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Observations of a Paternal Male with Bottlenose Dolphin Calf (*Tursiops truncatus*): A Case Study

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The rearing and socialization of bottlenose dolphin calves has been largely described as a female role, whether via direct maternal care or allomaternal parenting. Nevertheless, male associations have been observed but are rarely systematically investigated. This case study focused on the opportunistic occurrence of a single bottlenose calf and her associations with the mother, father and two unrelated allomothers in a captive setting. Observations were made postpartum of an adult male and his female calf multiple times per day over the course of the first year of the calf's life, including social (proximity and orientation), aggressive (tail slapping/swatting, threats, jaw popping, chasing) and tactile behaviors. For comparative analyses, data were simultaneously collected on mother-calf and allomother interactions. The results revealed that cohabitation of the paternal male and offspring was prosocial, with negligible levels of aggression (0.03%) even during maternal estrous. The male demonstrated minimal aggressive behaviors toward the calf (e.g., chasing), none of which resulted in injury. Rather, the male's interactions with the calf were considerably affiliative. Although the frequency of interactions between the paternal male and the calf were less than the mother's, father-calf interactions were significantly more frequent than were calf interactions with other dolphins. Over the course of the study, the number of interactions the calf had with mother, father, and allomothers decreased. Overall, these results confirm that care can involve the paternal male, although the relative size of the enclosed setting limits extrapolations to the wild. Nonetheless, these observations suggest that some dolphin fathers may play a role in their calves' social development and rearing. Although additional research on calf socialization is required, the dolphin father in this study established and maintained a social bond with his female calf that was clearly affiliative, and these associations occurred significantly more often than those between the calf and her allomothers.

Non-maternal provisionary care occurs in several mammalian species (e.g., Alcock, 2009; Kleiman & Malcolm, 1981; Vaughan, 1978), whereas male care is less prevalent and more commonly, though not exclusively, observed in monogamous species (e.g., Clutton-Brock, 1989; Geary, 2007; Woodroffe & Vincent, 1994). Absence of male care may potentially be due to the male's inability to contribute during both gestation and extended postpartum care (e.g., nursing; Clutton-Brock, 1991). Nevertheless, male care has been observed in several large-brained non-human mammals: primates (e.g., titi monkeys [*Callicebus*], owl monkeys [*Aotus*]; Fernandez-Duque, Valeggia, & Mendoza, 2009; savannah baboons [*Papio cynocephalus*]; Buchan, Alberts, Silk, & Altmann, 2003, and cotton-top tamarins [*Saguinus Oedipus*]; Price, 1990), as well as cetaceans (killer whales [*Orcinus orca*]; Woodroffe & Vincent, 1994), long finned pilot whales (*Globicephala melas*; Amos et al., 1993) and Baird's beaked whales (*Berardius bairdii*; Connor, Mann, Tyack, & Whitehead, 1998). It is suggested that male associations have evolved to support a greater survivorship of offspring, and it is possible that multi-mating opportunities are less beneficial to reproductive output than the participation in paternal care in non-obligated mammalian species (Gubernick & Teferi, 2000; Kleiman & Malcolm, 1981). Motivation for the evolution in reproductive strategies, such as shifting obligations from mating to parenting, is yet to be clearly identified among both human and nonhuman mammals (Geary, 2007) but may be due to biological, ecological, demographic, and/or social factors related to increasing the probability of offspring survival and genetic fitness (Gubernick & Teferi, 2000; Maestripieri, Ross, & Megna, 2002; Winterhalder & Smith, 2000).

Parental investment, although often not empirically investigated, is defined as an investment of time or energy that may increase the biological fitness of offspring at the expense of the caregiver (e.g., grooming, infant carrying, defense behavior [conflict, infanticide], nourishment) to ensure the reproductive success of a genotype (e.g., Alcock, 1998, 2009; Geary, 2005; Silk, 2007; Smuts & Gubernick, 1992; van Schaik & Paul, 1996). Although offspring success in mammals is not dependent upon male care, contributions from non-obligated individuals may assist in reproductive success by increasing offspring survival, maximizing mating opportunities, or sustaining prolonged relationships with specifically fit individuals (e.g., Birkhead & Møller, 1993; Owen, Wells, & Hoffmann, 2002). Reproductive strategies for both males and females are based upon ecological fitness cost-benefit trade-offs, with the ultimate goal to ensure genetic fitness. Trivers (1972) documented the fitness benefits mothers and fathers provide to their offspring by their investment in offspring care and the associated costs.

