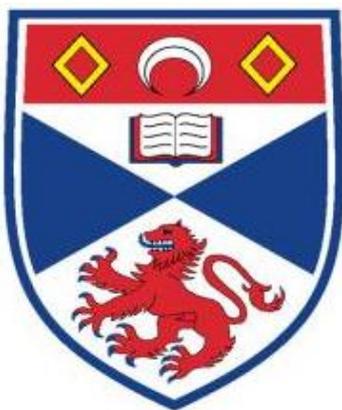


Is blood thicker than water?
The role of kin and non-kin in non-mother-calf
associations of captive bottlenose dolphins
(*Tursiops truncatus*)

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Declarations

I, Alexis Levensgood, hereby certify that this dissertation, which is approximately 11,500 words in length, has been composed by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree. This project was conducted by me at the University of St Andrews from September 2012 to August 2013 towards fulfillment of the requirements of the University of St Andrews for the degree of Masters of Research in Marine Mammal Science under the supervision of Dr. Vincent Janik.

Date..... Signature of candidate.....

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Abstract

Kinship is an important factor in the relationships of many social animals, including cetaceans. Yet, the occurrence and function of kin (aside from the mother) in delphinid calf associations, alloparenting, and/or calf rearing has hardly been investigated in the literature. As such, this study examined the role of kin and non-kin in non-mother-calf associations of a captive population of bottlenose dolphins (*Tursiops truncatus*) from 2006-2011 via underwater video and audio recordings. Event sampling of calf associations was used to determine if differences existed between kin and non-kin associations, specifically in the frequency and duration of events. Calves (N=13) were observed associating with an average of 6.62 ± 1.25 non-mother conspecifics each, though calves with kin present during the study (N=8) exhibited a higher average of associates (7.38 ± 1.36) than calves without kin present (N=5, 5.40 ± 2.50 associates). GLM results determined that calf identification, calf age, and associate age were significant predictors of the frequency of kin and non-kin associations. As for duration, however, kin and non-kin were not significant predictors of the mean duration of calf associations. Nonetheless, significant differences were observed between the proportion of time calves spent with kin and non-kin while in associations (kin= $15.58 \pm 6.11\%$, non-kin= $84.42 \pm 6.11\%$) and out of the total time in view (kin= $6.13\% \pm 3.33\%$, non-kin= $24.76\% \pm 4.42\%$). Still, no obvious differences between the context (such as the categories calf sex, associate sex, calf age, etc.) of the kin and non-kin calf associations were observed. Therefore, though calves with kin may surround themselves with a larger number of associates, the calves appear to preferentially socialize with non-kin over kin conspecifics. As such, calf associations do not follow the theories of kin selection, but rather indicate that other factors, such as age and individual calf personality, may have a larger influence on the associations involved in calf development.

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1. Introduction

A substantial diversity exists among animal social systems. Animals, from the non-nomadic to those that traverse great distances tend to form social relationships regardless of their degree of spatial association. As such, social relationships play an important role in the daily lives of many mammal species (Silk et al. 2003). Numerous social animals have shown preferences for particular individuals in their group (Smuts 1985; Cords 2002) and some species, such as monkeys and apes (Cords 1997; Silk et al. 2003), have even shown evidence of forming long-term, close, and enduring relationships with other group members.

For many social mammals, the mother-infant relationship is viewed as the strongest and one of the longest social bonds. This is likely due in part to the fact that mothers often are the sole provider for their young, and this is especially true for the majority of mammalian species (Vaughn 1978; Kleinman & Malcolm 1981). This relationship is often prolonged as infants are dependent upon their mothers in the beginning of their lives; however, the development of social mammals is a process involving not only the mother, but also other group members (Hrdy 1976; Altmann 1980; Hofer 1987; Nicolson 1987; Holekamp & Smale 1993). This likely explains the observed separations of infants from their mothers and the simultaneous association with other members of the population.

The number and type of social partners as well as the manner of social relationships are important to the socialization and developmental process of the infant (Suomi 1982; Champoux et al. 1991). One commonly observed social relationship is that of the infant and alloparent. Alloparenting (conspecifics associating with and caring for another's young) has been observed in over 120 species of social mammals (Hrdy 1976; Riedman 1982; Gittleman 1985). Alloparenting behavior patterns can vary considerably, not only within and among species, but also in the form that these actions take and the consequences that they present for all individuals involved (mothers, infants, and alloparents; Hrdy 1976; Riedman 1982; Mann & Smuts 1998), which has led to a wide variety of definitions of alloparenting in the literature. Many researchers now define the patterns of alloparental behavior, as one or more actions that benefit(s) an infant and that which would not be carried out by the alloparent if the young were not present (Woodroffe & Vincent 1994; Whitehead 1996). When defining alloparental behavior patterns, emphasis has been placed on quantifying the behavior(s) and assessing the costs and benefits involved in providing care to young.

Most cases of alloparenting in mammals have involved female over male alloparents, which is likely related to the aforementioned fact that, generally, females invest more in

parental care (Riedman 1982). This sex difference is supported by numerous reports of female alloparents from varying species providing for young, such as African and Indian elephants, *Loxodonta Africana* and *Elephas maximus* (Eisenburg 1972; Douglas-Hamilton 1973), rhesus macaques, *Macaca mulatta* (Rowell 1963), and bottlenose dolphins, *Tursiops truncatus* (Tavolga & Essapian 1957; Mann & Smuts 1998).

Nonetheless, there are several species where males have also been observed providing alloparenting to young. Male helpers, as stated by Woodroffe & Vincent (1994), are most prevalent among carnivores (e.g., dog and mongoose families), rodents, and primates (e.g., marmosets, tamarins, and macaques). Although male care is most common among these orders of animals, there are also various other species where male care has been observed, though less frequently, e.g., greater white toothed shrews, *Crocidura russula*, killer whales, *Orcinus orca*, and a single observation of Galapagos sea lions, *Arctocephalus galapagoensis* (Woodroffe & Vincent 1994). There are even species, such as the brown and spotted hyenas, *Hyaena brunnea* and *Crocuta crocuta*, where it is as common for males as it is for females to alloparent the young (Riedman 1982). Among both male and female alloparents, there are reports of varying age classes, differing levels of experience for females (those which have successfully reared young prior and those which have not), and varying degrees of kinship (from unrelated individuals to siblings) sharing the role of alloparent to the young (Hrdy 1976; Riedman 1982).

Kinship and the importance of kin assistance in rearing young has been studied in numerous species of mammals and birds, such as rhesus macaques (Harlow et al. 1966; Taylor et al. 1978) and the Florida scrub jay, *Aphelocoma coerulescens* (Emlen 1978). The focus on examining the role of kinship in social relationships stems originally from Hamilton's (1964) theory of inclusive fitness, which postulates that individuals will cooperate or aid genetic relatives to increase their own fitness. Hamilton's theory is based on the idea that cooperation among related individuals may be favored by kin selection, as individuals may directly benefit from reproductive success (Williams 1966) or may indirectly increase their own fitness through the reproductive success of genetic relatives (Hamilton 1964). This theorem is of direct relevance to the question, 'why do animals cooperate or exchange altruistic behaviors, when the benefits may be unequal among conspecifics?' Hamilton's (1964) theory is one of four developed to explain the evolution and maintenance of altruistic or cooperative behaviors among individuals, specifically by assuming relatedness between cooperating conspecifics. As a growing area of research with strong academic foundations,

his work establishes the role of kinship in founding and maintaining associations, alliances, and relationships among individuals.

Bottlenose dolphins, the focus of this study, represent a group of mammals where kinship research in associations and alloparenting is currently underdeveloped and where the above literature may be explored in practice. Bottlenose dolphins live in fission-fusion societies, where individuals develop flexible relationships involving groups that almost regularly change in size and composition. Nonetheless, many individuals maintain long-term, stable associations with selected individuals (Würsig & Würsig 1977; Wells et al. 1987; Smolker et al. 1992; Connor et al. 1992a, 1999, 2011; Möller et al. 2001). Among these stable associations are adult male pairs (Connor et al. 1992a, b), adult female pairs (Wells et al. 1987; Smolker et al. 1992), female kin (Wells et al. 1987), and, possibly the strongest bond of all (as with other social mammals), are mothers and their calves (Wells et al. 1987; Mann & Smuts 1999).

Bottlenose dolphin calves can be observed with their mothers well past the 18-36 month nursing period observed for both captive and wild dolphins (McBride & Kritzler 1951; Tavolga & Essapian 1957; Harrison & Ridgway 1971; Perrin & Reilly 1984; Evans 1987; Cockcroft & Ross 1990a, b; Wells et al. 1999; Mann et al. 2000). Within this time, the first year of life is critical for calves for both physical and social development, as well as infant survival (Cornell et al. 1987; Cockcroft & Ross 1990b). However, in both captivity (Chirighin 1987; Reid et al. 1995; Gubbins et al. 1999) and in the wild (Mann & Smuts 1999), following a period of dependence, calves begin a period of increasing independence until they are weaned from their mothers. Grellier et al. (2003) found that the proportion of time calves spent close to their mother decreased linearly over the first seven years of life. This increased autonomy is understood to be due to physical changes associated with maturity and the acquisition of behavioral skills (Cockcroft & Ross 1990b; Gubbins et al. 1999).

