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All Mothers are Not the Same: Maternal Styles in Bottlenose Dolphins (*Tursiops truncatus*)

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A dolphin calf's relationship with its mother is crucial for its survival and may be affected by the mother's preferred mode of interacting with her calf. Mothers from a variety of species exhibit individual differences and stable maternal styles. However, little is known about individual differences in the maternal behaviors of dolphins. We investigated the possibility of maternal styles in dolphins by identifying specific maternal care behaviors in 7 dolphin mothers at two facilities during the first year of each calf's life. The mothers exhibited different patterns of behavior including proximity maintenance, discipline, and initiation of separations and reunions with calves. These patterns of maternal behaviors suggest that dolphin mothers display a range of maternal styles that appear to be differentiated by level of maternal control. Moreover, a mother may also modify her individual style as her calf matures and as the social context changes.

The ability to rear one's offspring successfully to independence is influenced by a number of variables (Clutton-Brock, 1991). Food availability, the current physical environment, risk of predation, social ranking, reproductive status, age of the offspring, and previous maternal experience have all been shown to influence offspring care and survival in a variety of species including brown bears (*Ursus arctos*, Dahle & Swenson, 2003), dolphins (*Stenella frontalis*, *Tursiops* spp., Cornell, Asper, Antrim, Searles, Young, & Goff 1987; Delgado-Estrella & Romero-Tenorio, 2006; Mann & Smuts, 1998; Mann & Watson-Capps, 2005; Miles & Herzing, 2003), guinea pigs (*Cavia aperea f. porcellus*, Albers, Timmermans, & Vossen, 1999a, 1999b), pigs (*Suidae* spp., Herskin, Jensen, & Thodberg, 1998), and many species of primates (Altmann, 1980; Bard, 2002; Fairbanks, 1996; Maestripieri, 1998, 2001; Rogers & Davenport, 1970; Suomi, 1999).

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Clearly, the task of caring for one's offspring is difficult and there are many potential hazards for both mother and offspring. The task is even more daunting for mothers that care for their offspring over extended periods of time as they repeatedly encounter many different obstacles to the survival of themselves and their offspring.

Mother-offspring interactions include a wide range of behaviors such as feeding, protection, exploration, play, and nurturing. It is clear that all mothers do not respond identically while interacting with their offspring. For example, guinea pig mothers reliably differ from one another in terms of locomotor, affiliative, or aggressive behaviors display (Albers et al., 1999a, 1999b). It is also clear that these individual differences in maternal responses also influence later offspring behavior. For example, rat dams (*Rattus* spp.) displayed consistent individual differences in their rates of anogenital licking towards their offspring (for a review, see Fleming & Li, 2002). Mothers that display greater amounts of anogenital licking produce pups that are more curious and less fearful of novel situations than mothers who displayed lower amounts of anogenital licking. Similarly, the maternal behaviors (e.g., activity level and amount of rooting before changing positions) of sows differ between individuals, which directly affect piglet mortality and care (Spinka, Illmann, de Jonge, Andersson, Schuurman, & Jensen, 2000; Valros, Rundgren, Spinka, Saloniemi, & Algers, 2003). Research with many primates has further demonstrated the importance of maternal competence in rearing an infant successfully. The mother's own rearing conditions (e.g., isolated, peer-reared, or mother-reared), previous experience with infants, environmental conditions, and maternal personality characteristics impact the ability of individual primate mothers to rear their infants to independence (Bard, 2002; Bloomsmith, Kuhar, Baker, Lambeth, Brent, Ross, & Fritz, 2003; Fairbanks, 1996; Rogers & Davenport, 1970; Suomi, 1999).

Consistent individual differences in maternal care, exhibited by mothers during interactions with their offspring, have been termed maternal styles (e.g., Hrdy, 2004; Maestripieri, 1998; Mandara, 2003). Maternal style typically falls along a continuum that is characterized by the extent to which the mother nurtures, protects, and allows her young to explore their world (see Bard, 2002; Fairbanks, 1996, for reviews). In many primate species, maternal protectiveness involves nurturing behaviors that promote contact with infants, including maternal initiation of contact with her infant, physical restraint of the infant when it attempts to leave, and the inspection or grooming of the infant. Maternal permissiveness is characterized by the degree of freedom granted to the infant. For example, permissive mothers are more likely to allow their infants to explore their environment (Altman, 1980; Fairbanks, 1996). In contrast, restrictive mothers actively prevent the infant from exploring and leaving the mother's vicinity. Maternal rejection occurs when a mother aggressively prevents her infant from nursing and making contact with her. Although most primate mothers use all of these behaviors at some point during their infant's development, maternal style reflects the extent to which certain types of behaviors characterize a mother's interaction with her infant. Extreme maternal styles, characterized by overly permissive, restrictive, or rejecting mothers, are likely maladaptive and are rare as they fail to promote survival and independence (Altman, 1980; Fairbanks, 1996). Thus, moderate maternal styles

occur more frequently within primate species (Altman, 1980; Fairbanks, 1996; Fleming & Li, 2002).

In nonhuman primates, maternal styles have been documented formally in rhesus monkeys (*Macaca mulatta*, Berman, 1990; Hinde & Simpson, 1975; Hinde & Spencer-Booth, 1967; Suomi, 1999), vervet monkeys (*Cercopithecus aethiops*, Fairbanks & McGuire, 1987), pigtail macaques (*Macaca nemestrina*, Maestriperi, 1998, 2001), yellow baboons (*Papio cynocephalus*, Altmann, 1980), and chimpanzees (*Pan paniscus*, *Pan troglodytes*, De Lathouwers & Van Elsacker, 2004). Other non-primate species proposed to display maternal styles include red-necked wallabies (*Macropus rufogriseus*, as reviewed in Higgenbottom & Croft, 1999) eastern grey kangaroos (*Macropus giganteus*, as reviewed in Higgenbottom & Croft, 1999), African elephants (Lee, 1983; Lee & Moss, 1986, 1999), and dolphins (Cockcroft & Ross, 1990; dos Santos & Lacerda, 1987; Mann & Smuts, 1998, 1999). Anecdotally, mothers of these species have been observed to exhibit individual differences in their care of offspring.

