table 5
Age class segregation in non-kin dyads vs kin dyads

Mean HWIs within and between age class		
	Kin-Nonkin	Kin-Kin
Speckled-Speckled	0.19 (0.09)	0.21 (0.14)
Mottled-Speckled	0.15 (0.07)	0.26 (0.13)
Mottled-Mottled	0.13 (0.06)	0.23 (0.06)
Within	**0.17 (0.08)**	**0.22 (0.11)**
Between	**0.15 (0.07)**	**0.26 (0.13)**
Overall	0.16 (0.07)	0.25 (0.12)

Discussion

This study builds upon support for Hamilton's (1964) theory of inclusive fitness previously found in studies of primates (Smith et al., 2003; Widdig et al., 2001; Alberts, 1999; Goodall, 1986b). There is also newly found support for the theory in other species of dolphins (*S. coeruleoalba*: Gaspari et al., 2007; *T. aduncus*: Krutzen et al., 2003, *T. truncatus:* Parsons et al., 2003) and now this study contributes supporting data from *S. frontalis*. Association indices were significantly higher within families than between families, demonstrating preferential association among kin. This finding was supported by a positive correlation between relatedness and association indices of dyads.

General social trends in this study population were typical of other well-studied dolphin societies in that associations were stronger in same-sex pairs than mixed-sex pairs, and stronger between individuals in the same age class than between individuals in different age classes (Smolker, Richards, Connor, & Pepper, 1992; Wells et al., 1987). The most intriguing aspect of the results reported here is that sex segregation and age segregation were not observed in kin dyads as they were in the whole population. Although individuals in different age classes constituted the majority of the kin dyads in this study, their association values remained high. This effect is very interesting and warrants further investigation into the question of preferential association among kin.

Relatedness may be an important factor in the formation of relationships that define dolphin societies, and one that is overshadowed by more well-known factors. Factors such as reproductive status and age acting as primary influences on social structure are well documented (Wells et al., 1987). It may be valuable to now examine the effects of less predominant factors such as kinship. It is also important to note that the results from this project were drawn conservatively, as no paternal relatedness was assumed and not all individuals in the analysis were seen in each year. It is possible not only that some of the kin dyads analyzed were full siblings or were paternally related, but also that some of the dyads to which the kinship dyads were compared were paternally related. Paternally related dyads in the comparison

group of individuals of known maternal relations could have diluted the results.

If it was to be expected that related individuals should associate preferentially with one another based on the theory of inclusive fitness (Hamilton, 1964), there should also have been lower associations among aunt/uncle-nephew dyads than among sibling dyads. There was, however, no difference. In fact, aunt/uncle-nephew associations were higher on average. This observation could be a result of a greater degree of relatedness (paternally related individuals) among the aunt/uncle-nephew dyads than was assumed. Alternatively, this observation, along with the lack of age segregation in kin dyads, lends support to the idea that the mixed age-class groups observed in this society may be a means for cultural transmission (Bender, Herzing, & Bjorklund, 2008; Herzing, 2005; Rendell & Whitehead, 2001). In addition to forming mixed age-class groups, the individuals in this population are long-lived and are often observed in multi-generational family groups. It would follow from inclusive fitness theory that some groups are formed based on relatedness so that young dolphins are exposed to important behaviors by their relatives.

High associations among grandmothers and grandchildren should also be expected, according to inclusive fitness theory. These associations were not included in this analysis because three of the four grandchildren were calves and one was only observed in two encounters. The average HWI of the grandmothers, Blotches and Paint, with their three grandchildren that were sighted at least four times, was 0.31 (SE = 0.10), which is higher than the population mean index of 0.12.

Future Research

Analysis of a long-term data set may provide a more definitive answer to the question of whether dolphin kin preferentially associate. Long-term associations can be examined to determine if, for example, associations with kin are longer-lasting than non-kin associations. Another avenue of investigation may be to determine whether, as is the case in male bottlenose alliances in the Bahamas (Parsons et al., 2003), male spotted dolphin relatives form coalitions with one another. Unfortunately, the only male-male kin dyad in this study comprised two young individuals, Kai and Brulee, neither yet of age to join an alliance. Their association index during this study was strong however, at 0.39. Future investigations could look into the alliance participation of this dyad.

Research efforts in the future could also be put towards investigating further the relationships of related individuals that are far apart in age, including but not limited to grandparental relationships. Concentrating on those dyads could elucidate the results of this study by reducing the variable of reproductive status, which seems to predominately shape dolphin social structure. Genetic investigations of paternal relatedness in this population are currently underway (Green et al., 2007). The results from that study can be used in the future to research association between paternally related individuals and to detect significant differences or similarities between paternal and maternal sibling associations.

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