The separation of calves from their mothers is likely related to the development of calf social relationships. As calves are frequently seen swimming in association with nonparents (Waite 1988; Whitehead 1996; Mann & Smuts 1999), they are exposed to a relatively large number of associates from an early age (Gibson & Mann 2008). It is plausible that an increasing independence explains, to some extent, why calves are observed separated, albeit briefly, from their mothers at very early stages of their lives. Infants begin socializing (independent of their mother) at a young age, and have even been observed regularly socializing with others by the end of their second month after birth (Mann & Smuts 1999).

Gibson & Mann (2008) suggested that bottlenose dolphins must gain competence early, learning to navigate their social and physical environments by the end of infancy. During this time, calves work on developing skills and behaviors (Mann & Smuts 1999), which likely aid in preparing them for survival when fully independent from their mothers. These social interactions likely help shape the nature of learning and maturation that enables the calf to grow into a successful adult.

Alternatively, time away from the mother, may also be due to the mother needing assistance. Conspecifics may provide aid to mothers to allow them to hunt for food, rest, or socialize without their calf in tow. Among cetaceans, alloparental behavior patterns have been noted in both captive and wild bottlenose dolphins (Tavolga & Essapian 1957; Gurevich 1977; Leatherwood 1977; Wells 1991), spinner dolphins, *Stenella longirostri* (Johnson & Norris 1994), sperm whales, *Physeter macrocephalus* (Best 1979; Whitehead 1996), killer whales (Haenal 1986), and harbor porpoises, *Phocoena phocoena* (Anderson 1969). Among bottlenose dolphins specifically, Mann & Smuts (1998) reported that both experienced and inexperienced females assumed the role of alloparent, as well as kin and males; however, female kin and males were seldom seen in the role and inexperienced females were observed more than experienced females. Essapian (1963) also observed a male in the role of babysitter, while Tavolga & Essapian (1957) witnessed varying ages of females tending to the young. Still, there is very little reported on kinship with regard to alloparenting for dolphins. Mann & Smuts (1998) briefly mentioned related females as alloparents in their results, but removed them from their analysis as they were not equally available to the calves and not a focus of their study.

There is also little research focused on the associations of calves with any individuals outside of the mother-calf relationship, and even less on the level of kinship among these associations. In one of the only published studies where non-mother-calf associations were examined and compared to the associates formed with mother-calf pairs (Gibson & Mann 2008); kinship was not a focus and therefore not reported in the results; though it was mentioned that kin (specifically those who associate with the mother) could possibly be associates of less independent female calves.

There have been various studies over the past decade researching kinship among social associations in delphinids outside that with a calf, including those that examine male-male (Möller et al. 2001; Krützen et al. 2003; Owen 2003; Parsons et al. 2003; Welsh & Herzing 2009), female-female (Möller et al. 2006; Gaspari et al. 2007; Welsh & Herzing 2009; Frère et al. 2010), and male-female (Welsh & Herzing 2009; Wiszniewski et al. 2010)

bonds. Among these studies, however, no calves were included in their analysis. The lack of kinship studies among calves with associates (aside from the mother-calf relationship) is likely due to the challenges involved in re-sighting calves, which have few, if any distinguishing marks. This is further evidence of the deficiency of published data on the role of kin, outside the mother-calf relationship, in dolphin calf development.

Nonetheless, published studies of kinship among delphinid associations have shown differing levels of preference for kin associations. Two studies, Möller et al. (2001) and Owen (2003) found that male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of Southeastern Australia and Atlantic bottlenose dolphins of Sarasota Bay, Florida, did not preferentially associate or form preferential alliances with either maternal or otherwise genetically related kin. Meanwhile, Krützen et al. (2003) and Parsons et al. (2003) found that male bottlenose dolphins (Indo-Pacific and Atlantic) in both Western Australia and The Bahamas spent more time in (first and second degree) male alliance associations with closely related conspecifics. As for female-female relationships, Möller et al. (2006) discovered that associations were correlated to both maternal and genetic kinship in female Indo-Pacific bottlenose dolphins, while Gaspari et al. (2007) found that female striped dolphins (*S. coeruleoalba*) showed a significantly greater association to kin than males did. Moreover, Frère et al. (2010) uncovered a positive relationship between matrilineal and biparental (both maternal and paternal measured from nuclear DNA) relatedness in female Indo-Pacific bottlenose dolphin associations off Western Australia. There has also been evidence of preferential kin associations in male-female Indo-Pacific bottlenose dolphin associations in southeastern Australia (Wiszniewski et al. 2010). Further corroborating evidence of preferential kin associations can be found in Welsh & Herzing (2009), where male-male, female-female, and even male-female Atlantic spotted dolphins (*S. frontalis*) associated more with kin than non-kin conspecifics.

Because published kinship studies lack analysis on calves, the aim of the current study was to uncover the role of kin and non-kin in non-mother-calf associations in a group of captive bottlenose dolphins. The importance of kin assistance in rearing young has been studied in numerous other species, as mentioned previously, but there is currently very limited published research on calf associations, alloparenting, or any form of calf rearing, especially outside of the mother-calf relationship in dolphins. This study will help determine the importance of individuals involved in calf development and will provide new evidence toward the support, or lack thereof, for kin-selection theory in regards to male and female dolphin calf associations.

2. Materials & Methods

2.1 Study Site

Data were collected from 2006-2011 at Roatan Institute for Marine Science (RIMS), Anthony's Key Resort, Roatan, Honduras, by the Dolphin Communication Project (DCP) and represent a proportion of DCP's long-term, ongoing study of the dolphins at RIMS. The RIMS dolphin facility is located adjacent to Bailey's Key along the northwest coast of Roatan, approximately 27 miles north of mainland Honduras (Figure 1). The facility includes several pools within a natural lagoon that has a sea floor consisting of natural sea grass, sand, and coral (Figure 2). Depths range from shoreline to eight meters, with a total surface area of approximately 10,000 m².



Figure 1: World Map highlighting Honduras (in red) with enlargement of Honduras denoting Roatan Island (enclosed by a red box). Credit: Map adapted from www.naturalhistoryonthenet.com and WGS84 Coordinate System.



Figure 2: Aerial view of RIMS dolphin enclosure (on left) located adjacent to Bailey's Key. Anthony's Key is the island located to the right of Bailey's Key. The island of Roatan is the land mass "below" the two keys. Image credit: Anthony's Key Resort website.

2.2 Study Population

The RIMS dolphin population consisted of approximately 30 individually distinct (via rake and natural markings) bottlenose dolphins ranging in age from neonate to over 30 years old. Thirteen members of this study group (seven females and six males) were wild caught in local Honduran waters, whilst all other individuals were born at the facility. The total population per year ranged from 16 to 24 individuals depending on the year of study with a span of 8 to 12 females and 8 to 13 males present annually. From 2006-2011, there was an overall total of 13 females and 16 males in the study population. Over these six years, the population presented eight matriline with adult females having a total range of one to four offspring each (Appendix B).

2.3 Data Collection

Underwater video and audio data of the animals were collected by DCP researchers for approximately one hour per day from one to two week periods from 2006-2011 (Table 1). The underwater data were recorded during snorkel swims using a manually operated mobile video acoustic array (MVA) that permitted real-time synchronous video and stereo audio capture of dolphin behaviors and vocalizations (Dudzinski et al. 1995). Data collection was not conducted during the animals' training sessions or programs. Factors limiting underwater video included poor weather, sea, and visibility conditions (Dudzinski 1998). A focal-animal-follow and all-occurrence sampling protocol were employed to record underwater observations (Altman 1974; Mann 1999). Data collection at RIMS was conducted under permit to RIMS from the Honduran government. Additionally, ethical approval by the University of St Andrews Animal Welfare and Ethics Committee (AWEC) was granted for the use of this research.

Table 1: Hours of videotape footage per year of RIMS dolphins from 2006-2011.

	Year						Total Effort
	2006	2007	2008	2009	2010	2011	
Effort (Hours)	9.47	6.88	3.87	10.83	10.87	6.22	48.14

2.4 Data Processing

In the lab, individual dolphins were identified on underwater video by using rake and natural markings, as well as scars. Individual identifications were confirmed by a minimum of two trained DCP researchers.

All video data were event sampled for non-mother-calf associations, with the identity of the calf and non-mother associate documented per event. Age and sex of both the calf and associate were recorded. Exact age was known for all dolphins born in captivity; while all wild caught individuals were adults during the study period. Sex was based on visual confirmation of the genital area. Duration of each event and the relationship of the individuals (kin versus non-kin, determined by matrilineal relatedness, see Appendix B) were recorded for each association. Given that no two calves could be kin to one another, no calf-calf associations were recorded.