For example, previous studies with dolphin mothers, both in their natural habitat and in the care of humans, have suggested that mothers discipline their calves differently (Cockcroft & Ross, 1990; dos Santos & Lacerda, 1987; Mann & Smuts, 1998, 1999). Dolphin mothers also have been documented to display individual differences in their reactions to voluntary and involuntary separations from their calves (Mann & Smuts, 1998; McBride & Kritzler, 1951; McCowan & Reiss, 1995; Sayigh, Tyack, Wells, & Scott, 1990; Smolker, Mann, & Smuts, 1993). These observations, the extended length of offspring care, and their complex social structures and interactions suggest that dolphins may also exhibit maternal styles.

Characterized by interbirth intervals of two to six years (Wells, Scott, & Irvine, 1987), bottlenose dolphin (*Tursiops truncatus*) mothers care for their offspring for the first three to four years of life (Connor, Wells, Mann, & Read, 2000; Mann, Connor, Barre, & Heithaus, 2000; Smolker, Richards, Connor, & Pepper, 1992; Wells & Scott, 1999). During these years, mothers nurse, protect, play with, maintain proximity to, and discipline their calves. Similar to many ungulates and unlike many of their primate counterparts, dolphin calves immediately swim and follow their mothers at birth. This precociousness enables the calves to initiate separations from their mothers at any time, immediately following birth, and highlights the importance of proximity maintenance in the mother-calf relationship.

Dolphin mothers initiate the majority of the mother-calf interactions at the beginning and during the first year of a calf's life, including retrieving a calf that has strayed, guiding a calf away from a danger, or protecting the calf from others (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1998, 1999; Reid, Mann, Weiner, & Hecker, 1995; Smolker et al., 1992). As the calves develop and their behavioral repertoire becomes larger and more diverse, they begin to venture further from their mothers and spend less time with them (*Tursiops truncatus*, Cockcroft & Ross, 1990; Gubbins et al., 1999; Mann & Watson-Capps, 2005; *Stenella frontalis*, Herzing & Brunnick, 1997; Miles & Herzing, 2003). By the end of the first year of life, the calves initiate the majority of the mother-calf interactions (*Tursiops* spp., Mann & Watson-Capps, 2005; Mann & Smuts, 1998, 1999; Reid et al., 1995; *Stenella frontalis*, Miles & Herzing, 2003). Even as they increase their independence, calves frequently return

to their mothers in times of stress or fatigue (Cockcroft & Ross, 1990; Gubbins, et al., 1999; Tavalga & Essapian, 1957).

Despite our knowledge of individual maternal care activities and certain developmental trends, little research has been conducted on the existence of systematic individual differences in bottlenose dolphin mothers. The current study attempted to investigate two issues associated with dolphin maternal care. First, we wished to confirm the types and distributions of maternal care behaviors over the first year of life for dolphins in human care. As suggested by previous research, dolphin mothers were expected to change patterns of maternal care behavior as their calves developed. Second, we attempted to address the question of systematic individual differences in maternal care in an effort to identify stable maternal styles in bottlenose dolphins. Consistent individual differences in maternal care were expected, based on anecdotal reports of differing maternal responses by dolphins (Cockcroft & Ross, 1990; dos Santos & Lacerda, 1987; Mann & Smuts, 1998, 1999; McBride & Kritzler, 1951; McCowan & Reiss, 1995; Sayigh et al., 1990; Smolker et al., 1993). Finally, we were interested in the stability of maternal styles during the first year of a calf's life. It seemed possible that maternal styles might change as a calf matured, with mothers exhibiting more protective styles when calves were more vulnerable.

Method

Subjects

Seven mother-calf pairs of bottlenose dolphins (*Tursiops* spp.) in the care of humans were observed for the present study between June 1997 and October 2002. All mothers were collected within their natural habitat and had been in the care of humans for at least 10 years. None of the mothers were genetically related to one another.

Facilities

The mother-calf pairs were located at two facilities. Four pairs were housed at Marine Life Oceanarium (MLO) in Gulfport, Mississippi. The three remaining pairs were housed at the Marine Mammal Program (MMP) in San Diego, California.

MLO. Primarily an entertainment facility in which dolphins performed daily shows, MLO housed four mother-calf pairs and one adult male in a relatively stable social group. The facility was a multi-level, free-standing, concrete circular pool approximately 90 ft (27.30 m) in diameter and 25 ft (7.59 m) in depth. Although time of day, cloud layer, and the observer's location (i.e., top of pool, middle level, or bottom level) affected water clarity, the animals were generally visible 10 to 20 ft (3.04 to 6.07 m) from the observer's location. During the period of these observations (June 1997 to March 2000), the social group remained relatively stable. The only major change in the social group occurred approximately four months after the birth of the first calf when one adult female and four juvenile dolphins were relocated to a different pool. The remaining dolphins ultimately included one adult male and the four females and their calves.

MMP. Located in San Diego Bay, MMP was a training and research marine mammal facility. This facility consisted of a network of free-floating bay enclosures. The enclosures ranged in size from 30 ft by 30 ft (9.10 m by 9.10 m) to 60 ft by 60 ft (18.20 m by 18.20 m), depending on access. Due to tidal fluctuations, enclosure depth ranged from approximately 15 ft to 20 ft (4.55 m to 6.07 m) with water clarity between 3 ft (about 1 m, poor visibility) and 10 ft (3.04 m, excellent visibility). Mother-calf pairs were often grouped with each other during the period of these observations (June 2001 to October 2002). However, they were observed in a number of social groupings, including all three pairs together, groups of two pairs, or as individual pairs. Additionally, other adult females were occasionally housed with the mother-calf pairs.

Procedure

Data were collected for the first year of life for each mother-calf pair using a combination of several approaches: continuous behavior recording, instantaneous scan sampling for groups, and point sampling for individuals (Altmann, 1974/1996; Mann, 2000; Martin & Bateson, 1993).

MLO. Data used in this study were a subset of data that were collected as part of a longitudinal behavioral development study of bottlenose dolphins in human care. A number of different observers ($n = 17$) assisted with the data collection procedure during the three-year period encompassed by this portion of the study. All observers were trained by the first author. Training consisted of an in-depth review of the animals and their characteristics, a list of behaviors and their operational definitions, and the recording protocols. After the initial instructional sessions (one to two sessions), each observer participated in three to five additional sessions with the trainer, identifying animals and behaviors and practicing recording techniques. The observers collected data after demonstrating their knowledge of animal characteristics and behaviors.

