Contact Exchanges in Bottlenose Dolphin Mother–Calf Pairs

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Abstract

The relationship between a dolphin mother and her calf has been well studied, but details regarding tactile exchanges within these dyads are limited. Contacts between five adult female bottlenose dolphins (Tursiops truncatus) and their calves, with data from three pairs analyzed statistically, were examined from video collected in October 2017, 2018, 2019, and in January 2018. Of 289 contact events, calves initiated 65.7% (n =190), of which 82.6% (n = 157) were affiliative; 77.8% (n = 77) of mother-initiated contacts were categorized similarly. Thus, the overall trend for mother-calf contacts was affiliative. Mothers initiated contact with the dorsal fin less often (n = 3), while calves initiated with their dorsal fin more often (n = 40), especially one-year-old (C1) calves (n = 33). The body was used to initiate contact more by three-year-old (C3) calves (n = 47) and less by C1 calves (n = 22). Both results are likely an artifact of the infant position used by calves at different developmental stages. Only two-year-old (C2) calves initiated agonistic contact with their rostrum (n = 4); 75% of these contacts were initiated by one male calf. Mothers used the body to initiate contact with most calf ages, though contact by pectoral fin occurred more often than expected with their C2 calves (n = 11). Since 72.7% of these contacts came from one mother, a specific maternal style may be present. Only one mother used her rostrum with her C3 calf to initiate agonistic contacts; all others used the fluke. Several variables, including individual preference, calf sex, and maternal experience, may explain some of the contact patterns, but a larger sample size is needed to illustrate potential patterns among pairs. Still, these results support the notion that mothercalf dyads share more affiliative than agonistic contacts, expanding our knowledge on the tactile relationships of mother-calf pairs.

Key Words: behavior, mother–calf dyads, tactile contacts, bottlenose dolphins, *Tursiops truncatus*

Introduction

In most social mammals, the relationship between mother and offspring is documented as one of the strongest bonds and includes both affection and conflict (Zahavi, 1977). The details of this relationship have been studied in many species, from primates (e.g., Fitch-Snyder & Ehrlich, 2003; Nakamura & Sakai, 2014; Ross & Lehman, 2016) to marine mammals (e.g., Riedman, 1990; Schusterman et al., 1992; Mann, 2017), focusing on different behaviors to better understand mother-infant interactions. In primates, grooming is an important social behavior used to strengthen bonds (Nakamura & Sakai, 2014) and reduce tension (Schino et al., 1988), especially in larger groups (Dunbar, 1991). Infants groom their mothers at low levels that can fluctuate with age depending on the species (e.g., lorises: Fitch-Snyder & Ehrlich, 2003; and monkeys: Dettmer et al., 2016), but which never occurs more often than the mother grooming the infant (Fitch-Snyder & Ehrlich, 2003). Maternal grooming is also positively correlated with calm and easy interactions within the mother-infant relationship in monkeys (Vandeleest & Capitanio, 2012). Looking at proximity in lorises (i.e., being within 0.3 m without contact), mother-infant closeness can significantly increase with age (Fitch-Snyder & Ehrlich, 2003). In slow lorises (Nycticebus bengalensis), infants both initiate and end closeness more as they get older, while their mothers do not change rates of initiation or termination along the same timeline. Contacts are frequent and necessary in young primates as infants require near constant contact with their mother for a few weeks after being born (Nakamura & Sakai, 2014). Some species continue to maintain high rates of contact, even 9 wks after birth (blue-eyed black lemur [*Eulemur flavifrons*]; Volampeno et al., 2011). Nuances in contact events change as the offspring ages, with infants shifting from infant to adult types of contact and increasing the number of initiations, while mothers initiate fewer contacts (Fitch-Snyder & Ehrlich, 2003; Ross & Lehman, 2016).

Marine mammals also have important motherinfant relationships but are met with a different set of environmental challenges. In some species, such as sea otters (Enhydra lutris) and walruses (Odobenus rosmarus), young use the mother-offspring relationship to learn foraging skills (Mann, 2017). Other pinniped young use the mother as a back-up food supply while they practice independent foraging and social behaviors (Riedman, 1990). During motherpup reunions in California sea lions (Zalophus californianus), pups show an increase in locomotion effort as they age (Schusterman et al., 1992), which suggests they participate in reunion behaviors more as they mature. The increase in pup-initiated participation with age mirrors the shift in proximity maintenance documented in infant primates with their mother (Fitch-Snyder & Ehrlich, 2003; Ross & Lehman, 2016).

In cetaceans, the mother-infant relationship for mysticetes and odontocetes is somewhat different. The nursing period is usually much shorter in mysticetes compared to odontocetes, resulting in a short-term relationship (Mann, 2017). Within this shorter window, dive synchrony can be seen in humpback whales (Megaptera novaeangliae), as well as a shift in control of proximity toward the calf as it gets older (Tyson et al., 2012; Huetz et al., 2022). In contrast, most odontocetes have a longer period of maternal care that typically lasts 2 to 4 y for smaller delphinids (Connor & Smolker, 1985; Wells et al., 1987; Wells, 1991; Mann, 2019) to decades or more for killer whales (Orcinus orca; Bigg et al., 1990; Weiss et al., 2023). Prior to weaning, odontocete calves learn social and foraging behaviors primarily from their mothers (Wells et al., 1987; Mann, 2019) through various interactions that the calf increasingly initiates as it ages, including contacts, play attempts, proximity, and pair swims (belugas [Delphinapterus leucas]: Hill, 2009; Hill et al., 2013, 2015; Hill & Campbell, 2014; Krasnova et al., 2014; killer whales: Guarino et al., 2017). The development and use of pair-swim positions (e.g., echelon and infant position; Noren & Edwards, 2011; Mann, 2019) by mother-calf dyads are thought to provide hydrodynamic and social benefits to the calf (Noren et al., 2008; Noren & Edwards, 2011; Xian et al., 2012) and have received much interest in several species, including eastern spinner dolphins (Stenella longirostris; Weihs, 2004), bottlenose dolphins (Tursiops truncatus; Noren & Edwards, 2011), Yangtze finless porpoises (Neophocaena asiaeorientalis asiaeorientalis; Xian et al., 2012), and narwhals (Monodon *monoceros*; Charry et al., 2018). However, the species receiving the most attention for mother–calf relations is the bottlenose dolphin (*Tursiops* sp.).