Additionally, other relevant information was recorded including: date of occurrence, “real” time of event, experience of associate in rearing young, behavioral activity in the context of the association, association position or spatial state relative to each other, occurrence of tactile contact, frequency and duration of contact, whether the calf’s mother was in view and her activity, presence or absence of vocalizations, and which dolphin departed the interaction.

When the identification of an animal could not be confirmed the animal was designated unidentifiable. Experience of the associate was determined only for female associates and based on whether the female was multiparous (experienced) or not (inexperienced). The behavioral activity was determined by predominant activity sampling (PAS; Tyler 1979; Mann 1999), in which the activity that occurred for a minimum of 50% of the association event was chosen as the overall activity during the event; this included directed movement, rest/slow movement, milling, playing, socializing, and attempted/successful nursing. Association position focused on calf position (or spatial state) in relation to the associated dolphin and included whether the dyad was in echelon, infant, or other position. Mother’s activity included all of the categories from the association activity (except for nursing) and likewise was determined by which activity occurred for over 50% of the time the mother was in view. Departing individuals were determined by which individual left the association and could be denoted as neither (neither individual left or was responsible for ending the association), both (both individuals separated at the same time), the associate, or the calf, as well as the animals going out of view (in which the dyad was still in association but exited the viewing screen of the video). Definitions of all relevant terms mentioned above can be found in Appendix A.

2.5 Data & Statistical Analysis

All association events were documented from video-taped data. As such, all events with unidentifiable individuals involved in the associations were removed from the analysis. Therefore, only associations where the identity of both individuals could be confirmed were used for this study.

Statistical analyses were completed in the statistical program R (R Version 2.15.1, R Development Core Team 2012). Descriptive statistics were used to examine the occurrence of kin and non-kin associations of the calves, the age classes and sex of the associates, and the age(s) (< 1, < 2, < 3 years) and sex of the calves, as well as the behavioral activity of each event, the presence of tactile contact between associates, the visibility of the mother, presence of vocalizations, and the departing dolphin roles. Contingency tables were constructed to assess the data and expose possible relationships between these variables.

The total number of associates for each calf was calculated and averaged for all calves. Several calves, however, did not have kin available (aside from their mothers) and therefore, an additional total number of associates was computed and analyzed for calves with kin present and those without kin present. Averages were compared using the non-parametric Wilcoxon signed rank test.

Proportions of time spent in associations were generated for the total time each calf associated with non-mother conspecifics. However, calves without kin present (as mentioned above) were removed from further statistical analysis when comparing calf associations with kin and non-kin. As such, additional proportions of time were calculated for each calf (whose kin were present during the study period) for time spent in association with kin and non-kin. Proportions of time were estimated for both kin and non-kin among all associations, as well as kin and non-kin for the entire duration each calf was visible on screen. These values were then compared using the non-parametric Wilcoxon signed rank test.

A binomial based generalized linear model (GLM) was created to examine the occurrence of calf associations with kin and non-kin. The covariates for the GLM included: calf identification, calf age, calf sex, associate age class, associate sex, year, proportion of kin available, behavioral activity of the events, the presence or absence of tactile contact, and the presence or absence of vocalizations. The response variable was kin (1) or non-kin (0). A gamma based GLM was generated to assess the duration of kin and non-kin associations. The covariates for the GLM comprised of: relatedness (kin and non-kin), calf identification, calf age, calf sex, associate age class, associate sex, year, the proportion of kin present per year,

the behavioral activity, the presence or absence of tactile contact, and the presence or absence of vocalizations. The response variable was duration of association. Each model was generated in R to ascertain which covariates may explain the differences in the occurrences and durations of calf associations between kin and non-kin. Model comparison and selection were done by using Akaike's Information Criterion (AIC, with the lowest AIC value indicating the best fitting model) during dredge selection and analysis of variance (ANOVA) testing to determine significant covariates to include in the model. Akaike weights were then used to determine the relative support for each model (Burnham & Anderson 2002).

3. Results

3.1 Data Overview

A total of 750 association events were observed during the study period (48.14 hours of videotape). Of those events, 123 were deemed unidentifiable and were removed from further analyses, leaving 627 association events with both parties (calf and associate) identifiable.

Thirteen calves were present at varying times between 2006 and 2011. One calf, Mickey, had no kin, aside from his mother, but was observed associating with (non-kin) conspecifics the most (117 events; Figure 3). Four calves (Bailey, French, Jack, and Osgood) had siblings, but their kin were not present (either due to death or relocation, whether permanent or temporary). These four calves were observed in 28, 17, 44 and 0 events, respectively, associating with non-kin conspecifics (Figure 3).

Eight calves (representing 421 association events) had both kin and non-kin present to associate with during the study period; however, one calf, Cortez, with two kin present during the study period, was never observed associating with any conspecifics (aside from this mother) be they kin or non-kin (Figure 3). Additionally, another calf, Luna, was never observed associating with kin (with the exception of her mother). Nonetheless, Luna was observed in 11 association events with non-kin individuals (Figure 3). All other calves (Anthony, Dixon, Ken, Marg, Pigeon, and Vin) were observed associating with both kin and non-kin conspecifics. They were observed in 87, 97, 47, 57, 47, and 75 association events, respectively (Figure 3).

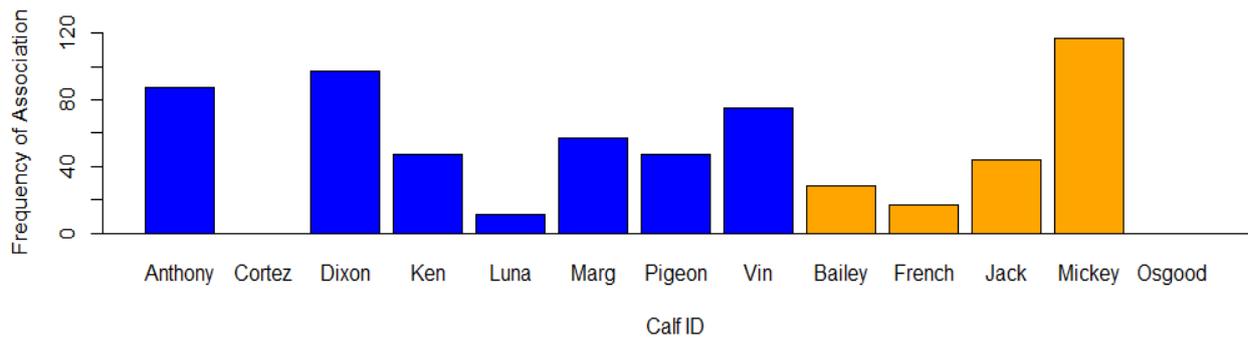


Figure 3: Total frequency of association events for all calves. Blue bars denote calves that had kin present, whereas orange bars represent calves that either had no kin or their kin were not present during the study.

3.2 Non-mother Associates

The total number of associates was tallied for each calf during the study period (Figure 4). The number of associates varied from zero to 15 individuals per calf during the total three year calf time period. On average, the calves had 6.62 ± 1.25 associates each. However, calves that had kin available were observed with an average of $7.38 (\pm 1.36)$ associates (median=8.50 associates); while calves without kin available to associate with were observed with $5.40 (\pm 2.50)$ associates (median=4.00 associates). If Mickey was removed from the analysis (as he was a likely outlier with a high number of associates), then calves without kin present had a mean number of associates of $3.00 (\pm 1.00)$ individuals. A Wilcoxon signed rank test revealed that when Mickey was included in the comparison, there was no significant difference ($p=0.237$) between the number of associates of calves with kin and calves without kin present (Figure 5). By removing Mickey from this examination a significant difference became evident ($p=0.039$, using a Bonferroni adjustment) between the two groups of calves (Figure 5).

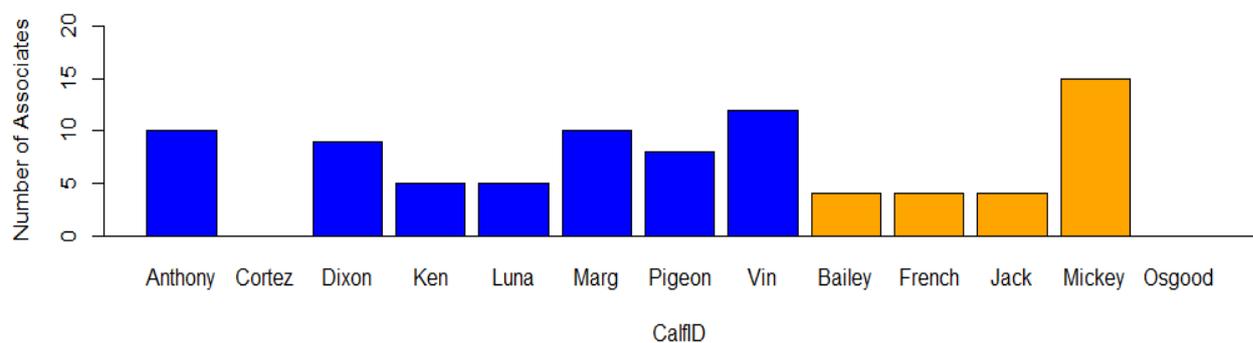


Figure 4: Total number of observed associates for each calf during the study period. Calves with kin available are indicated with blue bars, while calves without kin present are denoted with orange bars.

