

Behavioral Development of Two Captive Mother-Calf Dyads of Bottlenose Dolphins (*Tursiops truncatus*) in the Calves' First Year

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This study investigated the development of suckling behavior, spatial relations, social behavior, and play behavior in 2 mother-calf dyads of bottlenose dolphins (*Tursiops truncatus*). Each dyad was observed 4 hours weekly throughout the calves' 1st year. The dyads differed in calves' sex and mothers' parity. The dyad with the primiparous female needed more time to establish suckling and swimming routines. After the 3rd month, interactions with the mother (*flipper-rub*, *rest together*, *social play*, and *calf watches mother*) were significantly more frequent in the female calf, whereas interactions with the calves' father (*swim together*, *rest together*, and *social play*) were significantly more frequent in the male calf. The calves showed high rates of object play and social play. They seemed to modify their type of play according to the opportunities they were offered. A mentally stimulating object was preferred to simpler toys. The knowledge of the details of mother-calf behavior helps to develop appropriate breeding conditions that are vital for the survival and well-being of captive dolphin calves.

The study of bottlenose dolphins (*Tursiops truncatus*) revealed complex, fission-fusion type social systems (Connor, Read, & Wrangham, 2000; Connor, Wells, Mann, & Read, 2000) and remarkable cognitive abilities (reviews in Herman, 2006; Tschudin, 2006). The calves are generally nursed for three to six years (Mann & Smuts, 1999) and associate strongly with their mothers for the first few years (Smolker, Richards, Connor, & Pepper, 1992; Wells, Scott, & Irvine, 1987). With these features of dolphin biology, the mother-calf relationship can be expected to show a high level of complexity and variability. However, data on the details of the mother-calf relationship and its development are rare.

In the last decades, quantitative analysis of behavioral development in dolphins has concentrated on suckling behavior (Cockcroft & Ross, 1990; Eastcott & Dickinson, 1987; Mello, Nordensten, & Amundin, 2005; Peddemors, Fothergill, & Cockcroft, 1992; Reid, Mann, Weiner, & Hecker, 1995; Triossi, Pace, Terranova, & Renzi, 1998) and spatial relations (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999; Reid et al., 1995). In all dyads studied so far, suckling frequency declined in the first weeks post partum (Mello et al., 2005; Peddemors et al., 1992; Reid et al., 1995). Young dolphin calves predominantly swim in either the echelon position (the calf swims parallel and very close to its mother with its head next to the mother's dorsal fin) or the mother-calf position (the calf swims under its mother with its head touching her mammary region; also termed infant position in the literature). In the majority of observations, the echelon position decreased and the mother-calf position increased with the calf's age (Gubbins et al., 1999; Mann & Smuts, 1999). Proximity between mother and calf was primarily maintained by the mother and her contribution declined over time (Hill, Greer, Solangi, & Kuczaj, 2007; Mann & Smuts, 1999; Reid et al., 1995). Reid et al. (1995) studied two mother-

This study was part of a project supported by a habilitation grant of the German Research Foundation to Lorenzo von Fersen. We would like to thank zoo director Dr. Peter Mühling and the dolphin training staff for their assistance and cooperation. Many thanks go to Cornelia von Streit, Fritz Laux, and Ulrich Wiedenmann-von Streit for their vital support in data processing. Correspondence concerning this article should be addressed to Claudia von Streit, Achalmstr. 35, 72072 Tuebingen, Germany. (vonstreit@t-online.de)

calf dyads differing in parity. They observed that the calf of the primiparous mother suckled at high frequencies for a longer period of time than did the calf of the multiparous mother. Furthermore, the dyad with the primiparous mother also deviated from the general developmental patterns of the two major swimming positions: There was no developmental trend in the echelon position and instead of increasing the mother-calf position decreased.

An important aspect of dolphin calf behavior is play. Various functions of play have been proposed and it is generally thought to be crucial for the development of young mammals (reviews in Fagen, 1981; Martin & Caro, 1985; Spinka, Newberry, & Bekoff, 2001). Through play, young animals may practice motor (Byers, 1998; Byers & Walker, 1995), social (Bekoff & Byers, 1981; Maestripieri & Ross, 2004), and problem solving (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006) skills that will be useful later in life. Due to unlimited food resources and the absence of predators, captive animals can generally afford more time to play than their wild counterparts (Fagen, 1981; Thompson, 1996). Dolphins exhibited a rich repertoire of play behavior in both captive and free-ranging settings (review in Paulos, Trone, & Kuczaj, 2010; Connor, Wells et al., 2000; Kuczaj et al., 2006; Mann & Smuts, 1999; McBride & Hebb, 1948; Pace, 2000). Greene, Melillo-Sweeting, and Dudzinski (2011) found more object play in a captive than in a wild dolphin population. However, they discuss their results with caution, as sample size was substantially smaller in the wild setting. Thompson (1996) stated that play is an important means for captive animals to stay healthy, fit, and active and to avoid abnormal behavior such as stereotypy. For this reason, more data on play behavior in dolphin calves is necessary to provide captive dolphin calves with adequate stimuli for play.

Recent studies revealed an effect of the calves' sex and mothers' sociality on the social development of wild dolphin calves (Gibson & Mann, 2008a, 2008b). The authors found that sex differences in social behavior emerged as early as the first year of life. Calves showed same-sex preferences in association (Gibson & Mann, 2008b) and maternal influence on social development was stronger for daughters than for sons (Gibson & Mann, 2008a). Factors accounting for differences in mother-infant behavior, such as sex of the infant, or parity, dominance rank, and personality of the mother, have been extensively studied for primates (e.g., Nakamichi, 1989; Schino, D'Amato, & Troisi, 1995; Tanaka, 1989; reviews in Fairbanks, 1996; Hernandez-Lloreda & Colmenares, 2005). In contrast, the study of factors influencing mother-calf behavior in dolphins is in its infancy. One of the few studies addressing this topic suggested that differences in the mother's personality might be related to different maternal styles (Hill et al., 2007).