Care of non-related conspecifics has been observed in several cetacean species, and alloparental care typically occurs at a high cost for non-kin individuals. This type of behavior has been documented in white-sided dolphins (*Lagenorhynchus acutus*; e.g., Simard & Gowans, 2004), bottlenose dolphins (*Tursiops truncatus*; e.g., Caldwell & Caldwell, 1964, 1966; Mann & Smuts, 1999; Leatherwood, 1977; Tavolga & Essapian, 1957), spinner dolphins (*Stenella longirostris*; e.g., Johnson & Norris, 1994), spotted dolphins (*Stenella frontalis*; e.g., Herzing, 1996; Hill 2003, 2009; McCowan & Reiss, 1995), sperm whales (*Physeter macrocephalus*; e.g., Best, 1979; Whitehead, 1996), and killer whales (e.g., Waite, 1988). The behavior varies among and within species and may contribute to the survival of the calf through social learning, increased protection, and enhanced development (Gibson, 2002; van Schalik, 2000; Wells, 1991; Wolff & Peterson, 1998).

Much of the paternal research among mammalian species focuses on kin and non-kin interactions and the ability to discriminate (see for review Alcock, 2009; Geary, 2007). Male dolphins tend to skew resources towards multi-mating opportunities rather than offspring survival (e.g., Krützen, Barre, Connor, & Mann, 2004). Despite the fact that most research documents greater levels of allocare among kin related females (e.g., Mann & Smuts, 1998; Welsh & Herzing, 2008), adult males routinely practice prosocial behaviors among matrilineal and biparental kin (e.g., Indo pacific bottlenose dolphins [*Tursiops aduncus*]; Frère et al., 2010a, 2010b), assume the role as alloparent (e.g., bottlenose dolphin, Essapian, 1963), or occasionally act as a provisional escort (e.g., sperm whales, Whitehead, 1996; humpback whales, Megaptera novaeangliae; Danilewicz, Claver, Perez Carrera, Secchi & Fontoura, 2004; Valsecchi & Zanelatto, 2003). Although male cetaceans engage with calves, Gibson (2002) suggested that this phenomenon is a byproduct of large groups of mixed pods traveling together. Additionally, interactions with non-parental conspecifics may be influenced by age and sex of the calf, rather than kin associations (Levengood & Dudzinski, 2016). Research involving interactions with adult male dolphins and calves is minimal, with current studies largely limited to evaluations of aggressive and/or sexual behavior (Krützen et al., 2004; Patterson et al., 1998; Woodroffe & Vincent, 1994).

Postpartum is suggested to be a time of bonding between mothers and calves, with the mother being the primary influence in the calf's life (e.g., Bender, Herzing, & Bjorklund., 2009; Grellier, Hammond, & Wilson, 2003; Mann, 2001; Mann, Sargeant, & Minor, 2007; Marino, 2002; Quintana-Rizzo & Wells, 2001). Proximity, synchronicity, and total time spent associating is utilized to quantify social relationships among bottlenose dolphins (e.g., Connor, Read, & Wrangham, 2000; Gibson & Mann, 2008b; Hill, Greer, Solangi, & Kuczaj, 2007; Mann & Watson-Capps, 2005; Mann & Smuts, 1999; Quintana-Rizzo & Wells, 2001). Proximal relationships, specifically those of a mother and her calf, are crucial to calf survival, especially postpartum, as the calf is reliant on the mother for mobility and nourishment (e.g., Noren & Edwards, 2007). These relationships extended beyond protection from predators, as they increase sociability among other conspecifics

and may influence future bonds (e.g., Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999; Mann & Watson-Capps, 2005; Reid, Mann, Weiner, & Hecker, 1995).

Interactions with other conspecifics, including affiliative tactile behaviors, are suggested to represent bonding among individuals and are most commonly observed between mothers, calves, kin males and females, as well as other pair-bonded associates (e.g., Connor et al., 2000; Connor, Mann, & Watson-Capps, 2006; Levensgood & Dudzinski, 2016; Mann & Smuts, 1999; Samuels & Tyack, 2000). Affiliative tactile interactions are particularly salient between mothers and calves (Dudzinski, 1998; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Paulos & Dudzinski, 2008). This type of bonding is not limited by sex or age, wild or captive, and is widely observed among cetacean species, typically manifesting as gentle contact, petting, and rubbing (e.g., pectoral touch; Dudzinski, 1998; Dudzinski, Gregg, Melillo-Sweeting, Seay, Levensgood, & Kuczaj, 2012; Sakai, Hishii, Takeda, & Kohsima, 2003). The intensity and duration of bouts of petting and/or rubbing may indicate the degree of the association between conspecifics and the strength of bonds (e.g., Connor et al., 2006; Dudzinski, 1998; Kaplan & Connor, 2007). Synchronous contact swimming among dolphins is most frequently presented as pectoral fin touching (versus petting and rubbing) and is comparable to social grooming in great apes (e.g., Connor, 2007; Connor et al., 2006; Kuczaj, Highfill, Makecha, & Byerly, 2012). Although tactile interactions occur in aggressive contexts (e.g., dominance, sexual interactions), these interactions differ in intensity compared to petting and touching during affiliative contact (e.g., Brown & Norris, 1956; Norris, 1967; Östman, 1991).