Bottlenose dolphins are highly sociable mammals living in fission-fusion societies (Connor et al., 2000; Kogi et al., 2004). Studies focusing on behaviors used in their daily social interactions (i.e., pair-swim position: Noren et al., 2008; Themelin & Dudzinski, 2022; tactile contacts: Harvey, 2015; Dudzinski & Ribic, 2017) to develop and maintain their relationships are numerous (Themelin et al., 2020). The mother-calf relationship has received interest, but more aspects of this relationship need to be explored. Dolphin calves are highly precocious within the first few months of life, though they are still dependent on their mothers for survival (Mann & Smuts, 1999). Understanding their exchanges offers insight into how a young dolphin learns to navigate their social environment. For example, Levengood (2019) showed that the mother-calf relationship offers a foundation for a calf to build future social interactions because the calf shares the mother's friendship and avoidance relationships. Additionally, a better understanding of the complexities of the mother-calf relationship promotes more informed monitoring of calf development in managed care. Swim synchrony and mother-initiated interactions are high early in life, but older calves hold more responsibility in relationship maintenance as controlling maternal behaviors tend to relax (Mann & Smuts, 1999; Hill et al., 2007). Behavioral adjustment to the calf's development can be specific to individual maternal styles, which have been identified in bottlenose dolphins (Hill et al., 2007; Dudzinski et al., 2021b) and belugas (Hill et al., 2013) through each mother's distinct use of certain maternal behaviors such as herding, discipline, and pectoral fin contacts (PFCs). Maternal discipline is an agonistic behavior that can involve a tactile exchange such as tail slaps or calf pinning (Hill et al., 2007); however, aggressive behaviors are not common between mothers and calves and have not been fully studied in more than one or two populations (Scott et al., 2005). Dudzinski et al. (2021a, 2021b) documented variation in use of PFCs between mother-calf pairs compared to non-kin pairs finding the latter exchange significantly more contacts than the former. Still, other contact types, such as melon touches, maternal pushes, or body rubbing, likely represent most tactile exchanges observed between a mother and her offspring (Mann & Smuts, 1999; Nakamura & Sakai, 2014), but studies have not been conducted to understand subtle nuances in mother-calf tactile communication.

To investigate the exchange of all types of contact behavior within mother–calf dyads, we analyzed underwater videos collected as part of a long-term study by the Dolphin Communication Project (DCP) on bottlenose dolphins at the Roatan Institute for Marine Sciences (RIMS) in Roatan, Honduras (the supplemental video for this article is available in the "Supplemental Material" section of the Aquatic Mammals website). We hypothesized that mother-calf pairs use affiliative contact more than agonistic contact. We examined both mothers and calves in the initiator role during tactile exchanges, expecting overall that mothers initiate more contact with their calves than the reverse. However, as calves age from 1- to 3-y-old, we expected them to increase the number of contacts initiated with their mothers. We also investigated whether mothers or calves as initiators use specific body parts to exchange affiliative vs agonistic contacts. For affiliative contacts, we expected younger calves to initiate more pectoral fin-body contacts, specifically because of their use of the echelon position, though we expected older calves to have more body-body contacts because of their use of the infant position. Calves of all ages were expected to initiate agonistic contacts with their fluke more than their rostrum. For mothers as initiators, we expected more bodybody contact with their calves at all ages, whereas for agonistic contacts, mothers were expected to initiate more contact with their rostrums.

Methods

Data for this study were collected as part of an ongoing, long-term study of dolphin relationships and behavior by DCP (e.g., Dudzinski et al., 2010, 2021a, 2021b; Dudzinski & Ribic, 2017; Themelin et al., 2020). The dolphin group resides at the RIMS, Anthony's Key Resort (AKR) in Roatan, Honduras, which granted permission for DCP's longitudinal research.

Study Site and Population

Data were collected during 1-wk visits to the RIMS in October 2017 (n = 1.64 h), 2018 (n = 3.62 h), and 2019 (n = 3.32 h), and in January 2018 (n = 0.51 h), totaling ~9 h of video. This managed care group of common bottlenose dolphins resides in a natural lagoon sea pen with 8,000 m² of surface area adjacent to Bailey's Key on the northwest side of Roatan. Tactile and vocal behaviors expressed by these dolphins mirrored what had been observed in wild groups (e.g., Dudzinski et al., 2010; Dudzinski & Ribic, 2017). The dolphin population was subsampled to focus on five mother–calf pairs (or Mom–Calf), which included calves of three age groups (Table 1).

Table 1. Details of each mother–calf pair, including calf age and time on screen together. C1, C2, and C3 refer to a 1-y, 2-y, and 3-y-old calf, respectively; F = female and M = male.