Approximately 300 hours of observations were conducted at MLO using 30-minute sessions. All observations were conducted during daylight hours (i.e., between 7:00 a.m. and 6:00 p.m., depending on seasonal changes). Two restrictions were placed on the data collection procedure: (1) observations had to be completed 15 minutes before a show began, and (2) observations could not be started less than 20 minutes after a show ended. The periods before, during, and after shows contained many situation-specific behaviors and so including such periods in our observations would have biased the results. For example, immediately before a show, the dolphins engaged in more orientation and object search behaviors in preparation for the trainers' arrivals. After the show, the dolphins engaged in stereotyped behavior with miniature basketballs, which were always given to them at the end of a show.

Data were collected using a continuous behavior recording method in a written format. Observers recorded as many of the dolphins' behaviors as possible, including time, animals, sequences of events, duration of various behaviors, initiations and terminations, and any rare events. The written observations were later coded for frequency of individual behaviors.

MMP. As part of our ongoing longitudinal study of dolphin behavioral development, we began collecting data at MMP. For the current study, data were collected for a year and a half by a number of trained observers ($n = 30$). All observers at MMP were also trained by the first author using the same training protocol described above. The effectiveness of this training was assessed for five percent of the observations at MMP. Reliability sessions were conducted in which two observers independently observed the same set of animals from the same viewpoint for the duration of the session. Interobserver reliability was 93.8%.

Three hundred twenty-seven hours of observations were conducted at MMP using 30-minute sessions. All observations were conducted during the daylight hours (i.e., 6:30 a.m. to 5:00 p.m.) with one restriction: observations were not made during animal training/feeding sessions. If a training/feeding session was begun in the middle of an observation, the observation was ended, and the data were not used. As was the case at MLO, these restrictions were instituted to avoid biasing the results in terms of behaviors that occurred within a training context.

Instantaneous scan sampling and point sampling were used at MMP. Behavior samples were collected every five minutes for 30 minutes on a standardized behavioral ethogram. Each animal was observed for three to five seconds before categorizing the observed behavior. When two or more mother-calf pairs were housed together, an instantaneous scan sampling procedure (Altmann, 1974/1996; Mann, 2000; Martin & Bateson, 1993) was used such that the animals were scanned in a random fashion, depending on initial visibility and identification. When a single mother-calf pair was observed, a point sampling procedure was used because of the ease of identifying the animals. Additional qualitative data were collected during the time remaining in each interval.

Given that the primary concern of this study was the maternal behaviors exhibited by dolphin mothers, the analyses focused on the following behaviors: mother-calf swims, initiation of separations from and reunions with the calf, protective behaviors, discipline, social behaviors, and solitary activities. The discrete behaviors that comprised these categories are listed and defined in Table 1. Many of the behaviors identified were adapted from a variety of sources investigating bottlenose dolphin behavior in both human care and their natural environment (Cockcroft & Ross, 1990; Gubins et al., 1999; Mann & Smuts, 1998, 1999; Reid et al., 1995).

Table 1
Operational Definitions for Target Maternal Behaviors

Target Behavior	Operational Definition
Mother-calf swim	Mother and calf swim within 1m of each other and are synchronous
Contact	Mother or calf touches some part of the other's body with a body part
Left calf	Mother swims beyond 1m of calf
Return to calf	Mother swims within 1m of calf after being more than 1m away, an active maternal care behavior
Follow calf	Mother trails behind calf no more than 2m away as calf swims or interacts independently or with another animal other than mother, a passive maternal care behavior
Herd calf	Mother physically guides calf in specific direction using some part of her body, an active maternal care behavior
Intervention	Mother intercedes between calf and another dolphin or object by returning to calf and swimming between the calf and object of concern and/or removing the calf from the situation, an active maternal care behavior
Discipline	Behavior mother directs toward calf in response to calf's behavior, an active maternal care behavior
Pins down to bottom	Mother holds calf down against bottom of pool
Holds just under water	Mother holds calf under water with her body
Holds up above water	Mother holds calf partially out of water with either her rostrum or her belly if she is in a ventral position
Swim with other	Mother swims with animal other than her calf
Solitary activities	Independent activities that do not include any other dolphin (e.g., swims, floats, display behaviors such as breaches, dives)
Orients	Mother's eyes and head are directed at a person, object, or dolphin within or near enclosure, a passive maternal care behavior
Object play	Mother interacts with or manipulates an available object (e.g., toy)
Social interactions	Mother engages in play activities or aggressive activities with animals, including calf

Data Analyses

As the data from MLO were collected using a continuous behavior sampling approach, each pair of animals at this facility was observed a different number of times. This sampling issue combined with the inherent bias for conspicuous behaviors resulted in a recoding of the data into a zero-one coding system. Thus, if a behavior (i.e., an event) occurred at any time during a 30-minute observation, it was coded as a one, regardless of how many times it was observed. Behaviors that were not observed during a 30-minute observation were coded as a zero. Although exact estimates of behavior proportions cannot be obtained with this method and a substantial amount of data are ignored (Altmann, 1974/1996; Mann, Ten Have, Plunkett, & Meisels, 1991), it seemed the best alternative given the characteristics of the observations (e.g., the dolphins produced hundreds of observed behaviors). In order to compare the MLO and MMP data, the MMP data were coded and totaled in the same manner as the MLO data. The data on which these analyses were based are presented in Table 2.

Data analyses were performed with the total number of events per behavioral category (based on zero-one transformations) that were pooled across three-month periods (i.e., quarters) or across the year to account for individual months in which no or few observations occurred. Table 3 summarizes the total events observed per quarter for mothers and for the first year of the calf's life. It

also provides the total number of hours of observations made for individual mothers during each quarter.