Aggression and agonistic interactions among cetaceans are commonly observed between mothers and calves for disciplinary purposes, males herding females and consortships, as well as during competitive foraging events (e.g., Connor & Smolker, 1996; Herzing, 1996; Hill, 2009; Hill et al., 2007). Bottlenose dolphin calves that venture beyond provisioned areas will often be chased by the mother or allomothers (Mann & Smuts, 1998) in an effort to regain control of their offspring. Atlantic spotted dolphin mothers exhibit aggressive displays through inverted body posturing, chasing, as well as pinning their calves to the ocean floor (Herzing, 1996). Due to varying ages of females that assume the role of alloparent (Travalga & Essapian, 1957), one potential cost of allocare is active participation by inexperienced females, which may result in offspring injury or mortality (e.g., Goodall, 1986; Mann et al., 2007; Shopland & Altmann, 1987; Silk, 1980a, 1980b). A similar threat comes from male dolphins, documented directing aggressive behavior towards calves (e.g., Krutzen et al., 2004; Lusseau, 2007), and high levels of male aggressive behavior during female estrous cycles and mating are associated with infanticide (e.g., Connor, Richards, Smolker & Mann, 1995; Geary, 2005; Patterson et al., 1998; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005; Wolff & Macdonald, 2004).

Socialization among bottlenose dolphins, described as fission-fusion with significant fluidity in group size and composition, potentially on a daily basis (e.g., Connor et al., 2000), results in a variety of different social scenarios. Thus, the objective of this case study was to document interactions between an adult male dolphin, specifically the paternal male, with his calf post parturition through the first year. The study monitored an opportunistic animal management context in which a calf was housed with the paternal male, two non-related female cohorts (one pregnant), and the mother. Observations of the calf and her affiliations were charted and quantified for 780 total focal hours. Data were simultaneously collected on calf development, as well as maternal and allomaternal care for cross comparative analyses.

Method

Subjects and Setting

The focal calf (Julie) was born on 19 August 2007, and her interactions with cohorts, including her mother, father (validated through DNA testing), and two adult female allomothers (Table 1) were documented over the course of 12 months and four developmental stages: Stage 1 = 0 – 3 months, Stage 2 = 3 – 6 months, Stage 3 = 6 – 9 months, and Stage 4 = 9 – 12 months. All study subjects were housed at Dolphins Plus Oceanside Key Largo, Florida, characterized by semi-open, natural seawater lagoons, located adjacent to the Atlantic Ocean on a residential canal setting, with a 0.6 m – 1.2 m twice-a-day tidal exchange. For the first three months post parturition, the calf was housed with her mother and father in a single enclosure (mean depth and area: 4.5 m and 1500 m²). At Developmental Stage 2 (i.e., 3 months), the enclosure space was doubled (mean depth and area: 4.5 m and 3000 m²), and three adult females, including a deaf and non-social female, were added for permanent cohabitation.

At the time of the study, the other two social, female allomothers had each reared one successful calf, and one of them gave birth to a second female calf one month prior to the termination of the study. The deaf, rescued female exhibited few to no interactions with all other conspecifics, and as such, was excluded from the analyses.

Table 1
Study Subjects Demographic Data

Subject	DOB	Sex	Relation to Calf
Dinghy	°1977	F	Mother
Little Bit	°1978	M	Father
Samantha	°1984	F	Allomother
Sarah	°1984	F	Pregnant Allomother
Julie – calf	08/19/07	F	-

Note. ° - Estimated year of birth

Sampling

Data were collected over a period of 12-months post-parturition using a scan sampling method in which observational data detailing the calf's sociability with conspecifics were documented on one-minute time intervals for one hour per behavioral ethogram. This design and multiple observation periods per day (0800 hr; 1245 hr; 1445 hr) allowed for daily representations of social behavior. Due to varying weather conditions and daily operational constraints, observations were not always feasible; thus, a total of 780 hours of observations were recorded and analyzed. Observers ($N = 5$) were tested for reliability, and the results revealed a high reliability coefficient among observers, Cronbach's $\alpha = 0.979$.