Mom–Calf dyad	Calf sex	Year	Calf age	Time on screen (s)
Alita–Dory	F	2017*	C2	383
		2018	C3	631
		Total		1,014
Bailey-Tank	М	2017*	C1	494
		2018	C2	319
		2019	C3	776
		Total		1,589
Carmella-Stan**	М	2017*	C2	56
		2018	C3	86
		Total		142
Gracie-Shawn**	М	2017	C2	409
		Total		409
Tilly-Sandy	F	2019	C1	1,931
		Total		1,931

*Data from January 2018 session were included in 2017 because all calves were the same age as in October 2017.

**These dyads were not included in statistical analyses due to lack of data.

Data Collection

Video data were recorded with a mobile video/ acoustic system during opportunistic swims from an underwater perspective following a noninvasive protocol during which the observer did not interact with, touch, or feed the dolphins (Dudzinski et al., 1995, 2009, 2010). Any instances of dolphins being inquisitive of the recorder during data collection were not included in these analyses. Data were collected using a focal animal protocol (Altmann, 1974), and each session lasted from 22.45 to 56.05 min, depending on weather, current, and visibility conditions (Themelin et al., 2020). All contact behaviors between dolphins were coded using BORIS, Version 7.12.2 (Friard & Gamba, 2016), which allowed logging of contact exchanges in sequence using an event sampling protocol (Altmann, 1974; Dudzinski et al., 2009).

Definitions

Definitions of terminology used to describe contact events follow previous studies completed by DCP (Dudzinski et al., 2009, 2010, 2021b; Dudzinski & Ribic, 2017), and specific terms are also briefly explained below. Only contacts between pre-weaned calves and their mothers were included in this study. Calf ages were divided by year: birth to 12 mo were 1-y-olds (C1); 12 to 24 mo were 2-y-olds (C2); and 24 to 36 mo were 3-y-olds (C3). As this is a managed care study group, date of birth was known for all calves (Table 1).

Each physical contact between mothers and their calves was confirmed via direct observation (i.e., contact between bodies had to be observed on the video). Reliability between coders was confirmed at greater than 95%. Each contact event had the following: an initiator, the dolphin who started the contact, and a receiver, the dolphin who started the contact, and a receiver, the dolphin who was contacted (Dudzinski et al., 2009). The contact ended when one dolphin departed, both separated from each other, or the area of contact went out of view (e.g., off the video screen or behind another dolphin).

For both the initiator and receiver, the dolphin body was previously divided into 11 parts (see Dudzinski et al., 2009), which were grouped into affiliative and agonistic exchanges based on initiator's body part without assuming a functional affiliative or agonistic intent (following Themelin et al., 2020). Affiliative body parts included the body (i.e., side, back, face, belly, genitals, and peduncle/keel), pectoral fin, and dorsal fin, whereas agonistic body parts included the rostrum and fluke (Figure 1A). All contacts between each dolphin mother and her calf using any body part were documented.



Figure 1. (A) Dolphin body schematic depicting body parts categorized as agonistic (shaded in) and those categorized as affiliative (unshaded). The body, including the side, back, face, belly, genitals, and peduncle/keel, and the pectoral and dorsal fins comprise the affiliative body parts. The rostrum and fluke are identified as agonistic body parts. (B) Dolphin pair-swim diagrams depicting echelon (left) and infant (right) positions. Both images present a calf in the "calf role," but the mother can assume this position with her calf.

Statistical Analysis

Because of a small sample size for some contacts, descriptive analyses were applied to all five mother-calf pairs to assess general patterns of contact exchange. For the three mother-calf pairs (Alita-Dory, Bailey-Tank, and Tilly-Sandy) with adequate samples, the data were nonparametric and used a repeated measures design for analyses. The statistical tests follow Dudzinski et al. (2021a) by utilizing a chi-square test with a 10,000-simulation approach to determine the significance of the test statistic, with $p \le 0.05$ indicating significance (Rugg, 2003). Standard residuals were used to indicate variables of interest with a critical value of |1.96| or greater (Sharpe, 2015). For larger data tables, adjusted standardized residuals were used to indicate variables of interest, with a critical value of [2,58] or greater. This adjustment accounted for the larger interaction pool by considering row and column marginals in analysis (Sharpe, 2015). The statistical tests were performed using the Real Statistics Resource Pack (Release 7.6, 2013-2021, Charles Zaiontz; www.real-statistics.com) on Excel, Version 16.56.

Results

Overall, the five mother-calf dyads used affiliative contacts 80.1% of the time when all contacts were combined (n = 289; Table 2). Mothers and calves individually initiated affiliative contacts 77.8% (n = 99) and 82.6% (n = 190) of the time, respectively (Table 2). Carmella-Stan and Gracie-Shawn were the two dyads not used for statistical analysis. "Carmella" was not in the camera's viewfinder in January 2018, and Carmella and "Stan" were only on screen together for 56 s (of 98.43 min) in October 2017. Carmella and Stan exchanged five contacts during 86 s of screen time (of 217.48 min) in October 2018, and only one contact in 235 s of screen time (of 198.95 min) in October 2019. "Gracie" and "Shawn" were only present in October 2017 and presented low contact frequency in the video (Table 2).