Table 2
Annual Activity Budget and Mean Rates of Maternal Behaviors for Each Facility

	<i>M ± SD (%)</i>		Rate	
	MLO		MMP	
Herd calf	0.19 ± 0.32	<0.0001	1.01 ± 1.03	<0.001
Discipline	0.44 ± 0.77	<0.001	1.38 ± 1.03	<0.001
Return to calf	0.43 ± 0.44	<0.001	3.77 ± 2.57	0.002
Intervention	0.14 ± 0.10	<0.001	0.92 ± 0.63	<0.001
Orient	3.16 ± 0.89	0.02	1.57 ± 1.70	<0.001
Follow calf	0.31 ± 0.09	0.001	1.60 ± 1.79	<0.001
Left calf	0.06 ± 0.05	<0.001	0.79 ± 0.41	<0.001
Mother-calf swim	24.67 ± 4.24	0.12	65.28 ± 8.28	0.03
Contact calf	0.96 ± 0.24	0.004	1.09 ± 0.62	<0.001
Social interactions	2.35 ± 0.55	0.01	3.37 ± 0.92	0.001
Swim with other	1.29 ± 1.37	0.007	5.14 ± 2.30	0.002
Solitary activities	26.12 ± 2.05	0.13	13.70 ± 1.82	0.006
Object play	39.87 ± 5.62	0.20	0.38 ± 0.07	<0.001
TOTAL	~100		~100	

Rates of responses could not be calculated for individual behaviors given the transformed data. As a result, all behavior categories were examined proportionally, relative to one another. This activity budget was created with 13 mutually exclusive behavioral categories. Mann-Whitney *U* tests were conducted for all proportional behavioral categories to determine if facility differences existed as the different facilities produced different situational constraints. Only three behaviors demonstrated a difference between the facilities across the year: mother-calf swims (Mean ranks: MLO – 25.72, MMP – 63.23, Mann-Whitney *U* test, $z(81) = -7.05$, $p < 0.001$, Point Biserial $r^2 = .66$), object play (Mean ranks: MLO – 56.16, MMP – 18.95, Mann-Whitney *U* test, $z(81) = -7.14$, $p < 0.001$, Point Biserial $r^2 = .58$), and orients at environment (Mean ranks: MLO – 49.65, MMP – 28.42, Mann-Whitney *U* test, $z(81) = -4.07$, $p < 0.001$, Point Biserial $r^2 = 0.03$). These variables were then standardized within each facility for all remaining analyses. Variables for which facility differences did not exist were standardized across the facilities. Friedman’s Analysis of Variance by Ranks tests were performed to examine chronological trends in behavioral categories over the first year of life. Kruskal-Wallis Analysis of Variance tests were conducted to determine if individual differences existed between mothers on each maternal behavior examined. Finally, patterns of maternal behavior for mothers were initially explored qualitatively for the entire year and each quarter, using maternal rankings. K-means cluster analyses were then used to validate the qualitative approach.

Table 3
Quarterly Summary of Total Number of Events and Observation Hours per Mother

	<i>Number of events / Number of observation hours</i>			
	Q ₁	Q ₂	Q ₃	Q ₄
MLO				
<i>JAK</i> _{b,d}	237 / 24	270 / 19	150 / 6	146 / 9
<i>CHE</i> _{a,c}	333 / 27	572 / 73	774 / 78	2373 / 124
<i>KEL</i> _{b,d}	306 / 59	2431 / 143	1223 / 60	1022 / 38
<i>SHL</i> _{b,d}	524 / 66	2943 / 131	1117 / 65	715 / 25
MMP				
<i>POP</i> _{a,d}	252 / 29	427 / 29	86 / 11	164 / 18
<i>MU</i> _{b,c}	288 / 31	393 / 27	112 / 13	150 / 14
<i>BER</i> _{b,d}	324 / 24	186 / 20	136 / 12	178 / 19

Note: ^aPrimiparous mother. ^bMultiparous mother. ^cFemale calf. ^dMale calf.

Results

Tables 4 and 5 list the means and standard deviations for each of the targeted maternal behaviors across the first year of the calf's life and per quarter, respectively. Variability was much greater for some behaviors than for others. For example, the proportion of mother-calf swims ranged from 13.50% to 78.20% over the course of the year. In contrast, variability was quite small for behaviors such as maternally-initiated separations (range of 0% to 1.30%) and returns (range of 0.50% to 4.60%), perhaps because such events were relatively rare.

Table 4
Relative Proportion of Maternal Behaviors for the Year

	<i>M ± SD (%)</i>
Herd calf	0.63 ± 0.97
Discipline	0.94 ± 1.25
Return to calf	1.80 ± 1.47
Intervention	0.47 ± 0.38
Orient	4.34 ± 2.99
Follow calf	0.99 ± 0.65
Left calf	0.50 ± 0.45
Mother-calf swim	41.54 ± 28.01
Contact calf	1.21 ± 0.35
Social interactions	4.97 ± 1.10
Swim with other	1.51 ± 0.59
Solitary activities	18.24 ± 5.90
Object play	22.81 ± 20.59
TOTAL	~100

Table 5
Relative Proportion of Maternal Behaviors per Quarter

	<i>M ± SD (%)</i>			
	Q ₁	Q ₂	Q ₃	Q ₄
Herd calf	1.72 ± 2.46	0.04 ± 0.11	---	---
Discipline	1.22 ± 1.29	0.17 ± 0.31	1.00 ± 2.34	0.96 ± 1.61
Return to calf	3.73 ± 2.41	1.56 ± 1.47	0.20 ± 0.28	0.30 ± 0.62
Intervention	0.80 ± 0.98	0.60 ± 0.77	0.34 ± 0.56	0.04 ± 0.10
Orient	3.39 ± 5.75	4.17 ± 4.05	5.14 ± 7.14	3.42 ± 3.11
Follow calf	1.11 ± 0.87	0.88 ± 0.67	1.05 ± 1.69	0.35 ± 0.61
Left calf	1.13 ± 1.68	0.26 ± 0.28	0.37 ± 0.42	0.07 ± 0.12
Mother-calf swim	51.92 ± 26.89	46.87 ± 31.29	34.24 ± 22.08	35.66 ± 25.49
Contact calf	1.50 ± 1.85	1.38 ± 0.72	1.35 ± 0.84	0.59 ± 0.46
Social interactions	9.15 ± 5.94	3.80 ± 2.18	4.35 ± 3.29	3.85 ± 1.88
Swim with other	0.50 ± 0.59	1.30 ± 1.08	1.98 ± 1.86	1.72 ± 1.90
Solitary activities	13.38 ± 12.58	16.22 ± 9.49	27.34 ± 11.43	21.41 ± 10.43
Object play	10.25 ± 11.94	22.74 ± 21.89	22.66 ± 24.51	31.40 ± 30.41
TOTAL	~100	~100	~100	~100