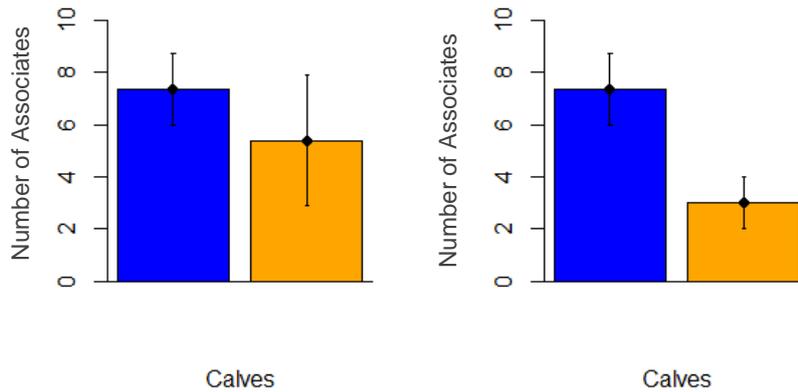


Figure 5: The mean (\pm SE) number of associates for the calves with kin (blue bars) and calves without kin available (orange bars). The plot on the left has all calves included in the analysis; while the plot on the right has Mickey (an outlier) removed from the analysis.

3.3 Frequencies of Association Events

When all calves were included, approximately five times as many non-kin as kin association events were observed (Table 2). Likewise, when only the seven calves who had kin present to associate with were analyzed (Cortez was not included as he was never observed in association with any individuals aside from his mother), calves still associated with non-kin more (approximately three times more) than with their kin (Table 3). Proportionally, more non-kin associates (approximately 12-19 individuals depending on the study year) were available than kin associates (1-2 individuals per calf per year) and as such, it was expected that more non-kin events would occur by random. The total duration for all calves (Table 2), as well as only calves with kin present (Table 3) was longer for non-kin association events, as would be expected (based on the frequencies). Still, although there were more and longer (in total duration) non-kin associations, the percentage of associations for calves with kin present, as well as each additional variable recorded for kin and non-kin events was very similar between the two groups (Table 3).

For both kin and non-kin associations (Table 3), as well as when all individuals were included (Table 2), male conspecifics were observed in association with the calves more frequently than females. Likewise, male calves exceeded the female calves in their frequency of associations with non-mother conspecifics (Tables 2 & 3). Associates (both kin and non-kin for calves with kin present and when all calves were included) were more likely to be juveniles, followed by sub-adults and finally adults (Tables 2 & 3). However, calves were found to be in a greater number of associations as they got older (Tables 2 & 3). There appeared to be minimal difference in the physical position calves swam in while in

Table 2: Contingency tables displaying the frequencies of calf association events (n=627) and additional information gathered for when all calves were included in the analysis. Relationship indicated by K (kin) and NK (non-kin). Sex denoted by M (male) and F (female). Associate age designated by A (adult), S (sub-adult), and J (juvenile). Other definitions can be found in Appendix A.

Association Events		Total Duration (min)		Associate Sex		Associate Age			Calf Sex		Calf Age			Behavioral Activity					
K	NK	K	NK	M	F	J	S	A	M	F	< 1	< 2	< 3	DM	Mill	Play	Rest/SM	Socialize	Nurse
96	531	28.23	165.85	363	264	309	202	116	484	143	28	209	390	66	189	92	116	164	0

Position		Contact		Vocalization		Mother Presence		Mother's Behavioral Activity					Departing Dolphin				
Echelon	Infant	Yes	No	Yes	No	Yes	No	DM	Mill	Play	Rest	Socialize	Associate	Calf	Both	Neither	Out of View
27	237	201	426	585	42	90	537	5	20	1	63	1	76	143	51	13	344

Table 3: Contingency tables displaying the raw data frequencies in parentheses and the percentage of kin and non-kin calf association events (n=421) and additional information gathered for the seven calves who had kin present to associate with during the study period. Relationship indicated by K (kin) and NK (non-kin). Sex denoted by M (male) and F (female). Associate age designated by A (adult), S (sub-adult), and J (juvenile). Other definitions can be found in Appendix A.

	Association Events	Total Duration (min)	Associate Sex		Associate Age			Calf Sex		Calf Age		
			M	F	A	S	J	M	F	< 1	< 2	< 3
K	(96) 22.80%	(28.23) 20.20%	(64) 66.67%	(32) 33.33%	(9) 9.38%	(21) 21.87%	(66) 68.75%	(76) 79.17%	(20) 20.83%	(9) 9.38%	(28) 29.16%	(59) 61.46%
NK	(325) 77.20%	(111.53) 79.80%	(208) 64%	(117) 36%	(52) 16%	(105) 32.31%	(168) 51.69%	(230) 70.77%	(95) 29.23%	(19) 5.85%	(90) 27.69%	(216) 66.46%

	Position		Behavioral Activity						Contact		Vocalization	
	Echelon	Infant	DM	Mill	Play	Rest/SM	Socialize	Nurse	Yes	No	Yes	No
K	(8) 8.33%	(9) 9.38%	(14) 14.58%	(29) 30.21%	(14) 14.58%	(15) 15.63%	(24) 25%	(0) 0%	(29) 30.21%	(67) 69.79%	(89) 92.71%	(7) 7.29%
NK	(38) 11.69%	(32) 9.85%	(31) 9.54%	(95) 29.23%	(47) 14.46%	(55) 16.92%	(97) 29.85%	(0) 0%	(116) 35.69%	(209) 64.31%	(308) 94.77%	(17) 5.23%

	Mother's Presence		Mother's Behavioral Activity					Departing Dolphin				
	Yes	No	DM	Mill	Play	Rest	Socialize	Associate	Calf	Both	Neither	Out of View
K	(29) 30.21%	(67) 69.79%	(0) 0%	(3) 3.13%	(0) 0%	(10) 10.42%	(0) 0%	(5) 5.21%	(27) 28.12%	(9) 9.38%	(3) 3.12%	(52) 54.17%
NK	(60) 18.46%	(265) 81.54%	(3) 0.92%	(14) 4.31%	(0) 0%	(42) 12.92%	(1) 0.31%	(42) 12.92%	(77) 23.69%	(24) 7.39%	(5) 1.54%	(177) 54.46%

association when comparing kin and non-kin (Table 3); yet the data with all calves included showed a higher number of calves in echelon position than in infant position (Table 2). When all individuals were included, the behavioral activity was most often milling followed by socializing, resting, playing, and finally directed movement (Table 2). The behavioral activity of the association between kin and non-kin was most often either socializing or milling; however, the percentage of events spent resting, playing and moving directly were observed almost equally between the two groups with resting occurring slightly more often than the other behavioral activities (Table 3). Nursing/attempted nursing was never observed from any individuals be they in kin or non-kin associations. Vocalizations were almost always present; while tactile contact was only observed in about one-third to one-half of the kin and non-kin associations, as well as the associations with all calves present (Tables 2 & 3).

Mothers of the calves were visible, but separated from their calves during few of the calf associations, regardless of who the calf was in association with (Tables 2 & 3). Nevertheless, mothers were observed to be visible slightly more often when kin associations occurred (Table 3). When the mother was visible nearby, she most often was seen resting in the distance or occasionally milling about (Tables 2 & 3). For when all calves were included, as well as those who had kin present to associate with, both individuals (calves and associates) were most frequently observed to go out of view together when association events ended, followed by the calf initiating a departure, or either the associate or both individuals exiting the association (Tables 2 & 3).

The binomial GLM created to examine the frequency of kin and non-kin associations suggested that the covariates calf ID, calf age, and associate age be retained through dredge selection and ANOVA. This indicated that the occurrence of kin and non-kin associations differed significantly based on these three covariates. Within these covariates, calf ID Dixon ($4.0 \pm 0.6\%$), calf ID Ken ($3.0 \pm 0.7\%$), calf ID Pigeon ($4.0 \pm 0.8\%$), calf age < 2 ($23.7 \pm 5.4\%$) and calf age < 3 ($21.1 \pm 4.6\%$) were significantly different $p=0.000$. Calf ID Vin ($1.0 \pm 0.5\%$) and the juvenile associate age class ($27.8 \pm 5.1\%$) were also found to be significant at the $p < 0.010$ level. Numerous covariates including, year, calf sex, associate sex, proportion of kin present, tactile contact, and the presence of vocalizations were not significant predictors of the frequency of kin and non-kin associations.

3.4 Duration & Proportion of Time in Association

There was variation in the total proportion of time each calf spent in association with non-mother conspecifics (Figure 6). Two calves (Cortez and Osgood) were never seen in association with any individuals aside from their mothers; while one calf (Dixon) spent approximately 65% of his time in association with conspecifics. On average though, the calves spent $22.60\% \pm 18.20\%$ of their time in association with non-mother conspecifics. The remaining time was either spent in association with their mothers or swimming alone.