The chi-square analysis showed a significant interaction between type of affiliative contact and initiator identified (INI ID) as mother or calf (χ^2 (2; n = 215) = 18.39; p = 0.0001). Calves used their dorsal fin more than expected, while mothers used their dorsal fin less. No other significant interactions

 Table 2. Number of contacts (CNT) for each dyad in each calf age observed, separated by initiator (INI) of mother (Mom) or calf. C1, C2, and C3 refer to a 1-y, 2-y, and 3-y-old calf, respectively.

		Affiliative CNT		Agonistic CNT		
Mom–Calf dyad	Calf age	Mom INI	Calf INI	Mom INI	Calf INI	All CNTs
Alita–Dory	C2	9	16	1	3	29
	C3	12	9	6	5	32
	Total	21	25	7	8	61
Bailey-Tank	C1	3	9	0	1	13
	C2	6	8	2	3	19
	C3	21	46	5	0	72
	Total	30	63	7	4	104
Carmella-Stan*	C2	0	0	0	0	0
	C3	1	2	2	0	5
	Total	1	2	2	0	5
Gracie-Shawn*	C2	6	10	4	0	20
	Total	6	10	4	0	20
Tilly-Sandy	C1	19	57	2	21	99
	Total	19	57	2	21	99
Grand Total		77	157	22	33	289

*These dyads were not included in statistical analyses due to lack of data.

	Mom as INI	Calf as INI	$\chi^2(p)$	
Affiliative	70 (-0.05)	145 (0.003)	0.00016 (1)	
Agonistic	16 (0.01)	33 (-0.007)	0.00016(1)	
Body	47 (0.67)	84 (-0.46)		
Dorsal fin	3 (-2.94)	40 (2.04)	18.39 (0.0001)	
Pectoral fin	20 (1.82)	21 (-1.26)		
Rostrum	3 (0.47)	4 (-0.33)	0.20 (0.00)	
Fluke	13 (-0.19)	29 (0.13)	0.39 (0.68)	

Table 3. Interactions of the initiator (INI) identity, mother (Mom) or calf, with type of contact, type of affiliative contact, and type of agonistic contact. Residuals are in parentheses, and chi-square of each group's interaction is listed with the simulated *p* value. Bold numbers indicate significant values for chi-square and critical values for residuals.

Table 4. Interactions between the calf-initiated (INI) contacts separated by calf age with type of contact, type of affiliative contact, and type of agonistic contact. Residuals are in parentheses, and the chi-square of each group's interaction is listed with the simulated p value. Bold numbers indicate significant values for chi-square and critical values for residuals. C1, C2, and C3 refer to a 1-y, 2-y, and 3-y-old calf, respectively.

	C1 as INI	C2 as INI	C3 as INI	$\chi^2(p)$	
Affiliative	66 (-0.67)	24 (-0.09)	55 (0.88)	6.61 (0.04)	
Agonistic	21 (1.41)	6 (0.19)	6 (-1.84)		
Body*	22 (-5.48)	15 (0.50)	47 (5.25)		
Dorsal fin*	33 (5.52)	4 (-1.31)	3 (-4.66)	38.98 (< 0.0001)	
Pectoral fin*	11 (0.68)	5 (0.97)	5 (-1.44)		
Rostrum	0 (-1.63)	4 (3.84)	0 (-0.78)	20.48 (0.0003)	
Fluke	22 (0.61)	2 (-1.43)	5 (0.29)		

*Indicates adjusted residuals were used.

existed for INI ID with type of contact (affiliative vs agonistic) or with type of agonistic contact (rostruminitiated vs fluke-initiated) (Table 3).

Overall, calves across all ages used significantly more affiliative than agonistic contacts (χ^2 (2; n =178) = 6.61; p = 0.035), but no specific age class initiated more contact than expected. The interaction of type of affiliative contact used by the three different calf age classes was significant (χ^2 (4; n = 145) = 38.98; p < 0.0001). C1 calves used more dorsal fin contacts than expected but fewer body contacts. C3 calves showed the opposite, using more body contacts than expected and fewer dorsal fin contacts. The interaction of type of agonistic contact varied among age classes (χ^2 (2; n = 33) = 20.48; p= 0.0003). The only notable value was for C2 calves using their rostrum more than expected (Table 4).

There was no significant interaction of affiliative vs agonistic contacts used by mothers in the INI role as their calves aged, but mothers used affiliative contacts 81.4% (n = 86) of the time. The type of affiliative contact used by mothers associated significantly with the age of the calf (χ^2 (4; n = 70) = 22.64; p = 0.0001). Mothers used body contacts less than expected but pectoral fin contacts more than expected when the calf was C2. These trends reversed when the calf was C3, with mothers using more body contacts than expected (Table 5). There was no significant interaction for the type of agonistic contact used by mothers as calves aged. However, 68.8% of the mother's agonistic contacts were toward C3 calves, which was the only calf age for which mothers used the rostrum to initiate contact.

and C3 refer to a 1-y, 2-y, and 3-y-old calf, respectively. Mom INI C1 Mom INI C2 Mom INI C3 $\chi^2(p)$ Affiliative 22 (0.56) 15 (0.09) 33 (-0.47) 2.91 (0.23) Agonistic 2(-1.17)3 (-0.19) 11 (0.98) Body* 17 (1.22) 3 (-4.39) 27 (2.63) Dorsal fin* 2(1.34)1 (0.51) 0 (-1.67) 22.64 (0.0001) Pectoral fin* 3 (-1.87) 11 (4.33) 6 (-1.82) Rostrum 0 (-0.61) 0 (-0.75) 3 (0.65) 1.68 (0.71) Fluke 2 (0.29) 3 (0.36) 8 (-0.31)

Table 5. Interactions between the mother-initiated (INI) contacts separated by calf age with type of contact, type of affiliative contact, and type of agonistic contact. Residuals are in parentheses, and the chi-square of each group's interaction is listed with the simulated p value. Bold numbers indicate significant values for chi-square and critical values for residuals. C1, C2, and C3 refer to a 1-y, 2-y, and 3-y-old calf, respectively.