Social interactions and physical proximity were organized and assessed with a behavioral ethogram that consisted of broad subsections: instinctual and social behaviors, as well as aggressive interactions (see Table 2 for definitions of all target behaviors). The ethogram was designed to assess various factors that influence social bonds and development among gregarious dolphins. All conspecifics adjacent to the calf were scored at each scan sampling point (60 s) if the proximity radius from the calf was 3 m or less. Ephemeral interactions (e.g., pass by swimming not obviously established in meaningful contact or connection with another conspecific), typically lasting less than 1 s, were excluded. Although the purpose of this study was to analyze adult male-calf interactions, data were simultaneously collected on mother-calf and allomother interactions as non-experimental controls, as well as calf solitariness. As such, the father's proximity (observed interactions) and social interactions (aggression, play, tactile) were examined and cross-compared to those of other conspecifics.

Table 2
Excerpts from Behavioral Ethogram Used for Analysis

Category	Target Behavior and Operational Definition
Interaction	<p>Configuration – Swimming formation of the calf and other conspecifics(s) (0 m – 3 m):</p> <p>Beside – Swimming parallel to one another</p> <p>Underneath – Dorsal fins are aligned vertically with one another</p> <p>Tucked (aka Infant Position) – Calf is under a conspecific and dorsal fin is aligned with peduncle</p> <p>Echelon – Calf is lateral to conspecific and calf's dorsal fin is in front of the subject's dorsal fin</p> <p>Other – Does not fit above descriptions</p> <p>Solo – All other subjects are greater than 3m distance</p> <p>Proximity – The distance between calf and other conspecifics:</p> <p>0 = Touching</p> <p>1 = ≤ 1 m</p> <p>2 = 1.1 m – 2 m</p> <p>3 = 2.1 m – 3 m</p> <p>4 = > 3.1 m</p>
Social Behaviors	<p>Tactile – Rubbing or petting; body-to-body contact with one or more conspecifics</p> <p>Play – Manipulating or interacting with an object in any way other than rubbing, including but not limited to: resting on, floating on, tapping, pulling, pushing, mouthing</p>
Aggressive Behaviors	<p>Headshake – Shaking or thrusting head towards another conspecific or an object in the environment (lagoon)</p> <p>Threat – Open mouth directed towards another conspecific</p> <p>Tail Slap/Sweep/Swat – Tail and/or peduncle are manipulated to make contact with the surface, sweep from side to side, or swat another individual</p> <p>Chase – Accelerated swim speed accompanied with pursuit of another conspecific; recipient is actively avoiding and fleeing</p>
Not Visible	<p>The calf is unobservable due to various environmental conditions; therefore, no social interaction or proximity scores can be assigned</p>

Data Analysis

To determine the existence of adult male provisionary care in the focus population, direct interactions between the father and the calf were documented and compared to the calf's interactions and sociability with other cohabitants. The yearlong study resulted in a total of 260 days and 780 hours of data collection. Calf behavior and affiliations with each conspecific were quantified and then standardized as proportions. Evaluations were made across developmental stages; Stage 1: birth – 3 months; Stage 2: 3 – 6 months; Stage 3: 6 – 9 months; and Stage 4: 9 – 12 months. Non-parametric statistics were utilized to analyze all behavioral data. Data for Developmental Stage 1 (0 – 3 months) were analyzed separately due to the absence of allomothers in the lagoon and included comparisons of the calf's interactions with the mother, father, or solo, as well as tactile and aggressive occurrences involving the mother and father. For Developmental Stages 2 – 4, sociality, aggressive interactions directed towards the calf, tactile events, and occurrences of play were analyzed for all subjects (mother, father, and allomothers), as well as how each variable changed over time.

Results

Observed Interactions with the Calf

The proportion of observed interactions between the mother and the calf were significantly greater than father-calf interactions during Developmental Stage 1, Mann-Whitney U , $U = 899.50$, $p < 0.05$. When analyzing all subjects for Developmental Stages 2 – 4, there was a significant difference in the proportion of time the calf spent interacting among cohabitants, Kruskal Wallis test, $\chi^2(3) = 375.57$, $p < 0.001$ (see Figure 1). Post hoc analyses revealed that mother-calf interactions occurred more frequently than all other subjects, and father-calf interactions were significantly greater than the two allomothers, $p < 0.05$.

The proportion of mother-calf and father-calf interactions differed significantly across developmental stages (1 – 4), Mother-Calf: Friedman's test, $\chi^2(3) = 70.33$, $p < 0.001$; Father-Calf: Friedman's test, $\chi^2(3) = 64.64$, $p < 0.001$. Post hoc analyses revealed that mother-calf interactions significantly and successively decreased as the calf aged and across each developmental stage (1 – 4), $p < 0.05$. Father-calf interactions significantly decreased from developmental stage 1 to 2, $p < 0.05$, and did not differ significantly between developmental stages 2 and 3. However, father-calf interactions significantly increased from developmental stage 3 to 4, $p < 0.05$.