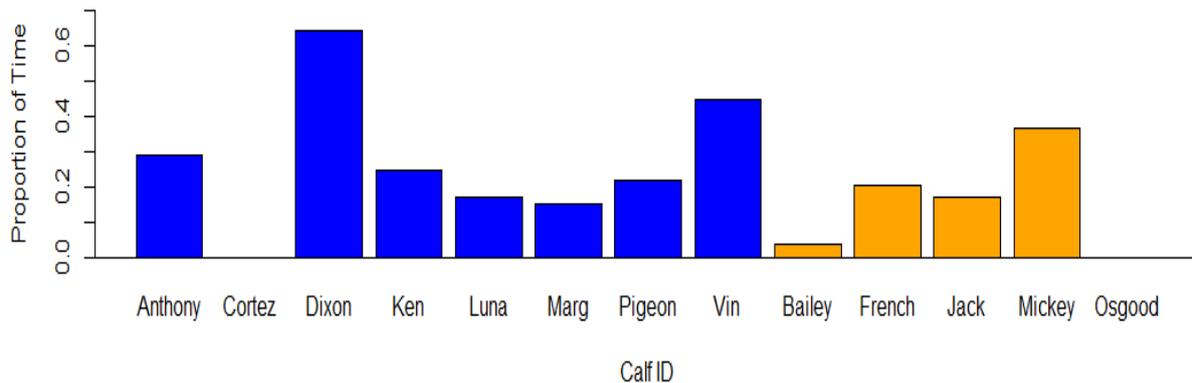


Figure 6: The total proportion of time each calf spent in association with conspecifics. Mother-calf associations were not included. Blue bars represent calves with kin present, while orange bars indicate the calves without kin present. Note both Cortez and Osgood were never observed in association with any individuals aside from their mothers and therefore, are displayed with zeros for their proportions of time in association with conspecifics.

According to the gamma GLM, the mean duration (seconds) of association events was significant by calf ID, calf age, associate age, proportion of kin present, behavioral activity, and tactile contact through dredge selection and ANOVA. The gamma GLM revealed significance within numerous covariates of the association event's mean durations. Two variables, calf ID Luna (29.68 ± 7.79 s) and associate age sub-adults (22.38 ± 3.54 s), were found to be significant ($p < 0.050$). Calf age < 2 (16.97 ± 3.15 s), calf age < 3 (21.63 ± 3.20 s), and calf ID Ken (16.32 ± 2.48 s) were significant at the $p < 0.010$ level. Two covariates, behavioral activity rest/slow movement (15.19 ± 2.79 s) and calf ID Vin (20.51 ± 3.26 s), were significant at $p < 0.001$. Lastly, numerous variables including, calf ID Dixon (29.45 ± 4.24 s), calf ID Marg (11.40 ± 1.78 s), calf ID Pigeon (11.36 ± 2.07 s), the proportion of kin present (18.49 ± 3.02 s), juvenile associate age class (17.40 ± 2.59 s), behavioral activity milling (19.58 ± 2.99 s), behavioral activity playing (12.21 ± 2.12 s), behavioral activity socializing (32.04 ± 4.83 s), and the presence of tactile contact (34.67 ± 5.46 s) were all found to be significant ($p = 0.000$). Other covariates such as, year, calf sex, associate sex, presence of vocalizations, and, most importantly to this study, kin and non-kin were not significant predictors of the duration(s) of association events. This was further supported by a non-

significant difference found using a Kruskal-Wallis non-parametric test of a randomized sample of kin mean durations and non-kin mean durations ($p=0.583$).

Although kin and non-kin were not significant predictors of duration of association events, there was variation in the proportion of time out of the total duration the calves were in view that they spent in association with kin and non-kin (Figure 7). Of the seven calves that had kin present to associate with, all but one calf (Luna) was observed associating with both their kin and non-kin. Luna, however, was never observed in association with her kin. All of the calves spent proportionally more time with non-kin than kin. On average, the calves spent $6.13\pm 3.33\%$ of their time with their kin (with a median of 2.52%), whereas they spent $24.76\pm 4.42\%$ of their time associated with non-kin individuals (and a median of 16.94%, Figure 8). From the total duration that the calves were in view, a Wilcoxon signed rank test revealed that at the 95% confidence interval there was a significant difference between the proportion of time that calves were in association with kin and non-kin ($p=0.016$).

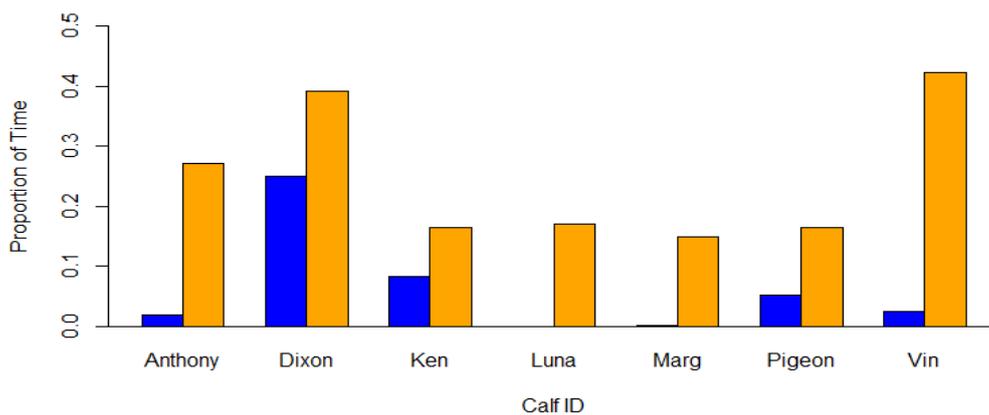


Figure 7: The proportion of time out of the total time each calf was in view, that they associated with kin (blue bars) and non-kin (orange bars). Associations were non-mother-calf associations.

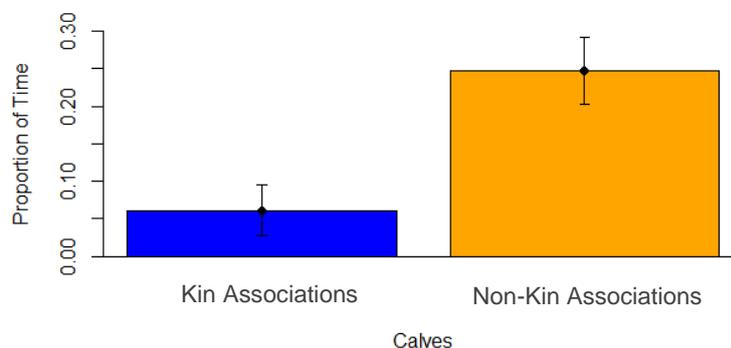


Figure 8: The mean (\pm SE) proportion of time out of the total time the calves were in view that they were in association with kin (blue bar) and non-kin (orange bar).

Furthermore, out of the total time each calf spent in association with individuals there were differences between time spent with kin and non-kin (Figure 9). Aforementioned, Luna

was never observed in association with her kin and therefore spent 100% of her association time with non-kin. On average, the calves were associated with their kin $15.58\% \pm 6.11\%$ (with a median of 6.47%) and with non-kin $84.42\% \pm 6.11\%$ of their time (with a median of 93.53%) when in association with conspecifics (Figure 10). During time spent in association with conspecifics, significant differences were observed at the 95% confidence level using a Wilcoxon signed rank test, between the proportions of time the calves spent in association with kin and non-kin ($p=0.016$). P-values for both Wilcoxon signed rank tests were equal due to the nature of the data for both tests being the same (the seven calves); thus, the p-value remained the same as the test ranks based off of the data set.

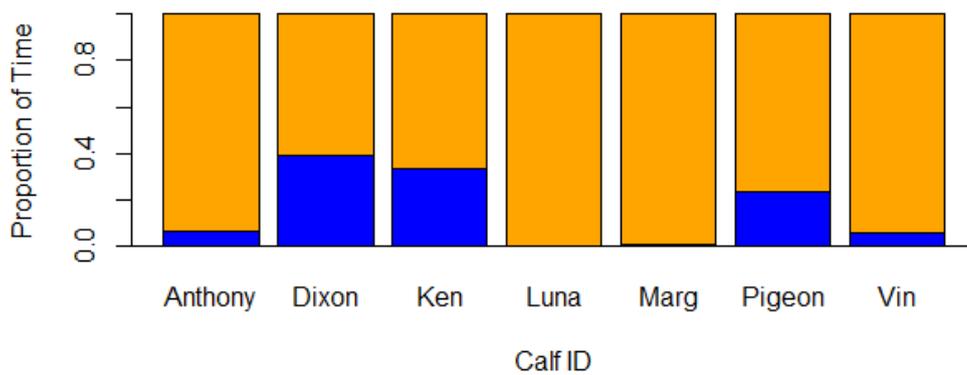


Figure 9: A stacked bar plot illustrating the proportion of time within non-mother-calf associations that the calves associated with kin (blue bars) and non-kin (orange bars).