The intent of this study was to add to the overall knowledge of dolphin mother-calf behavior. Even though this study is based on a small sample size, any information about dolphin calf development is important for successfully raising these animals in an aquarium setting. Two mother-calf dyads were observed in the zoological garden of Nuernberg, Germany throughout the calves' first year. The dyads differed in mothers' parity and calves' sex. Out of a more extensive ethogram (von Streit, Ganslosser, & von Fersen, 2011), we chose 14 behavioral categories in the areas of suckling behavior, spatial relations, play behavior, and social behavior for quantitative analysis. With regard to suckling behavior and spatial relations, we expected our data to support previous research. Consistent with the observations of Reid et al. (1995), we hypothesized a higher suckling frequency and a higher amount of time spent in the mother-calf position in the dyad with the primiparous mother and a higher amount of time spent in the echelon position in the dyad with the multiparous mother in the first weeks. Furthermore, we expected the following developments for the dyad with the primiparous female in the first weeks: A slower decline of suckling frequency compared to the dyad with the multiparous female, no developmental trend of

the echelon position, and a decrease of the mother-calf position. We measured the calves' frequencies and developments of locomotor play, object play, and social play and expected a high amount of play behavior after the first weeks. Finally, we investigated the rates of the five most frequent social behaviors (*swim together*, *rest together*, *flipper-rub*, *social play*, *calf watches mother*). Considering the results of Gibson and Mann (2008a, 2008b), we expected mother-calf interactions to be more frequent in the dyad with the female calf after the newborn period and interactions with the calves' father, who had access to the mother-calf dyads after about half a year, to be more frequent in the male calf. Although the small sample size precludes generalizations, we discuss if differences found between the two dyads might be attributed to the differences in mothers' parity or calves' sex.

Method

Subjects and Housing

We conducted the study in the dolphinarium II of the zoological garden in Nuernberg, Germany, established especially for breeding and research and not open to the public. It consists of two circular pools connected by two channels (Figure 1). Both females in this study were wild-caught. Eva was 25 and Emy 13 years old. The two calves were born within five days in November, 1993. Noah was Eva's third son and Neike was Emy's first surviving calf. The tank walls posed an injury risk for the calf of the inexperienced Emy and were therefore lined with a net. As the dolphin trainers feared aggression by Emy towards Eva and her calf, the two females were housed in separate tanks with the gates in the channels closed five months before the expected births of the calves (Figure 1). Eva and Noah shared their tank with Moby, the calves' father, but were separated from him by a net. Moby occasionally had access to Eva and Noah from Noah's 23rd week onward and to Emy and Neike from Neike's 33rd week onward. Altogether, Moby was in Eva's and Noah's section during 66 out of 112 hrs of observation from the 23rd week onward and in Emy's and Neike's tank during 36 out of 75 hrs of observation from the 33rd week onward. The calves had no physical contact to each other and only their interactions with their mothers and with Moby could be investigated. The gates in the channels were opened after the end of this study, when the calves were about one and a half years old. All animals were in good health throughout the study. From the fifth week onward, toys were present in the pools at all hours of observation, comprising balls of different sizes, hoops, cans, and ropes.

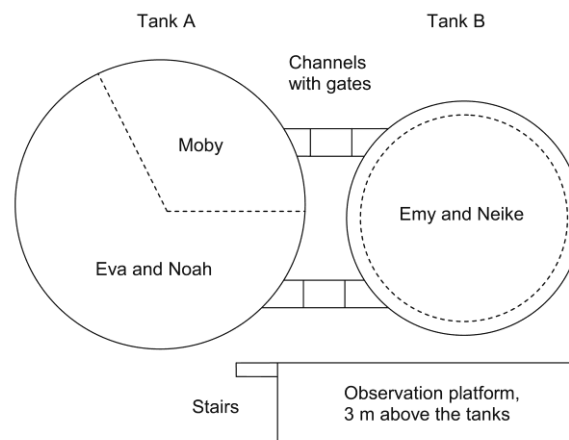


Figure 1. Plan of the dolphinarium II. Diameter of tank A is 15 m and diameter of tank B is 12 m. Water depths is 3.55 m. The tanks are connected by two channels with two gates each. A net (dotted lines) divides tank A into two sections. The wall of tank B is lined with a net for the calf's safety (dotted line). The dolphins living in the tanks at the time of the study are indicated. Reprinted from "Ethogram of two Captive Mother-Calf Dyads of Bottlenose Dolphins (*Tursiops truncatus*): Comparison with Field Ethograms," by C. von Streit, U. Ganslosser, and L. von Fersen, 2011, *Aquatic Mammals*, 37, p. 193. Reprinted with permission.

Measures

This study was part of a project on dolphin mother-calf behavior. An ethogram of the two dyads defining 51 behavioral categories was presented elsewhere (von Streit et al., 2011). Out of this ethogram we chose 14 behavioral categories in the areas of suckling behavior, spatial relations, play behavior, and social behavior for quantitative analysis (Table 1).

Table 1
Behavioral categories that were analyzed quantitatively in this study

Behavioral category	Definition
Suckling Behavior	
Suckling	Calf swims under the mother and holds its rostrum to her mammary slit for more than two seconds. It lies on its side, the fluke slightly bent towards the belly. Usually, the calf performs two or three suckling events in quick succession.
Side presentation	Mother stops her swimming movements, rolls onto her side, and turns her mammary region towards the calf.
Spatial Relations	
Approach	Dolphin swims towards another dolphin. Followed by an interaction.
Leave	Dolphin swims away from another dolphin after an interaction.
Echelon position	Mother and calf swim very close together. The calf's head is next to the mother's fin and its body slightly above the mother, touching or nearly touching the mother's body. The mother's swimming-movements are strong, the calf's weak or absent.
Mother-calf position	Calf swims under the mother, its head touching her mammary region.
Play Behavior	
Social play	Two dolphins interact playfully. The behavior can be vigorous with one dolphin chasing the other or both twirling around each other rapidly. Alternatively, it can be gentle, with the dolphins circling smoothly around each other or nudging each other.
Locomotor play	Only seen in the calves. Calf frolics through the pool: On its side, on its back, with changing speed, jumping, twisting its body in the air, sticking its fluke out of the water.
Object play	All activity addressed towards a toy placed in the tank. Toys are balls of different sizes, hoops, cans, or ropes.
Play with net	Only seen in Emy and Neike. They inspect the net that lines the wall of their tank and manipulate the cords that hold together the parts of the net.
Social behavior	
Swim together	Two dolphins swim in steady circles through the tank; the distance between them is less than one body-length.
Rest together	Two dolphins lie at a spot within a distance of maximum one body-length.

Flipper-rub	While swimming together, the calf rubs parts of its body or the whole body on its mother's pectoral fins. It turns different parts of its body towards the mother's pectoral fins, thus swimming sometimes on its side or its back. The mother remains horizontal. She sometimes sticks her pectoral fins towards the calf and moves them up and down.
Calf watches mother	Calf is close to its mother (<one body-length) and orients its rostrum towards the mother. Sometimes it circles the mother slowly and moves its head up and down as if watching its mother's activity, in most cases object play or – in Neike's case – Emy's play with the net.

