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The development of suckling behavior in two captive-born calves of bottlenose dolphins (*Tursiops truncatus*)

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Abstract

Few contrasting results have been obtained on nursing patterns of newborn and infant dolphin calves, so that the development profile of this behavior is still largely unknown. The aim of the present study was to observe, from birth to one year of age, the development of suckling behavior of two *Tursiops truncatus* calves that were born three weeks apart in the same aquarium. Duration, frequency, lateralization, and day/night patterns of attempted (AS) and successful (SS) suckling episodes were scored. Observations followed this rationale: (a) 1st week: 20 hours/day; (b) 2nd–8th week: 20 hours/week; (c) 9th–16th week: 20 hours/2 weeks; (d) 17th–52nd week: 20 hours/3 weeks. Overall, the ontogenetic profiles were rather similar in the two calves, and greater age-related changes were observed during the earlier compared to the later development period. AS frequency was high in the first postpartum phase. It readily decreased to very low levels thereafter, when SS frequency sharply increased, so that by the third day of life the correct behavior had almost totally replaced the attempts. SS duration increased over the first few days of life, and showed what appeared as a phase of adjustment around the second month. A circadian pattern was found during the first week of life for successful suckling, whose frequency and duration were higher during the night than during the day time. As for the last months of observation, individual developmental trends of suckling frequency appeared to be fairly consistent with the different time-courses of weaning. Finally, no definite evidence for any nipple preference appeared.

Introduction

When compared to other marine mammal species, maternal investment in bottlenose dolphins (*Tursiops truncatus*) is prolonged and intensive, and the duration of the mother–calf bond in the wild is highly variable, ranging from 2 to 11 years (Wells, 1990; Amundin, 1986; Caldwell & Caldwell, 1966; Cockroft & Sauer, 1990; Dudock van Heel & Mettivier Meyer, 1974; Hester, 1981; McBride & Hebb, 1948; Prescott, 1977). This long association also corresponds to a prolonged period of suckling. Although the estimated age at weaning in captive bottlenose dolphins is 18–20 months (McBride & Kritzler, 1951; Tavolga, 1966; Tavolga & Essapian, 1957), nursing can continue in the wild until beyond the age of 4.5 years (Wells, 1990). However, studies on feeding behavior in wild dolphins have generally been complicated by the fully aquatic nature of the animals and by the need to monitor individually recognisable dams and their offspring over periods of months or years (Wells, 1990). As a consequence, information has mainly been collected in captive conditions, which—although possibly influencing behavior with environmental constraints—allow for a continuous and detailed monitoring process (Norris, 1991).

Descriptions of suckling behavior in bottlenose dolphins have been provided by many authors (Cockroft & Ross, 1990; Essapian, 1953; McBride & Kritzler, 1951; Peddemors *et al.*, 1992; Tavolga & Essapian, 1957; Tayler & Saayman, 1972; Drinnan & Sadlier, 1981). Cockroft & Ross (1990), in a study carried out on a bottlenose dolphin calf, reported that suckling bouts were generally initiated by the calf. Usually, before suckling, it starts to swim underneath the mother, with either its dorsal fin or the top of the melon touching her genital region. It is possible that the duration of this bumping behavior is higher before the first suckling episode of each bout than between the following ones, and is required to initiate the 'let-down' of milk into the lactiferous canals (Cockroft & Ross, 1990; Kastelein *et al.*, 1990; Peddemors *et al.*, 1992; Tavolga & Essapian, 1957). Alternatively or additionally, such a behavior may provide the calf with information on the relative

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fullness of the mammary glands (Cockroft & Ross, 1990).

For the first month post-partum, the calve's feeding is generally associated to a sideways presentation by the dam, who arches her back and presents the calf with her mammary area (Cockroft & Ross, 1990; Eastcott & Dickinson, 1987). This posture may make suckling easier for the calf, whose respiratory and swimming efficiency is still low. Thereafter, suckling often occurs with the dam remaining in a vertical position, which possibly facilitates milk passage along the longitudinal lactiferous canals (Cockroft & Ross, 1990; Peddemors *et al.*, 1992). During suckling, she stops fluke movements and holds her peduncle high to allow the calf easy access to the glands. Possibly due to the initial mother's inability to provide milk and/or to the calve's inexperience, a great number of unsuccessful attempts to suckle—i.e. when infants do not succeed in inserting their mandibular tips into the mammary slit (see Methods for a better description)—can be seen during the first period after birth (Cockroft & Ross, 1990).