The proportion of interactions between the calf and allomothers did not differ across developmental stages (2 – 4), Allomother: Friedman's test, $\chi^2(2) = 4.70$, $p = 0.095$; Pregnant Allomother: Friedman's test, $\chi^2(2) = 1.43$, $p = 0.488$. Post hoc analyses revealed no significant differences in interactions between the calf and Samantha over time, but the pregnant allomother interactions with the calf significantly decreased between developmental stages 2 and 4, $p < 0.05$.

The proportion of time the calf spent alone differed significantly across all developmental stages (1 – 4), Friedman's test, $\chi^2(3) = 80.83$, $p < 0.001$. Post hoc analyses revealed solo occurrences increased significantly and successively from and between developmental stages 1, 2 and 3, $p < 0.05$, but no significant difference was observed between developmental stages 3 and 4.

Table 3

Mean Proportion and Standard Deviations of Target Behaviors for Developmental Stage 1 (Mother, Father, Calf) and Developmental Stage 2 – 4 combined (Mother, Father, 2 Allomothers, Calf)

		Mean Proportion of Target Behaviors with the Calf			
		<i>M(SD)</i>			
	Subject	Observed Interactions	Tactile Occurrences	Aggressive Interactions	Play Occurrences
Developmental Stage 1 (0 – 3 months)	Mom	0.742 (0.0204)	0.026 (0.040)	0.008 (0.023)	0.002 (0.006)
	Dad	0.424 (0.241)	0.005 (0.013)	0.0002 (0.002)	0.001 (0.003)
	Solo	0.116 (0.175)	–	–	–
Developmental Stage 2 – 4 (3 – 12 months)	Mom	0.484 (0.225)	0.138 (0.021)	0.002 (0.022)	0.005 (0.017)
	Dad	0.088 (0.095)	0.001 (0.005)	0.0001 (0.002)	0.001 (0.004)
	Non-Pregnant Allomother	0.049 (0.061)	0.005 (0.013)	0.0008 (0.010)	0.0009 (0.005)
	Pregnant Allomother	0.038 (0.059)	0.009 (0.025)	0.001 (0.013)	0.003 (0.018)
	Solo	0.258 (0.241)	–	–	–