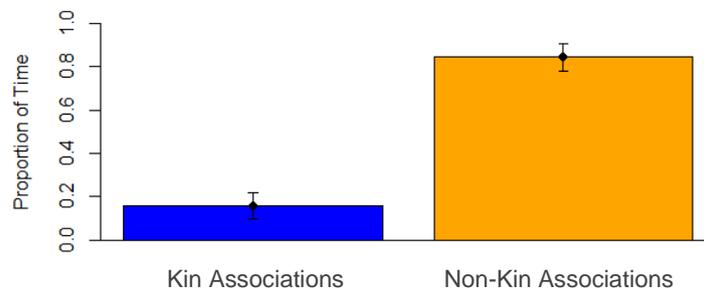


Figure 10: The mean (\pm SE) proportion of time within non-mother-calf associations that the calves associated with kin (blue bar) and non-kin (orange bar).

4. Discussion

Although the study of relatedness among cetacean associations has been increasing over the past few years, the role of kinship in calf associations, aside from the mother-calf bond has hardly been examined in any delphinid populations. This study has provided the first look at the similarities and differences in the frequency, duration, and to some extent, the context of the roles of kin and non-kin in non-mother-calf associations. These results provide information on the patterns of early sociality, the importance of individuals (in particular their relationship to the calf) involved in calf development and offer new evidence toward the

support, or lack thereof, for kin-selection theory concerning male and female dolphin calf associations.

4.1 Findings & Implications

There was clear variability (from no associations, to only associating with non-kin, to numerous associations with both kin and non-kin) among the calves. This was likely due to different personalities (distinct personalities have recently been detected in bottlenose dolphins; Highfill & Kuczaj 2007; Highfill & Kuczaj 2010) and social strategies among the individuals. What was most interesting were the calves who were never observed in association with kin or non-kin (Osgood and Cortez), as well as Luna who never associated with her kin. One might expect calves of a fission-fusion society to spend much of their time, especially as their independence increased, exploring new relationships with conspecifics. All three of these calves, in particular Osgood and Cortez, however, were rarely observed as they were seldom viewed near the camera, compared to the other calves. For Osgood, his mother Rita, was rarely captured on film and rarely approached the camera (K. Dudzinski, pers. comm., 2013). Cortez's mother, Alita, was seen more often on camera, but never as close as the other mothers in this group (K. Dudzinski, pers. Comm., 2013); thus, the lack of observation of these two calves might be related to their mothers' behavior more than their own. This discrepancy in amount of observation time for these two calves might, therefore, have caused a bias in the results, as Osgood and Cortez could have been in associations with conspecifics out of view of the camera, and only close to their mother or swimming by themselves the few times they were in view. As the nature of underwater video data only permits analysis of observations of what was in front of the screen, this bias should have been present for all individuals and therefore by calculating proportions of time, should have been minimized for differences in gregariousness among the calves.

Observations also revealed variation in the number of associates of the calves. More intriguingly, there appeared to be a difference in the number of associates of calves with kin present and those without kin present. Calves with kin available associated with conspecifics on average more than those without kin. This implies that calves with kin available may seek out or may encounter (through their kin) more individuals to associate with and therefore, ultimately have a larger social network of conspecifics. Being familiar with more individuals and having a larger social network may influence social bonds in later life stages and/or provide the calf with more social development by being around a greater number of conspecifics to learn from, communicate with, and create relationships with. On the other

hand, it is possible that calves without kin present, spent their time with fewer, but possibly “closer” individuals since they were lacking a kinship bond. The strength of associations was not analyzed for this project and thus the level of closeness of the bonds between dyads cannot be made with any certainty; however, if the bonds between calves without kin present and conspecifics were stronger than those with kin present, then two differing strategies (quantity versus quality) may exist in calf associations and early development. The strength of these bonds should be examined in the future to determine if these differing strategies are indeed in place among calf associations.

Mickey was the only exception to the calves without kin having fewer associates, as he had more associates than the calves with kin present. It is likely that Mickey was an outlier and when removed from the analysis the differences between the two groups were even more evident. Mickey has an extremely outgoing personality, no kin, and a mother who was frequently inattentive to her calf (K. Dudzinski, pers. Comm., 2013), sometimes known as a permissive or rejective maternal style (Altman 1980; Fairbanks 1996; Hill et al. 2007). It is possible (and more so in a captive setting where predators are non-existent) that the lack of the mother’s attention has equated to the calf being more social with other dolphins to possibly make up for the social short-comings of its mother. This would assume that the mother’s parenting style may have influence over the sociability of the calf, in terms of the number of associates. In human and non-human primates, offspring from mothers who exhibit permissive or rejection style parenting spend more time interacting with social companions than fellow offspring from more protective mothers (Hinde 1974; Simpson & Simpson 1986; Suomi 1987; Fairbanks 1996). Similarly, recent work has shown that maternal social patterns (who the mother associated with) influenced the number of calf associates in bottlenose dolphins of Western Australia (Gibson & Mann 2008). Although this does not mean dolphin mothering style has direct influence on calf associations, it does lend support to the notion being true.

Significantly more non-kin associations were detected than kin associations and based on the models, the difference was found to be related to calf identification, calf age, and associate age. Calf identification was likely a factor due to the quite drastic variability of sociality between the studied individuals, discussed above. Similarly, calf age was a likely explanatory variable, as a result of increasing independence with age, such that, as the calves aged the occurrence of associations increased. This is supported by previous findings (Gubbins et al. 1999; Mann & Smuts 1999; Grellier et al. 2003; Gibson & Mann 2008) that calves tend to separate from their mothers as they age; however, though the calves associated

more as their age increased, small differences were visible between kin and non-kin. Calves in kin dyads did spend slightly more time in association than those in non-kin dyads while at age one and two; whereas calves in non-kin pairs spent slightly more time in association at age three than those in kin associations. On the other hand, associate age worked in the opposite fashion, where younger conspecifics (juveniles) were observed in association with calves more than sub-adults and even more so than adults. These results coincide with the notion of assortative mixing, where individuals preferentially mix with conspecifics sharing similar traits, such as age (Wells et al. 1987; Lusseau & Newman 2004). The prevalence of assortative mixing may relate to the possible benefits gained by calves that associate with other individuals that share similar capabilities as them (Wiszniewski et al 2010), such as physical and developmental maturity. Like calf age though, slight differences were found between non-kin and kin associations. Calves in kin associations spent more time with juveniles than calves in non-kin associations, while calves in non-kin associations spent more time with sub-adults and adults than did kin dyads.

It appears as though calves preferred to associate (in terms of frequency) with non-kin over kin conspecifics. Interestingly, however, numerous other studies have found male-male (Krützen et al 2003; Parsons et al. 2003; Welsh & Herzing 2009), female-female (Möller et al. 2006; Gaspari et al. 2007; Welsh & Herzing 2009; Frère et al. 2010), and male-female (Welsh & Herzing 2009; Wiszniewski et al. 2010) delphinids (bottlenose, spotted, and striped dolphins) preferentially associating with kin. Although none of these studies included calves into their analysis, the results of this study are a significant deviation from previous findings. Only two published papers, Möller et al. (2001) and Owen (2003) found bottlenose dolphins (in Southeastern Australia and in Sarasota Bay, Florida, respectively) where males did not preferentially associate or form alliances with either their maternal or genetically related kin.

Despite the fact that the current study was not conducted on wild animals and therefore the association pattern(s) could be a product of captivity, these results still yield an interesting and different strategy for calf associations. The lack of preference for kin associations may in part be due to the strong mother-calf bond, which is the calves' primary relationship. It is possible that the calves, therefore, preferred to associate with non-related individuals to broaden their social network and relationships outside of their familial units, especially if much of their time was spent in close proximity to their mothers. Another possibility might be that bottlenose dolphins cannot or are unable to identify kin; however, this is extremely unlikely, as bottlenose dolphins are known to produce signature whistles, which appear to offer a reliable method of individual recognition and kin discrimination, by

communicating identity (Smolker et al. 1993; Janik & Slater 1998; Sayigh et al. 1999; Janik 2000). Furthermore, male calves share similar features of their whistles with their mother's (Sayigh et al 1990; Sayigh et al. 1995), and this acoustic signature may therefore function as a way to assess the matrilineal origin of fellow conspecifics.

Alternatively, other mechanisms may be more important than previously thought in determining the basis for these relationships. Age (of the calf and of the associate), in particular, might be influencing the differences in kin and non-kin associations more than expected, as age has been observed influencing associations in other studies (Wells et al. 1987; Gubbins et al. 1999; Mann & Smuts 1999; Grellier et al. 2003; Lusseau & Newman 2004; Gibson & Mann 2008) . These results correspond with the findings of age as significant predictors of kin and non-kin associations and could possibly explain the slight differences found in the percentage of occurrence of associations between the two groups. Although, it is possible that the small percentage differences in calf and associate age may have no significant meaning and are just products of the variability in the data. Nonetheless, the differences in age, especially in associate age classes, may have played a part in the functional role of the associate. It is possible that the older conspecifics were acting in a position of alloparent, by looking after the calves to aid the mothers. If this was the case, then it would appear that most calf associations were not of alloparenting contexts, unless some of the younger associates (juveniles) were alloparenting and learning the techniques used to take care of, protect, and watch the calves. This is quite possible as inexperienced females are often observed performing alloparenting behavior patterns (Mann & Smuts 1998). The possibility of alloparenting behaviors occurring during these associations will be addressed again further in this paper.