Chronological Trends

Maternal behaviors were examined by quarters to determine the nature of maternal activities over the course of the first year of life for their calves. Table 6 presents the results for the Friedman's Analysis of Variance by Ranks tests conducted for each maternal category. Mothers generally decreased herding of, initiations of returns to, and swims with their calves by the end of the year. It should be noted, however, that mother-calf swims only approached significance for mothers at MMP ($p = 0.060$). Mothers also decreased the proportion with which they interacted socially over the course of the year. Finally, mothers generally increased their solitary activities over the course of the year although this behavior varied across quarters. Similarly, mothers at MLO generally increased the proportion with which they engaged in object play over the year. Finally, no other trends were significant for the remaining maternal behaviors despite some fluctuation throughout the year.

Table 6
Friedman's Analysis of Variance for Chronological Trends in Maternal Behavior per Quarter

	<i>Mean Rank</i>				χ^2	df	N	<i>p</i>	τ^a
	Q ₁	Q ₂	Q ₃	Q ₄					
Herd calf	2.92	2.36	2.36	2.36	15.00	3	18	0.002	-0.09
Discipline	2.94	2.28	2.33	2.44	6.67	3	18	0.08	
Return to calf	3.47	2.56	1.78	2.19	20.53	3	18	<.0001	-0.13
Intervention	2.64	2.86	2.39	2.11	6.15	3	18	0.10	
Orient									
MLO	2.25	3.13	2.17	2.46	4.14	3	12	0.25	
MMP	2.58	2.17	2.83	2.42	1.21	3	6	0.75	
Follow calf	2.81	2.58	2.33	2.28	2.50	3	18	0.48	
Left calf	2.75	2.64	2.50	2.11	4.40	3	18	0.22	
Mother-calf swim									
MLO	3.38	2.38	2.33	1.92	8.35	3	12	0.039	-0.31
MMP	3.00	3.17	1.33	2.50	3.75	3	6	0.06	
Contact calf	2.56	2.69	2.69	2.06	3.81	3	18	0.28	
Social interactions	3.22	2.44	2.33	2.00	9.51	3	18	0.023	-0.05
Swim with other	2.22	2.69	2.94	2.14	6.73	3	18	0.08	
Solitary activities	2.17	2.06	3.25	2.53	9.47	3	18	0.024	0.06
Object play									
MLO	1.42	2.71	2.21	3.69	19.34	3	12	<0.001	0.44
MMP	2.67	2.75	2.08	2.50	2.11	3	6	0.55	

Individual Differences

Kruskal-Wallis Analysis of Variance tests indicated that mothers significantly differed from one another on the following behaviors: discipline, $\chi^2 (6, N = 162) = 12.69, p = 0.048, \eta^2 = 0.20$, contact with calf, $\chi^2 (6, N = 162) = 14.80, p = 0.022, \eta^2 = 0.11$, orient at environment, $\chi^2 (6, N = 162) = 24.53, p < 0.001, \eta^2 = 0.17$, mother-calf swims, $\chi^2 (6, N = 162) = 57.39, p < 0.001, \eta^2 = 0.74$, social interactions, $\chi^2 (6, N = 162) = 16.02, p = 0.014, \eta^2 = .12$, solitary activities, $\chi^2 (6, N = 162) = 15.32, p = 0.018, \eta^2 = 0.14$, and object play, $\chi^2 (6, N = 162) = 55.28, p < 0.001, \eta^2 = 0.64$. Table 7 provides the mean ranks for each behavior.

Table 7
Kruskal-Wallis ANOVA Mean Ranks for Individual Differences

	Mothers						
	JAK	CHE	KEL	SHL	POP	MU	BER
Discipline	47.25	34.88	34.33	36.83	49.41	34.73	50.55
Orient	50.17	46.21	54.83	47.38	21.50	20.32	43.45
Mother-calf swim	15.54	37.50	28.13	21.71	63.14	70.27	56.27
Contact calf	22.46	47.42	55.50	44.42	40.86	39.91	35.91
Social interactions	22.33	41.83	47.79	55.88	47.27	31.95	39.59
Solitary activities	33.96	39.58	51.38	52.92	35.59	22.64	49.68
Object play	65.00	46.42	54.71	58.50	18.05	17.41	21.41

Maternal Style

Both qualitative and quantitative techniques were used to determine if systematic individual differences existed and if these differences could be categorized into various maternal styles. Maternal styles were examined both across the year and within quarters. Qualitative analyses were initially performed and consisted of rank ordering mothers by their standardized rankings for each of the 13 targeted maternal behaviors. For example, when mothers were ranked using data collapsed across the year for the active maternal care behavior, discipline, the following trend occurred: JAK > BER > POP > MU = CHE = KEL = SHL. This procedure was used for each of the remaining active and passive maternal care behaviors as well as the nonmaternal care behaviors. An example of a rank ordering for a non-maternal behavior, social interactions, produced the following trend: SHL > POP > BER > KEL > CHE > JAK > MU. Although the 13 target behavior categories were mutually exclusive, the ranking procedure could have led to an individual mother ranking high on both a maternal and nonmaternal behavior (e.g., POP was high on discipline and on social interactions).

Overall analysis. Mothers (e.g., JAK and BER) that were ranked high (i.e., engaged in greater proportions) in active and passive types of maternal care behaviors and low on calf separations were also ranked low in activities not involving direct maternal care (e.g., contact, social interactions). Similarly, mothers (e.g., KEL & SHL) that were ranked low in active and passive types of maternal care behaviors were ranked high in activities not involving their calves (e.g., solitary activities). The qualitative findings were supported by the results of an exploratory

cluster analysis, which investigated if dolphin mothers differed quantitatively from one another in the care of their calves.