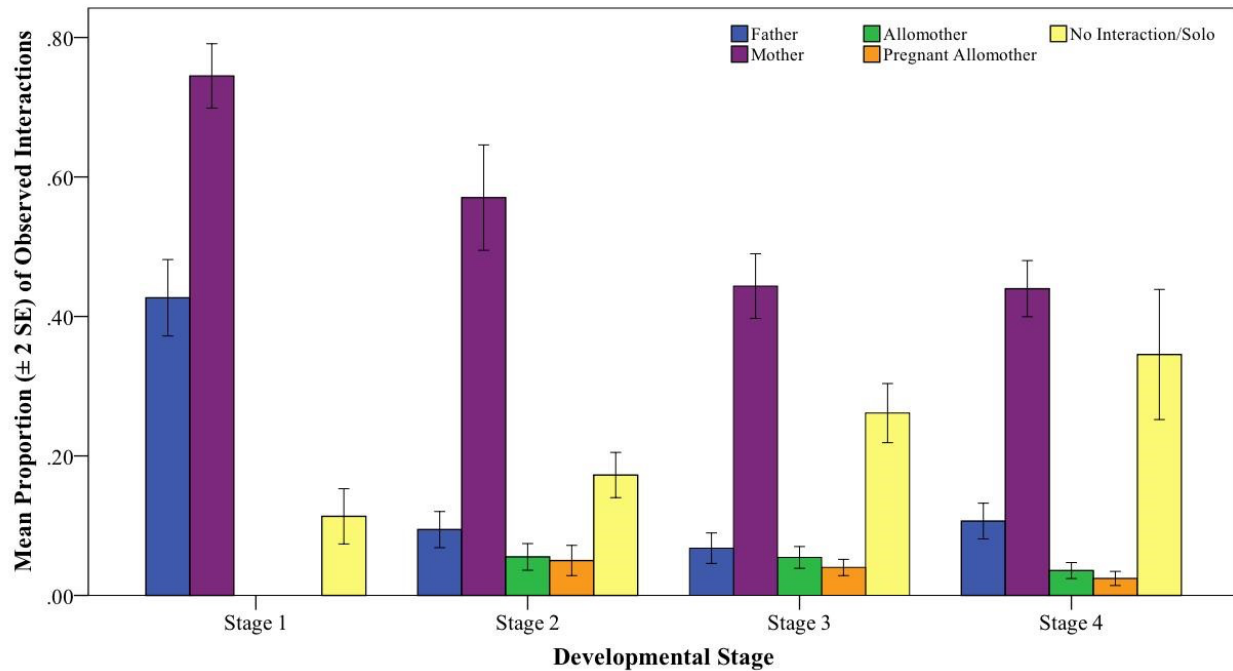


Figure 1. Mean proportion of all interactions (>3m from the calf) (± 2 SE) between the calf and the father, the mother, and two unrelated adult allomothers from birth to 1 year of age. Developmental Stage 1: 1 – 3 months; Developmental Stage 2: 3 – 6 months; Developmental Stage 3: 6 – 9 months; Developmental Stage 4: 9 – 12 months.

Play

During Developmental Stage 1 (0 – 3 months), play interactions with the calf did not differ significantly between the mother and father. For Developmental Stages 2 – 4, the proportion of play interactions between the calf and cohabitants differed significantly, Kruskal Wallis test, $\chi^2(3) = 22.87$, $p < 0.001$. Post hoc analyses revealed that the mother engaged in more playful interactions with the calf than all other conspecifics, $p < 0.05$; no significant difference was identified between the father and two adult allomothers.

Tactile

Mother-calf tactile interactions were significantly greater than father-calf tactile occurrences during the first developmental stage, Mann-Whitney U , $U = 1790.00$, $p < 0.05$. There were significant differences in the proportion of tactile interactions between the calf and cohorts across developmental stages 2 – 4, Kruskal Wallis test, $\chi^2(3) = 81.87$, $p < 0.001$ (see Figure 2). Mother-calf tactile occurrences were significantly greater than all other subjects, and father-calf tactile interactions occurred significantly less often than both allomothers, $p < 0.05$; tactile interactions did not differ significantly between allomothers.

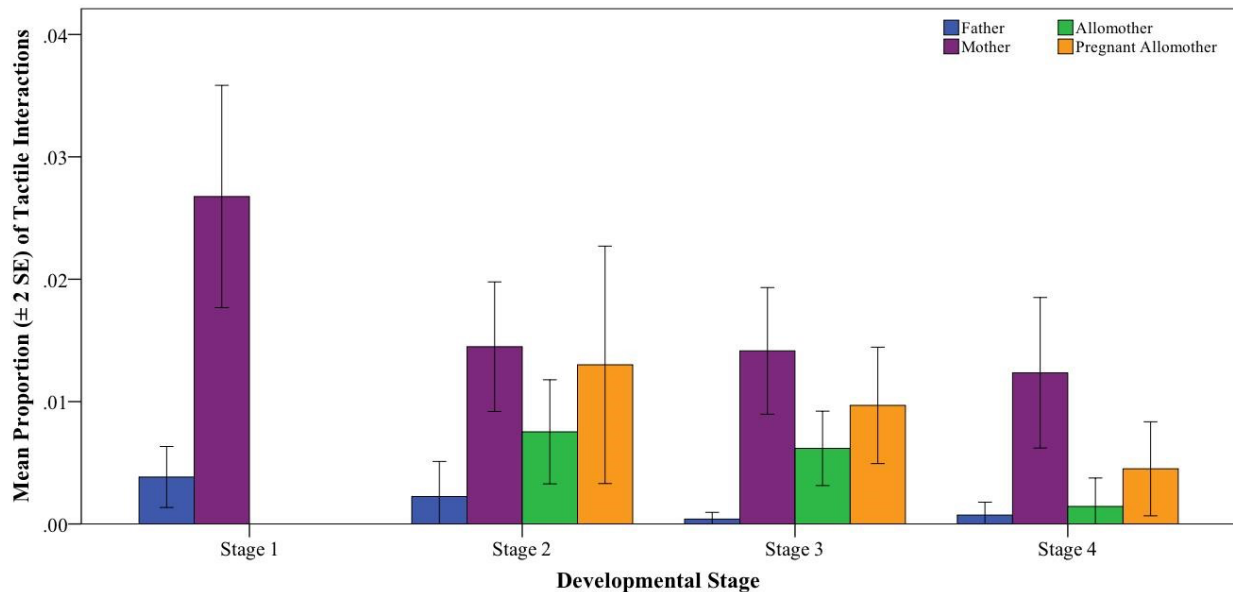


Figure 2. Mean proportion of tactile interactions (± 2 SE) between the calf and the father, the mother, and two unrelated adult allomothers from birth to 1 year of age. Developmental Stage 1: 1 – 3 months; Developmental Stage 2: 3 – 6 months; Developmental Stage 3: 6 – 9 months; Developmental Stage 4: 9 – 12 months.