*Indicates adjusted residuals were used.

Discussion

Affiliative contacts were the most common type of contact initiated by both mothers and calves as expected; however, these calves initiated more contacts than their mothers, contrary to what was predicted. During the nursing period, calves develop individual preferences and social skills (Krzyszczyk et al., 2017) while gradually improving their motor coordination (Mann & Smuts, 1999), so they may be less selective and "wigglier" when initiating contact with their mother. Alternatively, Mann & Smuts (1999) suggested that calves may be required to learn how to initiate reunions with their mothers early in their lives because foraging activities in natural environments necessitate frequent separations from the calf. Younger calves may initiate contacts regularly to communicate with their mothers as they learn other behaviors. There was limited significance between either initiator (whether mother or calf) and types of agonistic contact, which correlates with the lack of agonistic behaviors that have been reported between mothers and their calves (Scott et al., 2005). Still, agonistic contact, as defined in this study, did not assume intent; aggressive behaviors are dependent on the context of the interaction, including body posture and swim position (Dudzinski et al., 2009).

Across all five calves, no clear pattern was demonstrated regarding an increase or decrease in the number of contacts initiated by the calves as they aged. However, one calf, "Tank," did increase the number of contacts he initiated with "Bailey" as he aged from a 1-y-old (C1; n = 10) to a 3-y-old (C3; n = 46). Tank's pattern of increasing contact initiation followed the general trend of mother–infant behavior where initiation responsibility tends to shift from mother to older infant (e.g., Mann & Smuts, 1999; Fitch-Snyder & Ehrlich, 2003; Tyson et al., 2012; Ross & Lehman, 2016; Huetz et al., 2022). As Tank was the only calf in this study with data across all three pre-weaning years, more data across all ages on a greater number of calves is needed to know if this pattern generally persists or is an individual preference. Only 2-y-old (C2) calves used their rostrum to initiate agonistic contact, with Tank contributing most of these contacts, a possible further indication of preference. However, Tank was the only male calf analyzed statistically so this finding could suggest that male calves use their rostrum more than their fluke for agonistic contact.

Although the low sample size prevented sex comparison in this study, Krzyszczyk et al. (2017) found significant differences between calves of different sexes in the amount of time spent in rest and socializing, similar to beluga calves of opposite sex who spend differing amounts of time swimming with their mother (Hill et al., 2013). Furthermore, calves of opposite sex spend different amounts of time in groups with nonmothers (Gibson & Mann, 2008), which likely causes differences in the time spent with the mother. These differences in sociality between sexes may be further shown through tactile events between mothers and calves. For instance, male and female calves differed in how they initiated PFCs with their mothers compared to other dolphins (Dudzinski et al., 2021a), which extended to maternal brothers and sisters initiating PFCs differently with their shared mother (Dudzinski et al., 2021b). Having a larger sample size that includes more male and female calves may help elucidate any contact patterns regarding sex or individual preferences in calves.

When all calf age classes were combined, the dorsal fin was used more by calves and less by mothers when initiating contact with each other. These differences may be an artifact of the calf often occupying infant position when swimming with the mother (Noren & Edwards, 2011; Mann, 2019). Infant position places the calf below the mother's mammary and genital area which is convenient for nursing and offers hydrodynamic benefits to the calf (Noren & Edwards, 2011; Mann, 2019). In this position, a calf's dorsal fin could both purposely and inadvertently make contact with its mother's ventral body, although intent cannot be confirmed. Younger calves especially show this pattern in using the dorsal fin more than older calves, such as "Sandy," who contributed 77.5% (n = 31) of all calf-initiated dorsal fin contacts and was often seen in infant position despite being about a month old (DCP, unpub. data, 2019). At that age, and up to approximately 2 to 3 mo of age, calves are expected to use the echelon position predominantly (Noren et al., 2008), but an alternative hypothesis proposed that infant position has important social benefits that outweigh the higher hydrodynamic benefits of the echelon position (Weihs, 2004; Noren & Edwards, 2011). The high importance of socializing early in the group (e.g., Krzyszczyk et al., 2017) may encourage advanced use of infant position. Examining more closely the use of this position in younger calves will help indicate if this trend exists within the population or is an individual preference. In contrast, when older calves are in infant position, it places their melon under the mother's genitals and their dorsal fin further back due to longer body size. This shift in body positioning may be the reason older calves (C3) initiated body contacts more than younger calves (C1). These body contacts may also have a functional purpose as calves often bump their melons into the mother's mammary glands prior to nursing (Dudzinski, 1998; Mann, 2019). More detail on exact positioning, receiving body parts involved during contact, and behaviors following this action (e.g., nursing) should be examined to support possible function in pre-weaned calves.

Older calves in infant position could also explain the higher amount of fluke contacts initiated by the mother. The slight increase in fluke contacts from younger to older calves would support this explanation; the calf is growing longer and positioned more directly below the fluke, resulting in contact during swimming (see Themelin & Dudzinski, 2022). Conversely, mothers swimming below their calf (the "calf role" of infant position; see Figure 1B) may account for the high amount of fluke contacts initiated by calves, especially younger individuals. The gradual improvement of motor coordination with age may have led to fewer fluke contacts in older calves (Mann & Smuts, 1999). A closer look into the swim position of mothers and calves during contact events may help explain certain tactile patterns within this relationship.