Note. Adapted from “Ethogram of two Captive Mother-Calf Dyads of Bottlenose Dolphins (*Tursiops truncatus*): Comparison with Field Ethograms,” by C. von Streit, U. Ganslosser, and L. von Fersen, 2011, *Aquatic Mammals*, 37, pp. 195-196. Adapted with permission.

Procedure

We installed a video recorder for each pool on the observation platform (Figure 1). For reliability and repetition, we videotaped all hours of observation and analyzed the recorded sessions. To avoid disturbances by people, we carried out the recordings without trainers present (1200h to 1300h and 1700h to 1800h) when the first author was the only person in the dolphinarium. We recorded each dyad twice a week at noon and twice a week in the evening throughout the calves' first year. Altogether, 199 hrs of observation of Eva and Noah and 201 hrs of observation of Emy and Neike were included in this study.

We analyzed the videotapes with the *Observer 3.0* (Noldus Information Technology). Observation techniques were focal animal sampling and continuous recording (Altmann, 1974), with the mothers and calves as focal animals. The *Observer* calculated the frequency of the categories *suckling*, *side presentation*, *approach*, and *leave* and the duration of all other categories per hour (for the distinction between *events* and *states* see Martin and Bateson (1993)). To exclude an observer shift, we carried out an intra-observer reliability test after each quarter of a year. For each mother-calf dyad, we randomly chose two hours of observation from the beginning of each quarter and analyzed them a second time. The *Observer's* reliability analysis program tested both versions for correspondence. The degree of correspondence was high for both dyads in all four quarters, ranging from 76.2% to 95.7%.

Data Analysis

We used the statistic package SPSS 15 for statistical analysis. We summarized data in four-week intervals. As assumptions for parametric statistics (normal distribution, homogeneity of variance) were not always fulfilled, we calculated median values for each interval. Reid et al. (1995) and Mann and Smuts (1999) observed dolphin calves for nine and ten weeks, respectively. To examine the development of suckling behavior and spatial relations in the newborn period and to be able to compare our results to those of Reid et al. (1995) and Mann and Smuts (1999) we analyzed weeks 1-12 (that encompassed the periods of time studied by these authors) and weeks 13-52 separately. For continuity we maintained this distinction for the analysis of all behavioral categories.

We tested all behavioral categories listed in Table 1 for differences between the two dyads with a Wilcoxon matched pairs signed rank test. When a higher rate was hypothesized for one dyad due to the mothers' parity (*suckling*, *echelon position*, *mother-calf position*) or the calves' sex (all social behaviors), the test was one-tailed. We used the Spearman rank correlation coefficient (r_s) to assess significant age effects for the behavioral categories suckling, side presentation, echelon position, mother-calf position, and the approach-leave index (see below). As we expected specific developmental trends following previous studies, these tests were one-tailed. Furthermore, we tested the correlation between the rates of mother-calf position and suckling for the whole year with a Spearman rank correlation coefficient. A coefficient of 1 or -1 indicates a perfect positive or negative correlation and a coefficient of 0 indicates no correlation at all. Significance was set at $p < .05$ for all tests. When we used data for several tests, we adapted the level of significance using the sequential Bonferroni correction following Rice (1989).

To decide which partner was mainly responsible for the maintaining of proximity, we calculated an approach-leave index (Hinde & Atkinson, 1970): $I = [Ac / (Am + Ac)] - [Lc / (Lm + Lc)]$. The number of movements towards the partner (A = approaches) and away from the partner (L = leavings) was counted for both mothers (m) and calves (c). An index below -.1 indicated that the mother contributed more to the maintaining of proximity and an index above

+1 indicated that the calf contributed more to the maintaining of proximity. Values between -1 and +1 indicated equal responsibility of both partners.

Results

Suckling Behavior

Weeks 1-12. In the first 12 weeks, suckling frequency declined significantly in Eva and Noah (Spearman rank correlation: $r_s = -0.369$, $N = 47$, $p = 0.005$; Figure 2). Neike suckled at high frequencies for a longer period of time (Figure 3). Her suckling frequency also declined, but this trend was not significant after Bonferroni correction ($r_s = -0.278$, $N = 48$, $p = 0.028$; number of tests $k = 3$, adapted level of significance $p = 0.017$). Side presentation when nursing occurred in the first three weeks in Eva and in the first four weeks in Emy. It decreased significantly in Eva ($r_s = -0.844$, $N = 16$, $p < 0.0005$) and non-significantly in Emy after Bonferroni correction ($r_s = -0.442$, $N = 16$, $p = 0.043$; number of tests $k = 2$, adapted level of significance $p = 0.025$). There was no significant difference, either in suckling frequency (Wilcoxon matched pairs signed rank test: $Z = -1.420$, $N = 47$, $p = 0.079$) or in the frequency of side presentation ($Z = -0.157$, $N = 16$, $p = 0.894$; weeks 1-4) between the two dyads.

Weeks 13-52. In both calves, suckling frequency remained stable until week 28 (Figures 2 and 3). Neike started to consume fish regularly in week 30 and reduced her suckling frequency at that time. From week 13 to week 52 the decline of her suckling frequency was significant ($r_s = -0.602$, $N = 153$, $p < 0.0005$). In contrast, Noah, who did not eat fish in his first year, significantly increased his suckling frequency ($r_s = 0.229$, $N = 152$, $p = 0.002$). Although Noah suckled more frequently than Neike at the end of the first year, suckling frequency was significantly higher in Neike than in Noah in the entire period from week 12 to week 52 ($Z = -2.368$, $N = 147$, $p = 0.018$).