Aggression

The mean proportion of mother-calf aggressive bouts was significantly greater than father-calf aggression during the first developmental stage, Mann-Whitney U , $U = 2433.50$, $p < 0.001$. When analyzing developmental stages 2 – 4, there was a significant difference in the mean proportion of aggressive interactions among subjects, Kruskal Wallis test, $\chi^2(3) = 127.25$, $p < 0.001$ (see Figure 3). Mother-calf aggressive interactions were significantly greater than all subjects, and both allomothers displayed significantly more aggressive interactions towards the calf than the father, $p < 0.05$. Aggressive interactions did not differ significantly between the two allomothers.

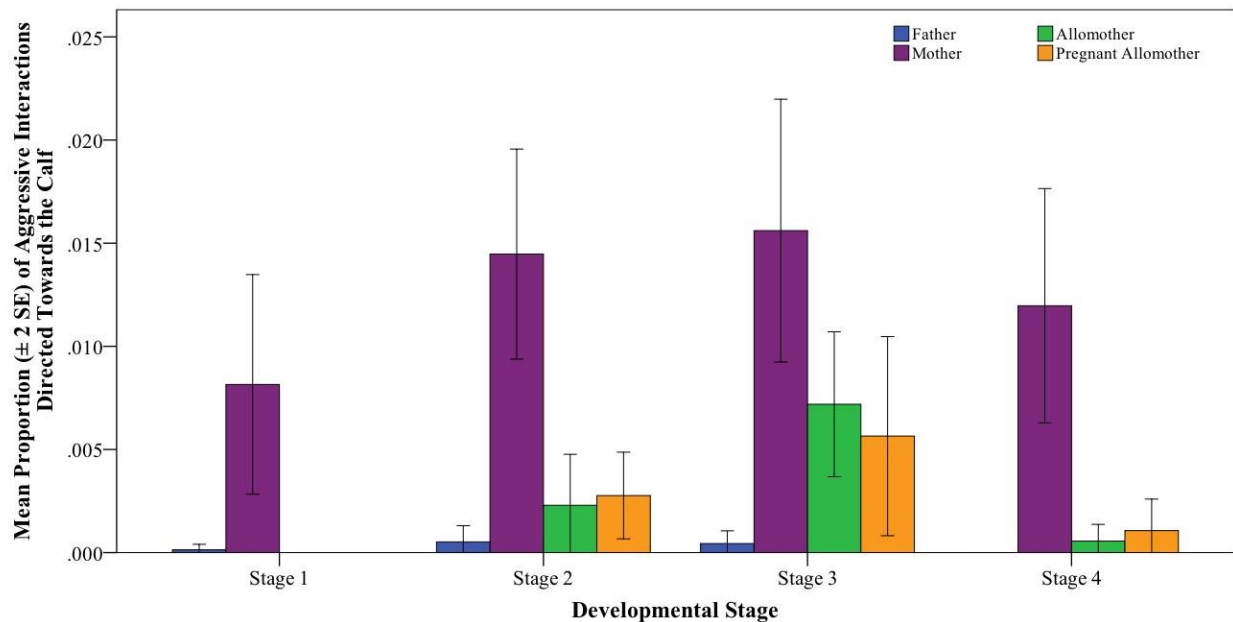


Figure 3. Mean proportion of aggressive interactions (± 2 SE) between the calf and the father, the mother, and two unrelated adult allomothers from birth to 1 year of age. Developmental Stage 1: 1 – 3 months; Developmental Stage 2: 3 – 6 months; Developmental Stage 3: 6 – 9 months; Developmental Stage 4: 9 – 12 months.

Discussion

Adaptations of male care have been reported across several mammal species, and researchers theorize that males in some non-obligated species may engage in offspring care to achieve increased genetic fitness, develop stronger bonds with fit mates, increase reproductive output, improve offspring survival, and/or decrease interbirth intervals (e.g., Gubernick & Teferi, 2000; Maestriperi et al., 2002; Ross & MacLarnon, 2000; Winterhalder & Smith, 2000). The data generated in this study, although sample specific, showed similar trends to previous studies of both captive and free ranging dolphins in regards to play behavior, independence, calf development, as well as maternal attachment with the mother and allomothers (e.g., Cockcroft & Ross, 1990; Connor, Wells, Mann, & Read, 2000; Gibson & Mann, 2008a, b; Hill et al., 2007; Mann & Smuts, 1998, 1999; Miles & Herzing, 2003; Reid, Mann, Weiner, & Hecker, 1995).