Though maternal style was not analyzed in this study, each observed adult female initiated contact with her calf somewhat differently relative to the others-for example, "Tilly" initiated 21 contacts with Sandy as a C1 calf, while Bailey initiated three contacts with her C1 calf, Tank (Table 2). These findings support the notion that individual maternal styles may impact the tendency for mothers to initiate physical contact with their calves (Hill et al., 2007; Dudzinski et al., 2021b). Across all calf ages, mothers mostly initiated contact with their body, except with C2 calves for which PFCs were the most common contact, with "Alita" initiating most of these contacts. Previously, Dudzinski et al. (2021b) categorized Alita in the "high PFC initiating group" compared to other mothers to differentiate her maternal style from others. Still, Alita did not consistently use PFCs with her calf, "Dory," across all of Dory's pre-weaned ages, indicating Alita might adjust her behavior based on calf development (Hill et al., 2007). While most mothers used their fluke for agonistic contacts, Alita was the only mother to use her rostrum with her calf, which could be another aspect of her maternal style. For motherinitiated contacts with C3 calves, Bailey initiated most of the observed body contacts with her calf, Tank, which might reflect her maternal style (Dudzinski et al., 2021b) or her individual preference for contact (Dudzinski & Ribic, 2017). Contact exchanges could be linked to the different types of swim positions used (i.e., infant or echelon) by the dyad, but both contact and swim positions could be an expression of maternal style. To identify potential patterns, and to better understand what was observed in our study, more data are needed on a greater number of females.

Overall, our results show frequent affiliative tactile exchanges between mothers and calves. Calves initiated more contacts than moms at all ages in their within-dyad exchanges, but calves did not increase their initiated contacts as they aged from 1- to 2- to 3-y-old with their mother. This suggests that calves take their social cues from their mothers as was reported by Levengood (2019) for wild Indo-Pacific bottlenose dolphin (Tursiops aduncus) calves who shared social friendships and avoidances with their moms. Alternatively, swim position of the calf was likely a factor in the observed contacts between mother and calf; the unexpected observation of infant position within the first month of life may have contributed to body parts (melon and dorsal fin) used by both calf and mother for tactile exchanges. Thus, the neonate (< 30 d) might be considered a fourth pre-weaned calf age to examine when assessing how contact between mother–calf dyads evolves as a calf develops.

Mothers were expected to use their bodies more than extremities to initiate contact with their calves; however, when observed exchanges deviated from the expected, it was related usually to individual variability (i.e., maternal style). For example, Alita primarily used her pectoral fin when initiating contact with Dory. Maternal style likely influences how contacts are initiated by the mother and, subsequently, the calf (see Hill et al., 2007; Levengood, 2019). Reproductive state regarding parity (Hill et al., 2007; Dudzinski et al., 2021b) and alloparenting experience (Riedman, 1982; Mann & Smuts, 1998; Dudzinski et al., 2022) of the mother may affect her maternal style and the use of contacts with her calf. These details on tactile exchanges offer a better understanding of the mother-calf relationship in a noninvasive manner that can be applied to observations of calf development. Moving forward, more details within the contact events, such as departing dolphin and receiver response, should be considered to accurately monitor the progression of these relationships. More data are already being analyzed, adding more mother-calf dyads, with calves observed during the full pre-weaned period. The ongoing analysis will allow exploration of contact exchanges between mothers and calves in greater detail to gain a better understanding of this particular relationship.

Note: The supplemental video for this article is available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10 &Itemid=147.

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Literature Cited

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227-267. https://doi. org/10.1163/156853974X00534
- Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb III, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. *Reports of the International Whaling Commission*, 12, 383-405.
- Charry, B., Marcoux, M., & Humphries, M. M. (2018). Aerial photographic identification of narwhal (*Monodon monoceros*) newborns and their spatial proximity to the nearest adult female. *Arctic Science*, 4, 513-524. https:// doi.org/10.1139/as-2017-0051
- Connor, R. C., & Smolker, R. A. (1985). Habituated dolphins (*Tursiops* sp.) in Western Australia. *Journal of Mammalogy*, 66(2), 398-400. https://doi.org/10.2307/1381260
- Connor, R. C., Wells, R., Mann, J., & Read, A. (2000). The bottlenose dolphins: Social relationships in a fissionfusion society. In J. Mann, R. C. Connor, P. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of whales and dolphins* (pp. 91-126). University of Chicago Press.
- Dettmer, A. M., Kaburu, S. S. K., Byers, K. L., Murphy, A. M., Soneson, E., Woodell, L. J., & Suomi, S. J. (2016). First-time rhesus monkey mothers, and mothers of sons, preferentially engage in face-to-face interactions with their infants. *American Journal of Primatology*, 78, 238-246. https://doi.org/10.1002/ajp.22503
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). Aquatic Mammals, 24(3), 129-142.
- Dudzinski, K. M., & Ribic, C. A. (2017). Pectoral fin contact as a mechanism for social bonding among dolphins. *Animal Behavior and Cognition*, 4(1), 30-48. https://doi. org/10.12966/abc.03.02.2017
- Dudzinski, K. M., Clark, C. W., & Würsig, B. (1995). A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals*, 21(2), 187-193.
- Dudzinski, K. M., Gregg, J. D., Paulos, R. D., & Kuczaj II, S. A. (2010). A comparison of pectoral fin contact behaviour for three distinct dolphin populations. *Behavioural Processes*, 84(2), 559-567. https:// doi.org/10.1016/j.beproc.2010.02.013