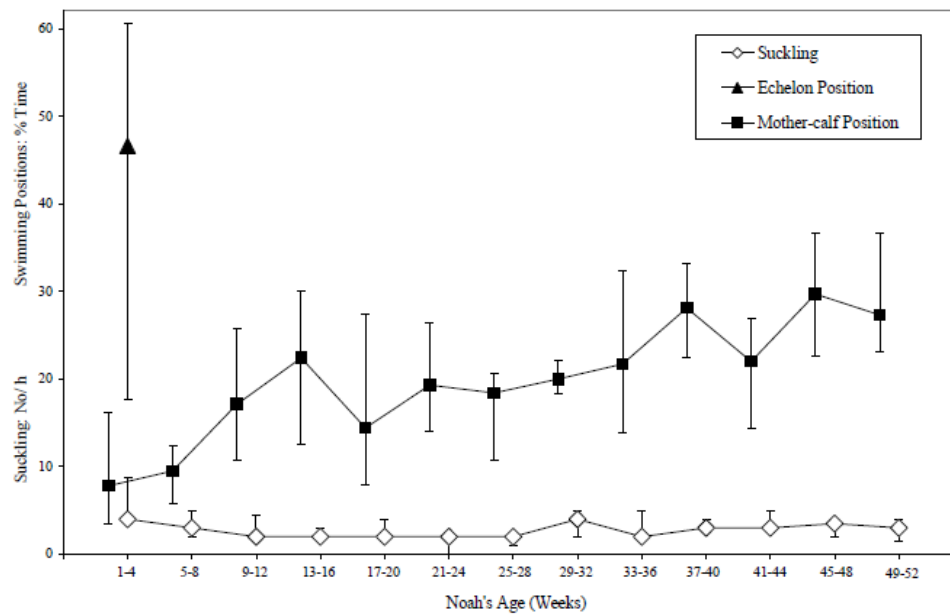


Figure 2. Developments of suckling frequency and of the proportions of time spent in the two major swimming positions in Noah's 1st year. Medians and 1st and 3rd quartiles are presented (see Appendix A for outliers). Median time spent in the echelon position was zero after week 4. Sample size was $N = 16$. Exceptions: $N = 15$ in weeks 5-8 and 41-44; $N = 14$ in weeks 33-36 and 37-40; $N = 13$ in weeks 29-32.

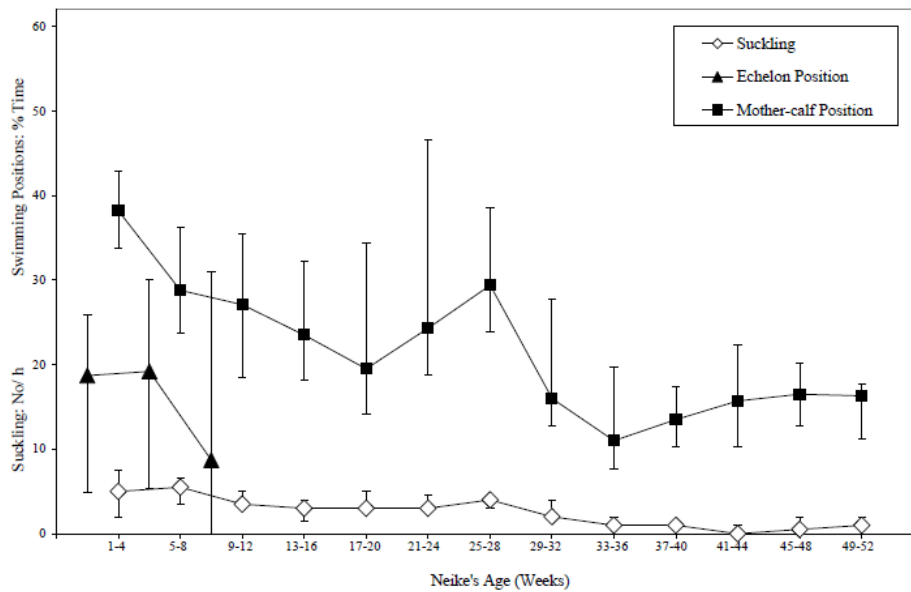


Figure 3. Developments of suckling frequency and of the proportions of time spent in the two major swimming positions in Neike's 1st year. Medians and 1st and 3rd quartiles are presented (see Appendix A for outliers). Median time spent in the echelon position was zero after week 12. Sample size was $N = 16$. Exceptions: $N = 15$ in weeks 25-28, 29-32 and 33-36; $N = 14$ in weeks 37-40 and 49-52.

Swimming Positions

Weeks 1-12. In Eva and Noah, the echelon position decreased significantly in the first 12 weeks ($r_s = -0.639$, $N = 47$, $p < 0.0005$) and the mother-calf position increased significantly ($r_s = 0.329$, $N = 47$, $p = 0.012$) (Figure 2). In contrast, the mother-calf position decreased significantly in Emy and Neike ($r_s = -0.266$, $N = 48$, $p = 0.034$) whereas no developmental trend was observed for the echelon position ($r_s = -0.219$, $N = 48$, $p = 0.067$) (Figure 3). The mother-calf position was significantly more frequent in Emy and Neike than in Eva and Noah ($Z = -5.238$, $N = 47$, $p < 0.0005$) whereas no significant difference between the dyads was observed for the echelon position ($Z = -0.194$, $N = 47$, $p = 0.426$).

Weeks 13-52. The echelon position was last observed in Eva and Noah in week 18. It was also rare in Emy and Neike after the 12th week. But it occasionally occurred in this dyad until the end of the first year and was significantly more frequent than in Eva and Noah ($Z = -3.176$, $N = 147$, $p = 0.001$). Concerning the mother-calf position, both dyads maintained the developmental trends we already observed in the first 12 weeks: a significant increase in Eva and Noah ($r_s = 0.314$, $N = 152$, $p < 0.0005$; Figure 2) and a significant decrease in Emy and Neike ($r_s = -0.367$, $N = 153$, $p < 0.0005$; Figure 3). There was no significant difference between the dyads for this swimming position ($Z = -1.464$, $N = 147$, $p = 0.144$).

A significant but rather low correlation was measured between the rates of suckling and mother-calf position in the first year in Emy and Neike ($r_s = 0.348$, $N = 201$, $p < 0.0005$). There was no significant correlation between these two behavioral categories in Eva and Noah ($r_s = 0.089$, $N = 199$, $p = 0.210$).

Maintenance of Proximity

Weeks 1-12. In Eva and Noah the medians of the approach-leave index were -0.53 in weeks 1 to 4, -0.36 in weeks 5 to 8 and -0.12 in weeks 9 to 12. Thus, Eva was responsible for the maintenance of proximity and her contribution significantly declined in the first 12 weeks ($r_s = 0.378$, $N = 34$, $p = 0.014$). In contrast, the corresponding three medians of the approach-leave index were zero in Emy and Neike, indicating equal responsibility of mother and calf. There was no significant developmental trend of the approach-leave index in Emy and Neike in the first 12 weeks ($r_s = -0.230$, $N = 34$, $p = 0.096$). Eva contributed more to the maintenance of proximity with her calf than did Emy, but this difference was not significant after Bonferroni correction ($Z = -2.029$, $N = 25$, $p = 0.042$; number of tests $k = 2$, adapted level of significance $p = 0.025$).