The results of a two-means cluster analysis ultimately led to the most meaningful and consistent conclusions regarding maternal styles. Two mothers separated into one category, JAK and BER, and the remaining five mothers grouped together with a distance of 4.78 between the final cluster centers. Mothers in the two groups, indicated by the two-cluster solution, differed in terms of orients at environment ($F(1, 5) = 60.997, p = .001$), initiation of separations ($F(1, 5) = 17.19, p = .009$), mother-calf swim ($F(1, 5) = 17.64, p = .008$), discipline ($F(1, 5) = 13.12, p = .015$), herding ($F(1, 5) = 10.97, p = .021$), and interventions ($F(1, 5) = 7.56, p = .04$).

The two mother group (JAK and BER) was characterized by a tendency to monitor and physically control their calves' activities. BER and JAK were more likely to herd, discipline, and intervene for their calves, and to actively monitor their environment. They were also less likely to initiate separations from their calves.

The five mother group consisted of mothers who rarely interfered with their calves' activities. These mothers were less likely to herd, discipline, and intervene for their calves. They were also less likely to monitor their surrounding environment. Finally, these mothers were more likely to initiate separations from their calves.

Quarterly analysis. Although the mothers exhibited some variation in their rankings of maternal behaviors when examined by quarters, six of the seven mothers maintained the same classification for maternal style determined from the overall analyses. The qualitative approach of rank ordering mothers on all behavior categories was also supported by the quantitative results of a two-means cluster analysis.

One mother, POP, was especially intriguing. In the overall analysis, POP was classified as a mother who engaged in few controlling behaviors. When examined by quarters, this pattern of behavior was observed during the latter half of the first year of life (7-9 months and 10-12 months). However, during the first half of the year, POP was identified as a mother who demonstrated high levels of controlling maternal care behaviors during the first two quarters. When her maternal care behaviors were examined individually, it was discovered that she ranked very high on herding, discipline, and intervention during the first two quarters.

Figure 1 displays specific maternal care behaviors for three mothers per quarter: JAK, SHL, and POP. As demonstrated in Figure 1, the mothers exhibited some flexibility in their maternal care behaviors over the year. JAK continued to display highly controlling behavior over the year but with decreasing frequency, as indicated by the smaller total percentage. SHL demonstrated a less controlling pattern of behavior over most of the year. However, she did appear to increase the frequency with which she monitored her calf's activities, as indicated by an increase in following her calf. Finally, POP appeared to exhibit a role reversal moving from very controlling behaviors early on to almost no controlling behaviors by the end of the first year. In summary, the quarterly analyses indicated that stable maternal differences existed over the course of the year, but variation within individuals also occurred.

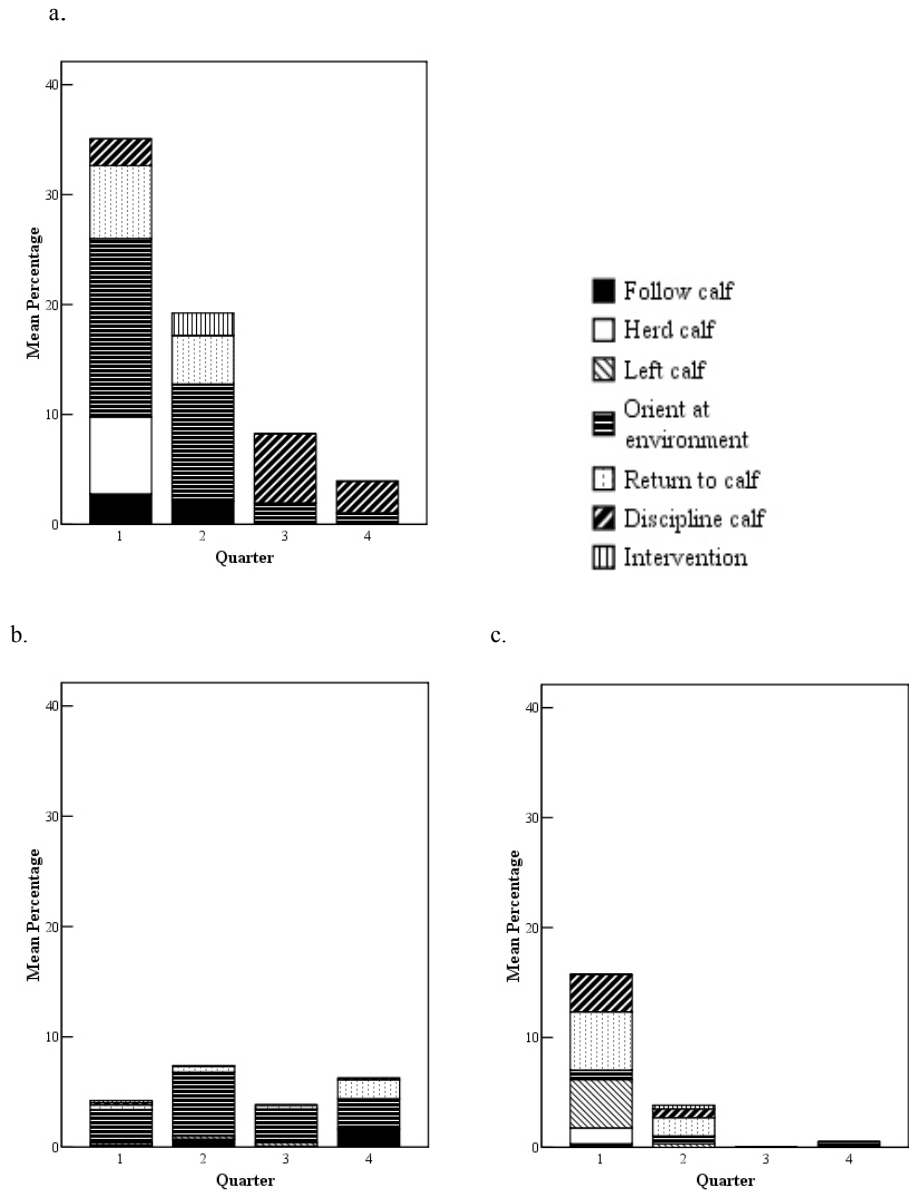


Figure 1. Average proportion of active and passive maternal care behaviors per quarter for three mothers. a. JAK – a highly controlling mother; b. SHL – a non-controlling mother; c. POP – Highly controlling first half of year, Non-controlling second half of year.