- Dudzinski, K. M., Gregg, J. D., Ribic, C. A., & Kuczaj II, S. A. (2009). A comparison of pectoral fin contact between two different wild dolphin populations. *Behavioural Processes*, 80(2), 182-190. https://doi. org/10.1016/j.beproc.2008.11.011
- Dudzinski, K. M., Ribic, C. A., Manitzas Hill, H. M., & Bolton, T. T. (2021a). Bottlenose dolphin calf initiated pectoral fin contact exchanges with mother, other kin, and non-kin. *Animal Behavior and Cognition*, 8(3), 376-390. https://doi.org/10.26451/abc.08.03.04.2021
- Dudzinski, K. M., Ribic, C. A., Manitzas Hill, H. M., & Bolton, T. T. (2021b). Evidence for maternal style among adult female dolphins when sharing pectoral fin contacts with their calves. *Animal Behavior and Cognition*, 8(1), 52-68. https://doi.org/10.26451/abc.08.01.05.2021
- Dudzinski, K. M., Themelin, M., Manitzas Hill, H. M., & Bolton, T. T. (2022). Allomaternal care and allonursing behaviors by a primiparous bottlenose dolphin. *Aquatic Mammals*, 48(6), 536-540. https://doi.org/10.1578/AM. 48.6.2022.536
- Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57, 121-131. https://doi.org/10.1159/000156574
- Fitch-Snyder, H., & Ehrlich, A. (2003). Mother-infant interactions in slow lorises (*Nycticebus bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). Folia Primatologica, 74, 259-271. https://doi.org/10.1159/000073313
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution, 7(11), 1325-1330. https://doi.org/10.1111/2041-210X.12584
- Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour*, 76, 375-387. https://doi.org/10.1016/j.anbehav.2008.01.021
- Guarino, S., Hill, H. M., & Sigman, J. (2017). Development of sociality and emergence of independence in a killer whale (*Orcinus orca*) calf from birth to 36 months. *Zoo Biology*, 36, 11-20. https://doi.org/10.1002/zoo.21338
- Harvey, B. N. (2015). The nature of social relationships in bottlenose dolphins (Tursiops truncatus): Associations and the role of affiliative, agonistic, and socio-sexual behaviors (Unpub. master's thesis). University of Southern Mississippi, Hattiesburg.
- Hill, H. M. (2009). The behavioral development of two beluga calves during the first year of life. *International Journal of Comparative Psychology*, 22, 234-253. https:// doi.org/10.46867/IJCP.2009.22.04.02
- Hill, H. M., & Campbell, C. (2014). The frequency and nature of allocare by a group of belugas (*Delphinapterus leucas*) in human care. *International Journal of Comparative Psychology*, 27(4), 501-514. https://doi.org/10.46867/ijcp.2014.27.04.08
- Hill, H. M., Campbell, C., Dalton, L., & Osborn, S. (2013). The first year of behavioral development and maternal care of beluga (*Delphinapterus leucas*) calves in human

care. Zoo Biology, 32, 565-570. https://doi.org/10.1002/ zoo.21093

- Hill, H. M., Greer, T., Solangi, M., & Kuczaj II, S. A. (2007). All mothers are not the same: Maternal styles in captive bottlenose dolphins. *International Journal* of Comparative Psychology, 20(1), 34-53. https://doi. org/10.46867/IJCP.2007.20.01.03
- Hill, H. M., Guarino, S., Crandall, S., Lenhart, E., & Dietrich, S. (2015). Young belugas diversify adult beluga (*Delphinapterus leucas*) behavior. *Animal Behavior and Cognition*, 2(3), 267-284. https://doi.org/10.12966/abc. 08.06.2015
- Huetz, C., Saloma, A., Adam, O., Adrianarimisa, A., & Charrier, I. (2022). Ontogeny and synchrony of diving behavior in humpback whale mothers and calves on their breeding ground. *Journal of Mammalogy*, 103(3), 576-585. https://doi.org/10.1093/jmammal/gyac010
- Kogi, K., Hishi, T., Imamura, A., Iwatani, T., & Dudzinski, K. M. (2004). Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science*, 20, 510-526. https://doi.org/10.1111/j.1748-7692.2004.tb01176.x
- Krasnova, V. V., Chernetsky, A. D., Zheludkova, A. I., & Bel'kovich, V. M. (2014). Parental behavior of the beluga whale (*Delphinapterus leucas*) in natural environment. *Biology Bulletin*, 44(4), 349-356. https://doi. org/10.1134/S1062359014040062
- Krzyszczyk, E., Patterson, E. M., Stanton, M. A., & Mann, J. (2017). The transition to independence: Sex differences in social and behavioural development of wild bottlenose dolphins. *Animal Behavior*, 129, 43-59. https://doi. org/10.1016/j.anbehav.2017.04.011
- Levengood, A. L. (2019). *The evolution of long-term social avoidances in a long-lived mammal* (Unpub. doctoral thesis). University of the Sunshine Coast, Sippy Downs, Queensland, Australia.
- Mann, J. (2017). Parental behavior. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 686-691). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00191-6
- Mann, J. (2019). Maternal care and offspring development in odontocetes. In B. Würsig (Ed.), *Ethology and behavioral ecology of odontocetes* (pp. 95-116). Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-030-16663-2_5
- Mann, J., & Smuts, B. (1998). Natal attraction: Allomaternal care and mother–infant separations in wild bottlenose dolphins. *Animal Behaviour*, 55(5), 1097-1113. https:// doi.org/10.1006/anbe.1997.0637
- Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, 136(5), 529-566. https://doi.org/10. 1163/156853999501469
- Nakamura, J., & Sakai, M. (2014). Social touch in apes and dolphins. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans: Field research and conservation* of complex mammalian societies (pp. 355-383). Springer Japan. https://doi.org/10.1007/978-4-431-54523-1_19