Weeks 13-52. With the exception of weeks 21-24, the approach-leave coefficient stayed below -.1 until week 44 in Eva and Noah, indicating a slightly higher role of Eva in the maintenance of proximity. At the end of the first year, Eva and Noah equally contributed to the maintenance of proximity. In Emy and Neike, we observed a slightly higher role of Emy in the maintenance of proximity in some weeks (17-20, 21-24, 33-36, 37-40, 49-52) and equal responsibility of mother and calf in others (13-16, 25-28, 29-32, 41-44, 45-48). We found no significant developmental trend of the approach-leave index in either dyad (Eva and Noah: $r_s = -0.024$, $N = 147$, $p = 0.385$; Emy and Neike: $r_s = -0.005$, $N = 140$, $p = 0.477$) and there was no significant difference between the dyads ($Z = -0.335$, $N = 130$, $p = 0.739$).

Play Behavior

Weeks 1-12. Social play started as early as in the second week in both dyads and there was no significant difference between the dyads ($Z = -1.205$, $N = 47$, $p = 0.235$). Locomotor play was first observed in week 5 in Noah and in week 7 in Neike. Again, there was no significant difference between the calves ($Z = -0.402$, $N = 47$, $p = 0.687$). In contrast, object play was significantly more frequent in Noah than in Neike ($Z = 2.666$, $N = 47$, $p = 0.008$). Noah started to play with objects in week 9, whereas Neike's first play with objects occurred after the newborn period in week 13.

Weeks 13-52. Both calves spent a high proportion of their time with play behavior, but preferred different types of play (Figures 4 and 5). Noah's most frequent play type was social play with Moby. Neike occupied herself mainly with the net, which lined the wall of her tank (Figure 1). Locomotor play was rare in both calves throughout the whole year. In contrast, both calves spent a considerable amount of time playing with objects. There was no significant difference between the calves in either locomotor or object play (locomotor play: $Z = -1.514$, $N = 147$, $p = 0.130$; object play: $Z = -0.706$, $N = 147$, $p = 0.480$). Social play was also a frequent play type in both calves, but they preferred different play partners. Whereas social play with the mother was significantly more frequent in Neike ($Z = -3.899$, $N = 147$, $p < 0.0005$), social play with Moby was significantly more frequent in Noah ($Z = -2.900$, $N = 36$, $p = 0.001$).

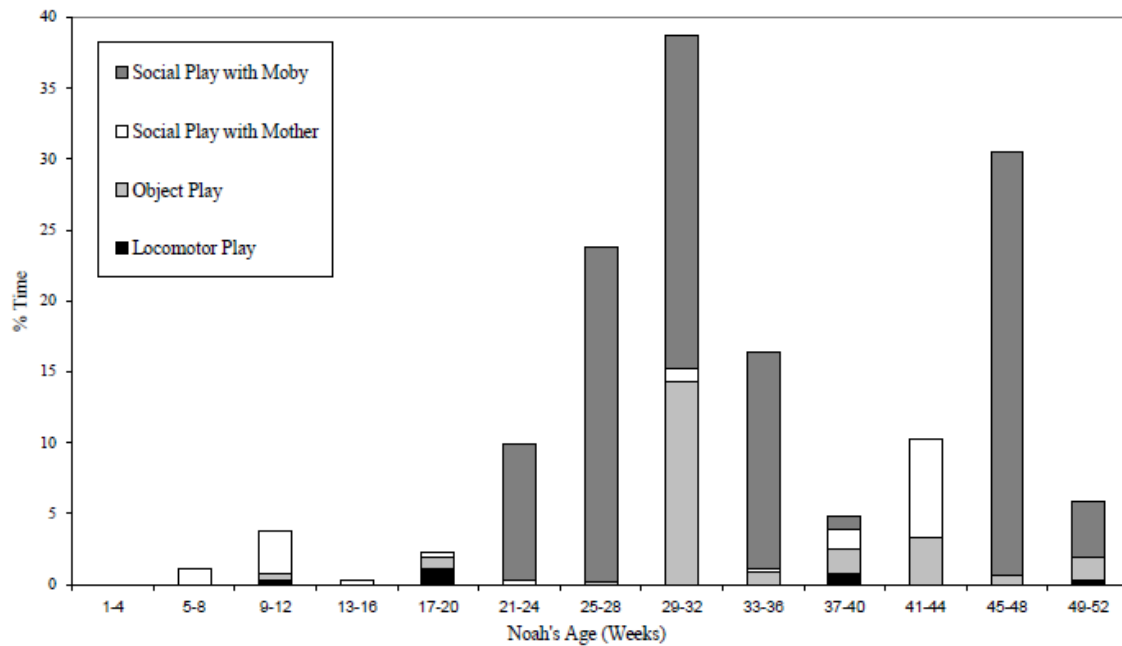


Figure 4. The median proportion of observation time that Noah spent for the different types of play (see Appendix B for 1st and 3rd quartiles and outliers). Sample size was $N = 16$. Exceptions: $N = 15$ in weeks 5-8 and 41-44; $N = 14$ in weeks 33-36 and 37-40; $N = 13$ in weeks 29-32. Moby had access to Eva's and Noah's section of the tank from the 23rd week onward.