Discussion

The current study explored maternal behavior by bottlenose dolphins in the care of humans. The first goal of the study was to examine the types of maternal behaviors and their development over the course of the first year of a calf's life. Maternal behavior included maternal care behaviors that directly impacted the calves' activities (e.g., discipline, proximity maintenance behaviors) and maternal behaviors that indirectly influenced calf development (e.g., contact, social interac-

tions). The second goal of the study was to determine if individual differences existed in maternal care behaviors, and to assess if these differences could group mothers into maternal styles during the first year of life.

Maternal Care Over the First Year of Life

As expected from previous research from both captive settings and natural environments (Cockcroft & Ross, 1990; dos Santos & Lacerda, 1987; Gubbins et al., 1999; Mann & Smuts, 1998, 1999; McBride & Kritzler, 1951; Miles & Herzog, 2003; Reid et al., 1995; Smolker et al., 1993; Sayigh et al., 1990), our mothers engaged in a variety of maternal care behaviors, including swimming with their calves, initiating reunions, maintaining proximity, initiating separations, disciplining, playing with their calves, and socializing with other dolphins. In general, our mothers, located at two different facilities, engaged in most of these behaviors with relatively similar proportions. Three maternal behaviors were significantly different between facilities: mother-calf swims, orients at environment, and object play. Specifically, mothers at the Marine Mammal Program (MMP) swam with their calves for a greater proportion of their total activities than mothers at Marine Life Oceanarium (MLO). Mothers at MLO engaged in greater proportions of play with objects and orients at environment as compared to mothers at MMP.

It is possible that these differences between facilities were due to a difference in the nature of the two environments. MMP was a very dynamic social and physical system. Housed within a bay environment where indigenous wildlife could enter enclosures at any time and social groupings were altered regularly, it is likely that this setting could have produced more calf-threatening situations (e.g., introduction of new dolphins, frequent changes to social milieu, wild marine life entering into bay enclosures, movement between enclosures) than the relatively stable social system and environment at MLO. Thus, safety issues may have played a role in the finding that mothers at MMP swam with their calves more often than mothers at MLO. Another issue was the difference between the facilities in terms of environmental enrichment devices (EEDs, such as toys and people). Mothers at MLO had constant access to EEDs as compared to mothers at MMP, who had a more limited access to similar objects. The difference in availability of EEDs at MLO, an entertainment facility, likely contributed to the differences observed in object play and orients at environment.

Despite different environmental constraints and some differences in the proportions with which mothers engaged in certain behaviors, all mothers exhibited expected maternal behaviors. Moreover, the maternal behaviors followed previously reported developmental trends. For example, our mothers rarely initiated separations from their calves and were generally responsible for reunions during the first few months of the calf's life, replicating earlier studies (Mann et al., 2000; Mann & Smuts, 1998, 1999; Miles & Herzog, 2003; Reid et al., 1995; Smolker et al., 1993). Additionally, the initiation of reunions by mothers, mother-calf swims, and proximity maintenance by mothers decreased over the course of the year, supporting previous research in which calves became more responsible for reunions and exhibited greater degrees of independence with increasing age (Gubbins et al., 1999; Mann et al., 2000; Mann & Smuts, 1998, 1999; Miles & Herzog, 2003; Reid et al., 1995; Smolker et al., 1993). The findings of the current study also

highlight the similar challenges dolphin mothers face while rearing their offspring within different settings and the general behavioral repertoire they draw upon to do so.

One behavior to note was the proximity maintenance behavior of herding. Herding, a very physical, active maternal care behavior, was exhibited by five of the seven mothers. This behavior only occurred during the first two months of a calf's life with a single exception occurring at four months. Herding appeared to be displayed only when physical intervention was necessary by a mother to redirect her young calf's swimming direction away from an object that was perceived as harmful by the mother. The absence of this active, proximity maintenance behavior during the second half of the first year of life may have indicated that it is no longer effective once calves were physically bigger and in greater control over their bodies (Mann & Smuts, 1999; Reid et al. 1995).

Individual Differences in Maternal Care and Maternal Styles

Mother dolphins cared for their calves in similar ways. However, they also exhibited individual differences in some aspects of their maternal care. For example, not all mothers herded their calves nor did all mothers use discipline. Some mothers were more likely to use discipline and to do so for longer periods of time. In fact, discipline became a significant maternal care behavior that was used to differentiate mothers into separate maternal styles

The individual variability and the consistency of such variability suggested that dolphins could be grouped into different patterns of behavior. Qualitative and quantitative analyses supported this observation as two patterns of behavior appeared to differentiate mothers. The two clusters seemed to differ primarily on the types and proportions of control techniques mothers exhibited when caring for their calves. Mothers who ranked high on active maternal care behaviors, such as discipline, herding, returns, and interventions, and high on passive maternal care behaviors, such as orients and follows, were considered to engage in more control techniques and were therefore identified as more controlling. Two mothers, JAK and BER, fell into this category.

In contrast, the remaining mothers tended to be lower on many of the active and passive maternal care behaviors and were considered less controlling. As this cluster held the remaining five mothers, there was greater variability in their maternal care behaviors. Two mothers, SHL and KEL, maintained the lowest rankings for controlling techniques. The other three mothers showed more variation in their use of controlling behaviors.

Thus, mother dolphins, like many other mammals including rats, guinea pigs, pigs, elephants, and nonhuman and human primates, exhibit stable patterns of behavior that may be organized into maternal styles. While maternal styles in some species are based on specific behaviors such as anogenital licking rates in rats (Fleming & Li, 2002) or the combination of grooming, ventral contact, and anogenital licking rates in guinea pigs (Albers et al., 1999a, 1999b), other species exhibit maternal styles centered around patterns of behaviors that are more global in nature. For example, the level of maternal control in offspring activities and degree of warmth and nurturing exhibited by mothers towards their offspring are two dimensions that differentiate between maternal styles in human and nonhuman pri-

mates (Altmann, 1980; Bard, 2002; Fairbanks, 1996; Hrdy, 2004; Mandara, 2003). Like their human and nonhuman counterparts, maternal styles in bottlenose dolphins in the care of humans may be characterized by a similar control dimension. The role of warmth and nurturing in dolphin maternal styles needs to be addressed.