Strong associations between mothers and calves (see Quintana-Rizzo & Wells, 2001) were observed throughout the study through position, social behaviors (e.g., play, tactile), and observed interactions, validating the mother as the primary influence in the calf's life (e.g., Grellier et al., 2003; Mann, 2001; Mann et al., 2007; Marino, 2002; Quintana-Rizzo & Wells, 2001). Additionally, the frequency of interactions between the mother and the calf remained constant between Developmental Stage 1 and 2, regardless of the enclosure size doubling and the introduction of two, non-kin allomothers, further validating the strength and importance of the mother-calf bond (e.g., Mann, 2001). Although the mother participated in the greatest frequency of all target behaviors, both the non-kin allomothers and paternal male also participated in these behaviors to varying degrees, suggesting different levels of association.

The paternal male in this study actively and routinely engaged in prosocial behaviors with the calf (e.g., play, tactile). Although male interactions with calves have been previously suggested to be the byproduct of male herds interacting with females (e.g., Gibson, 2002; Mann, 2001) or calves seeking attention from adult males (Mann & Smuts, 1999), the paternal male in this study was observed with the calf 42% of the time during Developmental Stage 1, often in dyad formation and unaccompanied by the mother. During this time (0 – 3 months), the calf had not gained full mobility or independence; thus, the father actively assisted the calf around the lagoon. Typically, the mother facilitates interactions with other conspecifics in order to encourage calf socialization (e.g., Miles & Herzing, 2003). In this case, the first time the mother was observed to actively direct and leave the calf with the father occurred seven days postpartum. The decrease in interactions with the father to 10% in Developmental Stage 2 may be a result of the addition of the allomothers, as well as the developmental trend of increased calf independence and other age-related changes (e.g., Mann & Smuts, 1998, 1999; Miles & Herzing, 2003). Though observed interactions with the paternal male and the calf remained relatively consistent across Developmental Stages 2 – 4, interactions between the calf and the mother and allomothers decreased between Developmental Stages 3 and 4, while increasing for the paternal male. Maternal social associations and strategies (e.g., Gibson & Mann, 2008a), as well as early social exposure (e.g., to the paternal male in Developmental Stage 1) (de Waal, 2006), may partially explain these results. Overall, the proportion of time the calf spent with her father, from birth to 1 year, was significantly greater than time spent with either of the allomothers, suggesting that rearing and care can involve fathers.

For the duration of the study, the mother, father, and calf were commonly observed swimming together (0 – 3 m) with no preference in positioning, although the calf was seen on the mother's side more frequently. The mother's behavior was altered on occasion, particularly when two other adult females were watching over the calf. The mother was observed chasing each of the allomother-calf dyads and actively trying to separate the two. Mann and Smuts (1998) suggested that provisional care provided by other mothers can be competitive and may cause social distress. Although the calf in this study was never overtly harmed during these interactions, the mother exhibited a heightened state of arousal and vigilance during several interactions between the calf and conspecifics, including father ($n = 2$), each allomother ($n = 8$).

Aggression towards calves by males (Connor et al., 1995; Krutzen et al., 2004; Mann & Smuts, 1999; Patterson et al., 1998; Wolff & Macdonald, 2004; Woodroffe & Vincent, 1994), allomothers (e.g., Mann & Smuts, 1998; Mann et al., 2007) and mothers, particularly as the calf ages (e.g., Miles & Herzing, 2003), has been documented among wild and captive dolphins. Aggression directed towards the calf was observed throughout the study by all subjects, successively increasing through Developmental Stage 3, followed by an overall decrease in Developmental Stage 4. Recorded aggressive interactions between the calf and her mother (1.1%) and the two allomothers (0.08% and 0.1%) were significantly greater than the comparatively negligible 0.03% of total aggressive interactions noted between the calf and her father. The frequency of aggression noted to occur between allomothers and the calf may reflect a lesser degree of maternal experience (Mann & Smuts, 1998), as each were primiparous at the time of the study, while the mother was experienced with four viable offspring. Although population specific, male interactions with the calf were generally affiliative, and there were no documented calf injuries as a result of the mother's, male's or allomothers' aggressive behaviors. Mating between the male and the other females occurred multiple times during the study, and despite the calf being present, she remained unharmed and uninvolved in these scenarios.

The major limitation with this study is the small population evaluated. Individual differences (e.g., Highfill & Kuczaj, 2007; Kuczaj et al., 2012), as well as decreased competition for resources in a captive setting, could account for the observations and verification of male involvement in offspring care. In order to

draw broader conclusions about how males interact with their young, additional studies are needed of both captive and free-ranging populations. Since many aspects of this study relevant to the calf and other females were congruent with previous research involving free ranging populations, it is possible that male dolphins interact with their offspring and may provide care. This differs from widely accepted theories regarding a broad lack of paternal care across many mammalian species and the notion that interactions between males and their offspring occur only fortuitously.

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