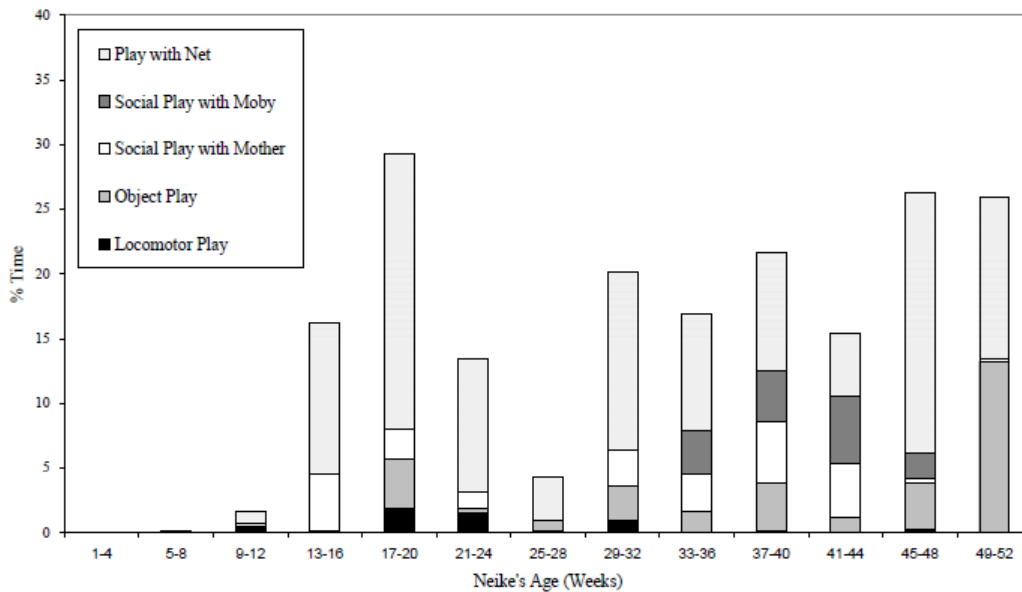


Figure 5. The median proportion of observation time that Neike spent for the different types of play (see Appendix C for 1st and 3rd quartiles and outliers). Sample size was $N = 16$. Exceptions: $N = 15$ in weeks 25-28, 29-32 and 33-36; $N = 14$ in weeks 37-40 and 49-52. Moby had access to Emy's and Neike's tank from the 33rd week onward.

Social Behavior

Weeks 1-12. The mother-calf interaction *swim together* was significantly more frequent in Emy and Neike ($Z = -2.053$, $N = 47$, $p = 0.040$). There was no significant difference between the dyads in the interactions *flipper-rub* ($Z = 0.639$, $N = 47$, $p = 0.533$), *rest together* ($Z = -0.059$, $N = 47$, $p > 0.999$), and *calf watches mother* ($Z = -0.022$, $N = 47$, $p = 0.989$).

Weeks 13-52. Swimming together was by far the most frequent mother-calf interaction throughout the whole first year and there was no significant difference between the dyads ($Z = -0.551$, $N = 147$, $p = 0.292$). In contrast, the dyads showed significant differences in nearly all other social behaviors. Whereas mother-calf interactions were more frequent in Emy and Neike (*flipper-rub*: $Z = -7.267$, $N = 147$, $p < 0.0005$; *rest together*: $Z = -6.440$, $N = 147$, $p < 0.0005$; *social play*: $Z = -3.899$, $N = 147$, $p < 0.0005$; *calf watches mother*: $Z = -5.482$, $N = 147$, $p < 0.0005$), most interactions with Moby were more frequent in Moby and Noah (*swim together*: $Z = -3.589$, $N = 36$, $p < 0.0005$; *rest together*: $Z = 3.010$, $N = 36$, $p = 0.002$; *social play*: $Z = -2.900$, $N = 36$, $p = 0.001$). The behavior *calf watches Moby* was the only interaction with Moby in which no significant difference was found ($Z = -1.254$, $N = 36$, $p = 0.150$).

Discussion

This study presents detailed information on the suckling behavior, spatial relations, play behavior, and social behavior of two captive dolphin calves, thus adding to the understanding of dolphin behavioral development. The two dyads differed in the development of suckling and

swimming behavior, suggesting an influence of the mother's parity in the first weeks. Differences in social behavior after the first weeks are suggestive of a potential effect of the calf's sex. The calves showed a high need for play and seemed to be flexible concerning the different types of play.

Suckling Behavior

Emy (primiparous mother) and Neike needed more time to develop appropriate suckling behavior than Eva (multiparous mother) and Noah: The frequencies of suckling and of side presentation declined more rapidly in Eva and Noah. For dyads with multiparous females, a steep decline in the first weeks was also observed by Mello et al. (2005), Peddemors et al. (1992), and Reid et al. (1995). In contrast, the dyad with a primiparous mother studied by Reid et al. showed a slow decrease, as was true for Emy and Neike. It seems likely that a lack of experience delays suckling routine. Future research in a greater sample size can hopefully clarify the influence of the mother's parity on early suckling behavior.

After the newborn period, Neike's suckling frequency further decreased, supporting previous research (Cockcroft & Ross, 1995; Mello et al., 2005; Peddemors et al., 1992). A marked decrease appeared when she started regular fish intake in week 30. The opposite trend, an increase in suckling frequency after the first months, seems to be less common. Apart from Noah, this development was observed in two calves by Triossi et al. (1998). The reason for this deviating pattern is unknown. The date of the regular consumption of fish might play a role, but can not be the only explanation: Although one of the calves studied by Triossi et al. (1998) as well as those observed by Cockcroft and Ross (1995) and Peddemors et al. (1992) started regular fish intake in the 11th month, Triossi et al. (1998) observed an increase in suckling frequency before this time whereas Cockcroft and Ross (1995) and Peddemors et al. (1992) found the opposite, a decrease in suckling frequency.

Swimming Positions

In the first weeks, the two dyads showed different developmental patterns in the two major swimming positions. In Eva and Noah, the rate of the mother-calf position significantly increased with Noah's age and the echelon position significantly decreased, replicating earlier studies of both captive (Gubbins et al., 1999) and free-living (Mann & Smuts, 1999) dolphins. In contrast, Emy and Neike as well as the dyad with the primiparous female in Reid's et al.'s study (1995) deviated from the general pattern. They showed a significant decrease in the mother-calf position and no trend in the echelon position. Possibly, parity affects the early development of the two major swimming positions. The competence of females to lead their calves in the appropriate position might be a vital factor for successful rearing.

In both our and Reid's et al.'s study (1995), the dyad with the primiparous female spent significantly more time in the mother-calf position than the dyad with the multiparous female in the first weeks. Lack of experience in nursing would be an explanation, if this swimming position was related to suckling, as was presumed by Gubbins et al. (1999) and Mann and Smuts (1999). In the present study, a significant but rather low correlation between the rates of suckling and mother-calf position in the first year was found for Emy and Neike, but not for Eva and Noah. Presumably, the mother-calf position serves more than one function. For example, Gubbins et al. (1999) suggested that the mother and calf also reinforce their bond by swimming in the mother-calf position. Suckling routine was easily achieved by Eva and Noah. On the other hand, they

engaged in less social behavior than Emy and Neike (see below). Thus, the social function of the mother-calf position might have outweighed its correlation to suckling in Eva and Noah.