We also examined if these maternal styles remained consistent within smaller time frames throughout the year, namely across quarters. The results indicated that mothers adapted their maternal care behaviors and overall maternal style to their calf's development and the current social environment. For example, the most controlling animal from the overall analysis, JAK, consistently engaged in the highest levels of controlling behaviors across all four quarters but appeared to use fewer of them by the last quarter. In comparison, POP began the first half of the year as a highly controlling mother and then became the least controlling mother the second half of the year. All mothers but POP either maintained their original maternal style or increased the frequency of control techniques they displayed as their calves matured.

Interestingly, the behaviors that mothers used to control their calves' activities appeared to change with the calves' increasing independence. Mothers engaged in fewer active forms of maternal control, such as herding and disciplining and more often displayed passive forms such as following their calves or observing them from a distance (i.e., orients), during the second half of the first year of life. These changes in control techniques may have corresponded to the potential dangers that calves encountered at different points during their development. For example, the first two quarters of the first year are critical for the calf's physical well-being and safety. Thus, mothers exhibited behaviors that allowed them to guide their calves' navigational, swimming, and nursing activities while avoiding obstacles like walls and gates. This conclusion is supported by previous observations that indicated mothers were much less "tolerant" of separations by their calves the first few months of life as compared to later periods (Mann & Smuts, 1998, 1999; Reid et al., 1995). In contrast, the second half of the year may be dedicated to monitoring the calf's social interactions and solitary activities. Thus, mothers may be less active in physically controlling their calves' behaviors but may be more vigilant in monitoring their calves' activities.

Flexibility in maternal care is a feature common to many species. Changes in food availability or the physical environment, the age and number of the offspring present, the presence of allomothers or aunts, maternal experience, and sex of the offspring influence patterns of maternal care and offspring survival in many mammals (Clutton-Brock, 1991; brown bears: Dahle & Swenson, 2003; elephants: Lee, 1983; Lee & Moss, 1986; pigs: Herskin et al., 1998; Spinka et al., 2000; Valros et al., 2003; primates: Altmann, 1980; Bard, 2002; Fairbanks, 1996; guinea pigs: Albers et al., 1999b; Kemps & Timmermans, 1984; Maestripieri, 1998; rats: see Fleming & Li, 2002 for a review). Although allomaternal behaviors have been observed for many species, including dolphins, in human care, allomaternal care was relatively rare in our sample of dolphin mothers. Only one mother, POP, was regularly observed swimming with a calf other than her own, and these swims often appeared to be more social than maternal in nature. That is, her swims with these calves usually consisted of fast swims that created large bow waves, which the calves "surfed" upon.

Parity and maternal-care behaviors have also been shown to influence the likelihood of dolphin calf mortality, whether in the care of humans or in their natural habitat (Cornell et al., 1987; Delgado-Estrella & Romero-Tenorio, 2006; Mann & Smuts, 1998; Mann & Watson-Capps, 2005). Given that all of the calves survived the first year and no extreme maternal styles were observed (e.g., rejecting), our exploratory findings suggested that, like many animals, dolphin maternal styles may consist of a range of adaptive maternal behaviors. Thus, a more controlling maternal style is neither better nor worse than a non-controlling maternal style, under non-extreme circumstances. Moreover, our mothers may have adapted some of their maternal care behaviors to account for changing calf demands throughout the year.

The current study could not empirically assess the relationships between maternal style and parity and maternal style and sex of the offspring, with only seven mother-calf pairs – two primiparous mothers and two female calves. It is unclear whether primiparous mothers should be more or less controlling of their calves. Research with rhesus monkeys has indicated that maternal experience often interacts with the mother's personality characteristics (e.g., high anxiety versus low anxiety), the infant's temperamental tendencies (e.g., high reactivity versus low reactivity in novel environments), and the current social environment (e.g., presence or absence of dominant animals, as reviewed by Bard, 2002; Suomi, 1999). Other research has suggested that some mothers of various species may invest differing levels of time and care depending on the sex of their offspring (e.g., African elephants, Lee & Moss, 1986; sea lions, Ono & Boness, 1996). It seems unlikely that the sex of a dolphin's calf would influence maternal style as few sex differences in dolphin calf behavior have been noted or observed.

The findings from the current study should obviously be interpreted with caution due to its very specific sample. The environmental constraints of dolphins in human care may alter maternal care behaviors, strategies, and their developmental course. However, although the findings may not directly generalize to dolphins in their natural habitat, we would like to argue that one of the strengths of this study is within its limited sample. That is, the current study demonstrated similarities in the types and trends of various maternal behaviors including maternal care and non-maternal care behaviors between mothers located at two very different types of facilities. Moreover, these behaviors were consistent with previous research conducted with both captive and wild dolphin populations (Gubbins et al., 1999; Mann et al., 2000; Mann & Smuts, 1998, 1999; Miles & Herzing, 2003; Reid et al., 1995; Smolker et al., 1993). Like many other species with extended maternal care periods, maternal styles in dolphins should be a fairly consistent phenomenon across different populations both in the care of humans and in their natural habitat. The current study identified various maternal behaviors that future investigations of maternal styles should target using larger and more varied samples of dolphins. Additionally, larger samples will allow the influence of factors such as previous maternal experience, offspring sex, and the personality characteristics of mothers (e.g., level of anxiety) and calves (e.g., level of reactivity) to be examined.

Finally, future research should also investigate the interaction between maternal style and calf behavior. The current study did not specifically investigate the influence of maternal style on calf behavior nor did it investigate the influence of

calf behavior on maternal style. Research with human and nonhuman primates has documented different developmental outcomes for offspring with mothers of varying maternal styles (for reviews, see Fairbanks, 1996; Hrdy, 2004). For example, human children who experienced consistent, appropriate, and warm interactions with their mothers were more confident and trusting in their relationships with others as compared to children without those same maternal experiences (for a review, see Mandara, 2003). In nonhuman primates, rejection rates are similar among rhesus monkey mothers and their daughters (Berman, 1990). The influence of maternal style on developmental outcomes has also been observed in offspring reactions to novel environments, exploratory behavior, and initiations of social interactions (Fairbanks, 1996; Hrdy, 2004). Evidence from a variety of species demonstrates that maternal style can influence offspring development, but offspring behavior also affects maternal style. Although much remains to be learned about the parenting behavior of dolphins, the role of dolphin calves in their behavioral development and rearing process is even more poorly understood and is in need of further investigation.

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