Although there was a clear difference in the occurrence of kin and non-kin associations, there was not a significant difference between kin and non-kin in the duration of associations. Kinship was not a significant predictor of association durations, while numerous other variables (e.g., age, behavioral activity, calf identification, etc.) were. Despite no difference in the durations, significant differences were detected in the proportion of time calves spent in association with kin and non-kin. For both, total duration in view and duration within an association, calves were observed spending proportionally more of their time in association with non-kin individuals.

This further supports the idea that calves prefer non-kin associates to kin associates, in both frequency and duration of association events. Though there was no difference in mean durations between the two groups, the clear difference in the proportion of time spent with

each group suggests that the amount of time per event was being shared equally among associates, but the overall proportion of time was being preferentially spent with non-kin. As was stated with the occurrence of association events, the preferential proportion of time spent with non-kin alludes to the idea that calves favor spending time with non-kin associates to potentially expand their social network and relationships with non-related individuals. Additionally, it is quite possible that calves spent time with their kin while also in association with their mothers and therefore when on their own to associate chose different/“unique” individuals to increase their social bonds.

The context of the association events presented no obvious differences between kin and non-kin associations. Trends were relatively consistent between the two groups with only slight differences in the proportions for some variables (e.g., the differences in ages mentioned previously). Male calves and male conspecifics were observed in the associations more than females, which is not surprising as some male bottlenose dolphins tend to form strong, stable alliances with other males of roughly the same age (Connor et al. 2000). When formed, strong social bonds between male bottlenose dolphins do not begin before the juvenile age class (Wells 1991; Connor et al. 2000); therefore, it is quite possible that the male calves were associating with more individuals to assess future alliance possibilities and/or to examine other, older male alliances. Nonetheless, both male and female calves were observed in association with individuals of the opposite sex and as such, not all associations involving males likely concerned alliance prospects/formation. Additionally, it is unlikely that the majority of these events involved alloparenting since there was such a large discrepancy, favoring males, between the proportions of associate sex. One would expect a larger proportion of the associates to be females if alloparenting was occurring, as females are most often observed performing alloparental behavior patterns in mammals (Riedman 1982; Woodroffe & Vincent 1994), and specifically in delphinids (Tavolga & Essapian 1957; Gurevich 1977; Leatherwood 1977; Mann & Smuts 1998).

Of the documented associations, vocalizations were present in almost all events, while tactile contact was observed in an estimated one-third to one-half of the associations. These results suggest that acoustic communication and tactile contact were relatively important during association events, and therefore, may have a vital role in both social associations and development of the calves (Dudzinski 1998). Communication and tactile contact among associates may have shaped and strengthened the bond between the dyads (Seyfarth & Cheney 1984; Tyack 1986; Dudzinski 1996; Mitani & Gros-Louis 1998), allowing the individuals to explore their relationships through varying means.

Mothers were seldom visible during calf associations for both kin and non-kin, but were more visible during kin associations. Yet, when mothers were visible they were most often observed resting/moving slowly followed by milling for both kin and non-kin associations. Therefore, the context of the mother's visibility did not vary between the two groups, even though the occurrence was slightly higher for kin events. The purpose for this difference is unknown, but it is possible that the mothers lingered around when their calves were with kin as they may have previously just been swimming in a kinship group or about to join their kin. This may be especially true if the kin associates were juveniles or relatively young individuals, as juvenile bottlenose dolphins usually remain loosely associated with their mothers. Weaned offspring for some bottlenose dolphins associate more closely with mothers when younger siblings are born (Wells 1991), thus possibly explaining why the mothers were more visible for kin associations. On the other hand, mothers may have been watching older siblings (kin) to be sure the interactions were beneficial to both offspring. Though these reasons may explain the slight difference in mother visibility, it is very possible that the mother's presence was not truly different between kin and non-kin. Mother's may have been present equally between the two groups, but not in view of the camera during the observations. Therefore, the visibility of the mother and the small differences found between kin and non-kin associations should be taken with caution as this difference may only be evident as a product of the methods used in this study.

Interestingly, calves were seldom seen in echelon or infant position while in associations with conspecifics, regardless of kin or non-kin. This is somewhat surprising as bottlenose dolphins have most commonly been observed in these two states when with their mothers (Essapian 1953; Tavalga & Essapian 1957; Cockcroft & Ross 1990b; Mann 1997; Gubbins et al. 1999; Mann & Smuts 1999). Gubbins et al. (1999), however, detected that infant position was rarely observed between the calf and another conspecific. Tavalga & Essapian (1957) also noted that calves moved into the infant position when startled or tired and felt that this position may have provided "safety" for the infant; Gubbins et al. (1999) documented a similar response into infant position. If the associations were alloparental, one might expect calves to be in echelon and infant position (considered positions of care and safety) more often during these events; however, this was not the case.

Results of this study on the lack of observed calf position were in agreement with findings that a larger portion of behavioral activity was recorded as socializing: the animals were much more active than during some of the other behavioral activities. Additionally, one might expect calves to spend more of their time resting/moving slowly or even possibly

moving directly if alloparenting (in particular care) was occurring; yet over half of the associations were either socializing or milling for both groups. Nonetheless, it is possible that play and/or social events were happening during alloparenting and therefore the possibility of alloparenting occurring cannot be eliminated. Calves also departed the associations proportionally more than the conspecifics, which would probably be unlikely if the association events were alloparental, as has been supported in wild chimpanzees where most often mothers retrieved their offspring or the alloparents returned the young to the mother (Nishida 1983).

While, it does not seem that the majority of the documented association events involved alloparenting, it is possible that a few did, especially because of the fact that there is considerable variability within alloparental behavior patterns (Mann & Smuts 1998). Additionally, there were no obvious differences in the behavioral activities found between kin and non-kin that would assume one group exhibited alloparenting events more than the other. As neither care, nor the costs and benefits were tested for in these associations it is difficult to say for certain if the non-mother calf associations were alloparental in behavior. Still, based on the observed context of the events, the majority of both kin and non-kin associations for calves were not likely alloparenting events, but rather social associations. Regardless of whether the function of these association were specifically alloparental or social, the developing social bonds likely influenced or provided important functions to the behavioral, social, and skill(s) development of these calves.

The culmination of these results leads to the question of whether kin selection theory in regard to non-mother-calf associations was supported or not by these findings. Kin selection theory (Hamilton 1964) suggests that individuals should preferentially associate with kin whenever the inclusive fitness benefits outweigh the costs. Therefore, if assistance was needed for infant rearing, whether in terms of social development or care and protection, then kin should have been preferred due to the potential gains through inclusive fitness. The calves' documented preference for associating with non-kin based on frequency and proportion of time, however, leads one to believe that kin selection theory was not at work in calf associations of this population. Therefore, this study does not build upon support (as many other delphinid studies recently have) for Hamilton's (1964) theory of kin selection.

Relatedness may be an important factor in the formation of relationships for other age classes of delphinid species, but it appears that at least for bottlenose calves outside of the mother-calf bond, there are other factors influencing their associations. Factors such as age, calf personality or individual level of sociality, and the behavioral activity characterizing the

associations may have more of an influence on with who calves associate. This is supported by age segregated groups and associations in several long-lived species (McComb et al. 2001; Widdig et al. 2001; Corr 2003; Silk et al. 2006; Evans & Harris 2008; Fraser et al. 2008) and in dolphins, specifically (Shane et al. 1986; Scott et al. 1990; Wells 1991). Additionally, Wiszniewski et al (2010) proposed that although the effects of personality traits on social network structure are not well understood for numerous species, a few studies on humans (Asendorpf & Wilpers 1998; Kalish & Robins 2006; Roberts et al. 2008), other primates (Weinstein & Capitanio 2008), and fish (Pike et al. 2008; Croft et al. 2009), as well as the detection of distinct personalities in bottlenose dolphins (Highfill & Kuczaj 2007; Highfull & Kuczaj 2010), suggest that individual personalities may influence dolphin networks and therefore social bonds.

Although the results of this study may be slightly surprising to some due to the recent discoveries in support for kin selection theory in inter- and intra-sex specific bonds (e.g., Krützen et al. 2003; Möller et al. 2006; Welsh & Herzing 2009; Wiszniewski et al. 2010), there may be some explanation(s) as to why kin selection was not supported for associations among these calves. For example, Parsons et al. (2003) proposed that selection against kin-biased behaviors in dolphins might be expected between individuals where little variance in relatedness exists. This quite possibly could be the case among the members of this population, as the level of relatedness, aside from maternal kin is not known among all the individuals (e.g., relatedness is based on maternal lines and not paternal contribution for this study). Additionally, Goldberg & Wrangham (1997) suggested that relatively long inter-birth intervals (as seen in cetaceans) would make it less likely for maternal siblings to become close affiliates, as they would be fairly dissimilar in age and reproductive status. Hence, since all kin available in this population were siblings, this may possibly explain the discrepancy in associations.