The relevance of the echelon position was restricted to the newborn period. After the first weeks, it was absent in Eva and Noah and very rare in Emy and Neike. In contrast, the mother-calf position became more important in Eva and Noah as was true for the dyads studied by Gubbins et al. (1999). In Emy and Neike, we observed a different pattern. They showed high rates of the mother-calf position until week 30, when Neike started to consume fish regularly and her suckling frequency dropped. Hence, the decrease of the mother-calf position in this dyad might in part be explained by the correlation between the rates of suckling and mother-calf position. However, since the correlation was rather low we suspect that more factors are involved that still need to be addressed.

Maintenance of Proximity

Eva was responsible for the maintenance of proximity in the first weeks and her contribution declined over time. This development was also observed by Mann and Smuts (1999) and Reid et al. (1995). But whereas Reid et al. found no difference between the dyad with the primiparous female and the dyad with the multiparous female, Emy and Neike deviated from this pattern. Both mother and calf were equally responsible for maintaining proximity and no developmental trend was observed. Possibly, factors other than parity have more effect on this behavior. In rhesus macaques, *Macaca mulatta*, the mother's personality (Stevenson-Hinde, 1983) influenced the role of mother and infant in maintaining proximity more than parity did. Dolphins also demonstrated different and relatively stable personalities (Highfill & Kuczaj, 2007, 2010), and the mother's personality might effect mother-calf behavior in this species as well. Furthermore, Hill et al. (2007) observed individual differences in the proximity maintenance of dolphin mothers that were in all probability linked to differences in maternal style.

By the end of the first year, both mother and calf equally contributed to the maintenance of proximity. The development was more distinct in Eva and Noah than in Emy and Neike. In the only study examining proximity maintenance in dolphins for more than a year (Chirighin, 1987) calves became more responsible around the end of the first year. However, this study involved only 1.8 hr of observation. In southern right whales, *Eubalaena australis*, the transition in responsibility from mother to calf also took place when the calf was about one year old and calves were more responsible at the beginning of the second year (Taber & Thomas, 1982). Compared to other mammals, the mothers of these two cetacean species remained responsible for the maintenance of proximity for a long period of time. Infants assume responsibility after the first months in rhesus macaques (Berman, 1980; Hinde & Spencer-Booth, 1967) and Savanna baboons, *Papio cynocephalus* (Altmann, 1980) and even as early as at the end of the first week in hyenas, *Crocuta crocuta* (Rifkin & Glickman, 2004).

Play Behavior

Locomotor play is a frequent play type in cetaceans especially in the wild, including wake-riding, surfing and intentional stranding (review in Paulos et al., 2010). Neike and Noah did not have the opportunity to engage in these activities, which might explain why locomotor play was their least relevant play type. By contrast, object play was abundant and rich in variety, especially in the second half year. Objects were present in the pools in all hours of observation from the fifth week onward. The opportunity to play with objects might have supplanted some of

the locomotor play. There was no significant difference in the amount of object play between the two calves, but it seemed that the calves preferred different toys. Noah's favorite objects were balls of all sizes and Neike favored ropes, hoops, and objects where cans and ropes were attached to each other. Similarly, Greene et al. (2011) found significant differences between two study groups of dolphins in the choice of objects, but not in the frequency of object play. In rhesus monkeys and human children, the infant's sex affected toy preference (Hassett, Siebert, & Wallen, 2008). It would be interesting to study toy preference in dolphins in a greater sample size in order to determine if sex, personality, or further factors shape the choice of favored objects.

The net in Neike's tank, which had been installed for her safety, proved to be a highly attractive play object, especially the cords that held together the parts of the net caught her attention. At one spot, the cords became unfastened. The inspection of the ends of the cords and the developing hole in the net turned into manipulation and she even succeeded in unraveling the knots. From the 13th week onward, Neike's occupation with the net exceeded the time she spent with other objects or social play. Given the high intelligence and cognitive abilities of bottlenose dolphins (review in Herman, 2006), it is not surprising that Neike preferred an object that required problem solving (how to unravel the knots of the cords) to objects that provided less opportunities for manipulation (toys). It can be concluded that objects that stimulate the calves mentally form a beneficial type of enrichment for bottlenose dolphin calves.

As soon as Moby had access to Noah's part of the tank (week 23), social play with him became Noah's predominant play type and was much more frequent than social play with Eva. Possibly, Noah and Moby would have shown a high amount of social play even earlier. Social play with Emy and with Moby were also major types of play in Neike, but were exceeded by her occupation with the net. We do not know whether different play partners would have induced more social play in Neike and whether Noah would have preferred a mentally stimulating object to playing with Moby. It seemed that the calves were flexible and modified their type of play according to the opportunities they were offered. A high variability and flexibility in dolphin play behavior was also reported by Greene et al. (2011), Kuczaj et al. (2006), and Paulos et al. (2010).

Social Behavior

The two calves differed in their social behavior. The interactions *flipper-rub*, *rest together*, *social play*, and *calf watches mother* were more frequent in Emy and Neike than in Eva and Noah. *Flipper-rub* is thought to be an affiliative behavior in dolphins (Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Sakai, Hishii, Takeda, & Kohshima, 2006). At three study sites, dolphins preferred same-sex, same-aged rubbing partners (Dudzinski, Gregg, Melillo-Sweeting, Seay, Levengood, & Kuczaj, 2012) and Sakai et al. (2006) suggested that flipper rubbing behaviors could be used as a measure of social relationship between individuals. If this was true, the relationship between Emy and Neike was stronger than that between Eva and Noah after the newborn period. On the other hand, interactions with Moby (*swim together*, *rest together*, and *social play*) were more frequent in Noah than in Neike. Furthermore, two behaviors that were thought to be affiliative in dolphins (*flipper-rub*: Dudzinski et al., 2009; Sakai et al., 2006; *mother-calf-position*: Gubbins et al. 1999) were observed in Moby and Noah – though rarely – but never in Moby and Neike. This might indicate a closer social relationship between Moby and Noah than between Moby and Neike. The differences between Neike and Noah in social behavior might in part be attributed to their sex. In bottlenose dolphins, males form strong and stable alliances with other males, whereas females maintain a large social network with other females (Connor, Wells et al., 2000). Calves must learn to meet sex-specific social demands and sex

differences in social behavior emerged as early as in the first year of life (Gibson & Mann, 2008a, 2008b). However, other factors, for example the mothers' experience or the mother's or the calf's personality, could also have contributed to the differences we observed. For example, Dudzinski et al. (2012) supposed that an individual dolphin's personality might play a role in the expression of its flipper rubbing behavior.