- Noren, S. R., & Edwards, E. F. (2011). Infant position in mother-calf dolphin pairs: Formation locomotion with hydrodynamic benefits. *Marine Ecology Progress Series*, 424, 229-236. https://doi.org/10.3354/meps08986
- Noren, S. R., Biedenbach, G. H., Redfern, J. V., & Edwards, E. F. (2008). Hitching a ride: The formation locomotion strategy of dolphin calves. *Functional Ecology*, 22(2), 278-283. https://doi.org/10.1111/j.1365-2435.2007.01353.x
- Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review* of Biology, 57, 405-435. https://doi.org/10.1086/412936
- Riedman, M. (1990). The pinnipeds: Seals, sea lions and walruses. University of California Press, Los Angeles. https://doi.org/10.1525/9780520320086
- Ross, A. C., & Lehman, S. M. (2016). Infant transport and mother–infant contact from 1 to 26 weeks postnatal in Coquerel's sifaka (*Propithecus coquereli*) in northwestern Madagascar. *American Journal of Primatology*, 78, 646-658. https://doi.org/10.1002/ajp.22529
- Rugg, D. (2003). TableSim—A program for analysis of small-sample categorical data (General Technical Report NC-232). U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN. https://doi. org/10.2737/NC-GTR-232
- Schino, G., Aureli, F., & Troisi, A. (1988). Equivalence between measures of allogrooming: An empirical comparison in three species of macaques. *Folia Primatologica*, 51, 214-219. https://doi.org/10.1159/000156374
- Schusterman, R. J., Hangii, E. B., & Gisiner, R. (1992). Acoustic signaling in mother-pup reunions, interspecies bonding, and affiliation by kinship in California sea lions (*Zalophus californianus*). In J. A. Thomas, R. A. Kastelein, & A. Ya. Supin (Eds.), *Marine mammal* sensory systems (pp. 533-551). Plenum Press. https:// doi.org/10.1007/978-1-4615-3406-8_34
- Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L., & Connor, R. C. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behavior. *Behaviour*, 142(1), 21-44. https:// doi.org/10.1163/1568539053627712
- Sharpe, D. (2015). Your chi-square test is statistically significant: Now what? *Practical Assessment, Research & Evaluation*, 20. https://doi.org/10.7275/tbfa-x148
- Themelin, M., & Dudzinski, K. M. (2022, August). Exploring bottlenose dolphins pair swimming position patterns in non-mother/calf dyads. *Proceedings of the 24th Biennial Conference on the Biology of Marine Mammals*, West Palm Beach, FL.

- Themelin, M., Ribic, C. A., Melillo-Sweeting, K., & Dudzinski, K. M. (2020). A new approach to the study of relationship quality in dolphins: Framework and preliminary results. *Behavioural Processes*, 181, 104260. https://doi.org/10.1016/j.beproc.2020.104260
- Tyson, R. B., Friedlaender, A. S., Ware, C., Stimpert, A. K., & Nowacek, D. P. (2012). Synchronous mother and calf foraging behaviour in humpback whales *Megaptera novaeangliae*: Insights from multi-sensor suction cup tags. *Marine Ecology Progress Series*, 407, 209-220. https://doi. org/10.3354/meps09708
- Vandeleest, J. J., & Capitanio, J. P. (2012). Birth timing and behavioral responsiveness predict individual differences in the mother–infant relationship and infant behavior during weaning and maternal breeding. *American Journal of Primatology*, 74, 734-746. https:// doi.org/10.1002/ajp.22024
- Volampeno, M. S. N., Masters, J. C., & Downs, C. T. (2011). Life history traits, maternal behavior and infant development of blue-eyed black lemurs (*Eulemur flavifrons*). American Journal of Primatology, 73, 474-484. https://doi.org/10.1002/ajp.20925
- Weihs, D. (2004). The hydrodynamics of dolphin drafting. *Journal of Biology*, 3(2), 8. https://doi.org/10.1186/ jbiol2
- Weiss, M. N., Ellis, S., Franks, D. W., Nielson, M. L. K., Cant, M. A., Johnstone, R. A., Ellifrit, D. K., Balcomb III, K. C., & Croft, D. P. (2023). Costly lifetime maternal investment in killer whales. *Current Biology*, 33, 1-5. https://doi. org/10.1016/j.cub.2022.12.057
- Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin* societies: Discoveries and puzzles (pp. 199-225). University of California Press, Berkeley.
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy* (Vol. 1, pp. 247-305). Plenum Press. https://doi.org/10.1007/978-1-4757-9909-5_7
- Xian, Y., Wang, K., Jiang, W., Zheng, B., & Wang, B. (2012). The development of spatial positions between mother and calf of Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) maintained in captive and seminatural environments. *Aquatic Mammals*, 38(2), 127-135. https://doi.org/10.1578/AM.38.2.2012.127
- Zahavi, A. (1977). The testing of a bond. Animal Behaviour, 25, 246-247. https://doi.org/10.1016/0003-3472(77)90089-6