As such, it seems as though calf associations, outside of the mother-calf bond, may deliberately involve more non-kin individuals, at least for this study. Calves may therefore encounter their “fill” of kin conspecifics when with their mothers and consequently choose to associate more often with new, unique members of their population to expand their social and developmental surroundings. This technique may be very useful for them, as they may gain more knowledge, behavioral skills, and future allies by broadening their associate repertoire, ultimately benefiting them as they mature into adult members of the community.

4.2 Errors, Methodological Weaknesses, & Limitations

No study is without weakness and, as is often the case with captive studies, the sample size for this group was small, originally 13 calves. Still, this number was reduced further to only seven calves for kin and non-kin comparisons as several calves did not have kin present during the study period or were never observed in association with any individuals aside from their mothers. As such, the conclusions drawn, including extrapolation to other populations must be done with caution. Small sample sizes could lead to biased results, since low statistical power has a reduced chance of detecting a true effect, as well as a reduced likelihood that a statistically significant result reflects a true effect. Though only seven calves were used for kin/non-kin association comparisons, they generated 421 association events, which was a much better sample size to work with and allowed for comparison with less concern of bias.

Of the calves observed, documented and included in this study, not all were represented for all three years of the age class. Additionally, all individuals in this group, including the calves, had differing levels of sociality. As stated earlier, both of these issues were addressed by calculating proportions of time the calves were in association with kin and non-kin and therefore eliminating the potential errors contributed by variation between individuals and effort. Nevertheless, mothering techniques might have impacted calf sociality (Hill et al. 2007). It is likely that mothers had influence on the level of sociality of their calf, which may have affected the frequency and duration of calf associations, or even the number of associates, as seen in Gibson & Mann (2008). Maternal strategy was not examined during the study and is a topic that could be looked into further during future research.

As a captive study group, the size of the population was naturally limited as compared with any wild study group; thus, the number of kin available to each calf was variable between individuals and generally low. Among all calves, there was considerably more non-kin present and available for interaction as compared with kin conspecifics. This discrepancy was accounted for by calculating the proportions of kin present for each calf in each year and included in the GLM models. Also, calf associations with non-mother conspecifics, indicated in part by separation from the mother, were relatively limited since all individuals were constrained by the enclosure in their movements and opportunities for separation. Moreover, predation risk was removed and the need to forage was not encountered by members of this study group; therefore, separation behavior could be different from that found in wild dolphin populations.

Another concern includes the fact that, although the collected data were a representative sample and indicative of calf associations, only an estimated 48 hours of videotape observations were gathered over six years for this study. Having a more robust data set may have allowed for different association patterns and trends to emerge. This study also relied only on maternal kinship as DNA testing and paternity were not available. Though maternal kinship has been used in numerous studies and proven reliable even when DNA was analyzed (Parsons et al. 2003; Möller et al. 2006), all results presented should be considered conservative as not all biological kin could be potentially determined for this study.

Lastly, errors became apparent when conducting some of the statistical tests. All assumptions were met except for the autocorrelation assumption for both GLMs, where positive autocorrelations were found in the residuals. This was likely caused by an unobserved explanatory variable that was related to the response variables (frequency and duration) and whose values changed systematically through time/space, thus causing an unexplained pattern in the residuals. Consequently, the broken assumptions warrant additional caution when examining or extrapolating the results. Though it is likely that the parameter estimates were minimally affected, the standard errors and confidence intervals might be negatively biased, which would increase the risk of concluding an explanatory variable was significant when in reality it was not. This concern could and should be minimized in the future by using different statistical tests that account for these problems (limited time prevented better tests to be conducted presently). For example, using a generalized estimating equation (GEE) would account for correlation and could be fitted to the data to give a less biased result. For that reason, a better model fit for both models may be possible and would be desirable as model fit was relatively poor ($R^2=0.340$) for the frequency GLM and only okay ($R^2=0.583$) for the duration GLM. Using GEEs for the future would greatly improve the confidence of the results presented here.

4.3 Future Studies

There are numerous other studies that would enhance and expand upon this research. Analyses of long-term data sets from other captive facilities may provide insight into whether the trends of kin and non-kin calf associations found here were simply artifacts of the dynamics of this population or are indicative of other populations as well. Facilities where a larger number of maternal kin are available (such as aunts, uncles, grandmothers, etc.) and/or

where paternity/DNA details are known would likely present a more accurate representation of kin and therefore potentially yield different results or corroborate the results of this study.

Applying the methods from this study to a wild population would also be ideal, though potentially challenging. That is, the wild study group would need to be a well-studied population with a long-term data set. Additionally, and likely the larger caveat, is that the wild population would have to have reliably identifiable calves, and known or determinable matrilineal kin and/or paternity/DNA. This would be a considerable challenge for most wild populations, but there are a few on-going longitudinal studies that could potentially have the right combination to make this type of study work for a wild dolphin group.

It would also be useful to determine whether different delphinid or other cetacean species (whether captive or wild) exhibit similar roles for kin and/or non-kin in calf associations. A comparison of how these roles and relationships vary between species could present exciting results as to how sociality, the importance of kinship, and their role in calf development varies (or does not) between species.

Another avenue of investigation would be to examine the differences and/or similarities in paternally related individuals to those of maternally related conspecifics, specifically looking at their role in calf associations and rearing. This could possibly produce interesting results as to how maternal and paternal investment differs even in extended family members.

Research efforts in the future could also be put towards investigating the associations of kin and non-kin as calves continue to age into juveniles, sub-adults and even adults. Comparing the patterns of association and the possible changing roles of kin and non-kin associates as development changes in the calf may yield some clues on how relationships change as a calf ages.

4.4 Conclusions

Similarities and differences were observed between kin and non-kin non-mother-calf associations. Calves with kin available associated with more conspecifics than calves without kin, suggesting that there may have been different social strategies occurring between these two groups. Nonetheless, calves associated more, in both frequency and proportion of time, with non-kin individuals. This was contrary to numerous recent studies that showed male-male, female-female, and male-female dolphin associations (excluding calves) being highly correlated with kinship. Yet in the calf associations, it seemed that calf age and

personality/sociality, as well as the associate age may have played a more important role than relatedness in who calves associated with outside of the maternal relationship. Additionally, no obvious differences in the functionality/context of the associations of calves with kin and non-kin conspecifics were found. As such, it appears as though calves preferentially associated with non-kin individuals, possibly to expand their social relationships through the acquisition of knowledge, behavioral skills, and future allies. Consequently, these results do not support the notion of kin selection theory in male and female calf associations. Still, the small sample sizes and assumptions broken during modeling warrant caution when discussing and extrapolating the conclusions. Nonetheless, with more robust data (including larger sample sizes), better analysis methods, and further questions, it could be possible to definitively understand the role of kin and non-kin in calf associations, both in captivity and in the wild. Overall, this study has provided the first glimpse into the role of kin and non-kin in calf associations, which in turn, has afforded further information on social development in captive bottlenose dolphin calves.

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6. Appendices:

Appendix A: Relevant Definitions in alphabetical order

Term	Definition
Associate	A male or female (non-calf) conspecific in association with a calf that is not its offspring
Association	The interaction between calf and associate, (swimming within 1.5 m distance of one another) with the simultaneous separation of the calf (>2 m) from the mother
Directed Movement (DM)	Deliberate, swift movement in a predetermined direction (>2m/s)
Echelon Position	Calf swimming at associates side, roughly parallel, above their midline (usually within 0.5m distance)
Experienced (female) Associate	A multiparous adult female
Inexperienced (Female) Associate	A female that has not had a calf
Infant Position	Calf swimming under associate (with melon or head very close to or lightly touching the associates abdomen)
Kin	Relatedness between individuals based on maternity
Milling	Non-directional, random movements with no to little net movement in any one direction
Non-kin	No matrilineal relatedness between individuals
Nursing/ Attempted Nursing	The successful or not successful acquisition of milk from a lactating female. Requires the calf's rostrum to be in contact with the mammary slits of a female
Tactile Contact	Contact between any body parts of one dolphin to another dolphin. This can involve active movement (rub) or static contact (touch)
Playing	Swift movements, chases, fast circular swimming, oriented directly (and close) to the camera, and/or pushing, pulling or mouthing objects or conspecifics
Rest/Slow Movement (Rest/SM)	Low level activity, dolphins moving at slow speeds (<2m/s)
Socializing	A minimum of two dolphins engaged in acoustic and/or non-acoustic (tactile contact such as rubbing) communication, includes mounting
Unidentifiable (unID)	When the identity of a dolphin is impossible to determine (whether due to distance, visibility, or speed). If identity is unknown often (but not always) sex, age, and affiliated characteristics (such as kin or non-kin) are unknown as well

Appendix B: Matrilineal Relatedness