Our study demonstrates the diversity of dolphin behavioral development. As the dyads differed in mother's parity and calf's sex, we discussed the possible effect of these two factors on dolphin mother-calf behavior. However, it can be expected that other variables also influence mother-infant behavior in dolphins, as was shown for different species of primates (for example individual differences in temperament and personality: review in Fairbanks, 1996; mother's age, dominance rank, and group composition: review in Schino et al., 1995). Emy was younger and livelier than Eva. Possibly, the mothers' ages and personalities as well as the small group size also contributed to the differences we observed. Further research into the role of various factors in dolphin mother-calf behavior will increase our understanding of dolphin behavioral development, which is important for successfully breeding dolphins in aquaria.

Our results suggest that dyads with primiparous mothers need more time to find a suckling and swimming routine and thus should be undisturbed for a longer period of time than dyads with multiparous mothers. Additional information on early social behavior could help to compose suitable breeding groups. Furthermore, future research into the play behavior of dolphin calves is desirable, especially with regard to toy and partner preference and the design of mentally stimulating objects.

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Appendix A

Supplement to the Medians Presented in Figures 2 and 3: Outliers in the 4-Week Intervals in Suckling Frequency (No/ Hour) and the Two Major Swimming Positions (% Observation Time) for Both Calves

Neike' age (weeks)	Suckling		Echelon position		Mother-calf position	
	Noah	Neike	Noah	Neike	Noah	Neike
1-4	18; 20	23				0; 8.2; 56.9
5-8					28.3	
9-12	10		20.9; 24.1		51.9	
13-16	0		60.0	53.9		54.2
17-20			37.0	1.0; 4.3; 12.9		
21-24				15.5; 37.7; 43.8		
25-28	5	6				70.8
29-32				2.7; 6.5; 13.8	0.7; 13.5;	59.2
					32.4; 34.8	
33-36				1.4; 1.9; 33.4		36.7
37-40	0; 7	0; 1		1.7	5.2	
41-44				4.2		
45-48						31.4; 33
49-52	8			1.0; 9.5		30.5

Appendix B

Supplement to the Medians Presented in Figure 4: 1st and 3rd Quartiles and Outliers of the Different Types of Play in Noah's 1st Year. Moby had Access to Eva's and Noah's Section of the Tank from the 23rd Week onward.

Noah's age (weeks)	Locomotor play			Object play			Social play with Eva			Social play with Moby		
	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers
1-4	0.0	0.0		0.0	0.0		0.0	1.8	6.0			
5-8	0.0	1.1	3.2; 14.9; 38.8	0.0	0.0		0.0	7.6	21.2; 25.0			
9-12	0.0	3.3	8.2; 16.2	0.0	3.3	16.6; 36.0; 41.5	0.0	12.4				
13-16	0.0	0.5	1.3; 3.9; 8.3	0.0	16.7	52.3	0.0	11.5				
17-20	0.0	2.7	11.2; 15.3	0.0	2.8	10.7; 28.3	0.0	4.0	14.8; 20.8; 27.3			
21-24	0.0	2.3		0.0	2.4	7.4; 12.5	0.0	2.0	12.1; 13.5; 16.8	4.6	17.2	
25-28	0.0	0.6	2.4; 3.2	0.0	0.0	4.3; 7.4; 13.1	0.0	1.1	3.0; 3.4; 3.8	2.5	35.4	
29-32	0.0	0.7		5.8	20.8	50.8	0.0	1.1	4.4; 19.2	2.5	46.4	

Noah's age (weeks)	Locomotor play			Object play			Social play with Eva			Social play with Moby		
	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers
33-36	0.0	0.4	1.5; 2.4; 6.9	0.0	5.3	26.6; 29.9	0.0	4.4	11.0; 20.3	4.1	27.8	
37-40	0.0	3.3	21.4	0.0	24.7	91.5	0.0	2.5	13.6	0.0	8.6	34.8
41-44	0.0	0.6	2.4; 3.0; 9.4	0.3	11.2	41.6; 68.2	0.1	8.0		0.0	20.3	
45-48	0.0	0.7	6.5; 8.5	0.0	3.3	11.9; 72.5	0.0	0.1	0.2; 4.0; 8.4	3.2	48.6	
49-52	0.0	1.0		0.1	13.4	38.5	0.0	1.6	5.4	0.0	13.1	

Appendix C

Supplement to the Medians Presented in Figure 5: 1st and 3rd Quartiles and Outliers of the Different Types of Play in Neike's 1st Year. Moby had Access to Emy's and Neike's Tank from the 33rd Week onward.

Neike's age (weeks)	Locomotor play			Object play			Social play with Emy			Social play with Moby			Play with net		
	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers
1-4	0.0	0.0		0.0	0.0		0.0	0.8	2.8				0.0	0.0	
5-8	0.0	0.0	0.6; 2.7; 10.4	0.0	0.0		0.0	8.5	32.7				0.0	0.6	1.3; 5.5
9-12	0.0	7.2	25.7; 26.2	0.0	0.0		0.0	7.5	19.9; 41.6				0.0	11.0	62.3
13-16	0.0	3.8		0.0	5.4		0.0	18.0					0.0	26.5	
17-20	0.0	7.6		0.3	8.9	21.8	0.6	11.3	32.1; 40.2				4.7	33.5	
21-24	0.1	4.0		0.0	2.3	17.1; 24.5	0.0	5.2	12.3; 34.2				0.1	19.9	
25-28	0.0	0.7	1.9; 4.7	0.0	3.9	12.6; 15.4	0.0	9.3					0.7	9.8	25.1; 34.8

Neike's age (weeks)	Locomotor play			Object play			Social play with Emy			Social play with Moby			Play with net		
	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers	1 st Q	3 rd Q	Outliers
29-32	0.1	3.6		0.8	14.8	47.2	0.2	12.6					7.1	18.5	
33-36	0.0	0.8	3.5; 4.0; 5,1	0.0	17.3		0.7	7.4		0.0	7.2		0.3	22.4	
37-40	0.0	1.5	4.8	1.0	16.4	46.0	3.2	10.8	39.4	0.0	9.4		5.5	15.6	33.2
41-44	0.0	0.0	1.6; 2.5; 2,6	0.0	5.4		0.4	10.7	30.4; 31.2	2.3	8.0		0.8	13.5	38.7
45-48	0.0	1.3	3.1	1.4	8.1	23.2	0.0	4.7	33.7	0.0	11.1		4.7	28.5	
49-52	0.0	0.1	1.8	2.8	30.1		0.0	12.3	36.4	0.0	1.2	10.8	6.8	21.7	50.0