As for the study of the developmental trend shown by the occurrence of suckling bouts, Eastcott & Dickinson (1987) found that the first, unsuccessful, attempt to suckle occurred approximately 17 h after parturition, whereas the first successful one was observed 4 h later. These authors also reported that the frequency of attempted suckling episodes was high on the first few days after birth, markedly decreasing thereafter. In addition, Peddemors *et al.* (1992) observed a rapid decrease in suckling frequency—scored irrespectively of successfulness—during the first week of life, and suggested that such a phenomenon may be due to the initially high and subsequently decreasing number of unsuccessful attempts.

However, apart from a few studies, often reporting occasional observations or concerning scattered and/or short periods of the behavioral ontogeny of one single calf (Cockroft & Ross, 1990; Eastcott & Dickinson, 1987; Peddemors *et al.*, 1992), little has been done to gather quantitative data to characterize the development of suckling behavior in the bottlenose dolphin. The aim of the present work was to address such an issue by carrying out a longitudinal observational study based on a continuous and systematic time sampling of suckling episodes from birth throughout the first year of life of two calves. The hypotheses of a circadian suckling pattern (Eastcott & Dickinson, 1987; Harrison, 1968; Peddemors *et al.*, 1992) and of a nipple preference (Cockroft & Ross, 1990; Peddemors *et al.*, 1992), i.e. other issues which in bottlenose dolphins have been given few and inconsistent answers, were also investigated.

Materials and methods

Animals and breeding

The subjects of the study were two newborn male bottlenose dolphins (*Tursiops truncatus*) and their mothers, all housed in the 'Aquatic World' dolphinarium (Cattolica, Italy). The calves, named Tabo and Golia, were born in the pool during the early summer of 1993 (15 June, Tabo, and 6 July, Golia), three weeks apart from each other. Tabo's mother, Candy, was approximately 15-years-old, came from Texas, and was kept in captivity from the age of 4 years. The primiparous mother of Golia, named Isa, was approximately 7-years-old, came from Cuba, and lived in captivity from the age of 2 years.

During the last four months of gestation, parturition, and the four months thereafter, the pool housed one more dolphin, an unrelated sub-adult male, approximately 7-years-old, which came from Cuba and was at the dolphinarium from 5 years (in October this animal was transferred to another dolphinarium). The father of both calves lived in the nearby dolphinarium of Riccione ('Adriatic Sea World'), was approximately 15-years-old, came from Texas, and was kept in captivity from the age of 4 years.

Apparatus and procedures

The study was carried out at Cattolica's aquarium, where the open-air oval pool (19 × 15 m; capacity: 1000 m^3; surface: 300 m^2; maximum height: 3.6 m) is equipped with six underwater windows (80 × 70 cm). Hygienic conditions were controlled by means of a close-circuit water system, and the pool's conic bottom promoted the animals' waste matter concentration. Water was checked weekly for the presence of bacteria, and *Colibacilluses* were kept under 20 colonies/100 ml. A chemical conditioning system controlled the intake of sodium hypoclorite-based disinfectants, and such compounds were constantly kept in the range of 0.4–0.7 p.p.m. pH was kept between 7.7 and 7.9, and the water density was approximately 25–33 gr/l. The water temperature oscillated, depending upon the season, between 13 and 27°C.

Suckling behavior was constantly monitored from birth to 52 weeks of age. A total of 600 h of observation, corresponding to 300 sessions each lasting 120 min for each mother–calf pair, was carried out. To obtain a more thorough evaluation of the first post-partum period but also maintain a standard time sampling as to obtain comparable data sets throughout the whole year, observations were carried out according to the following temporal schedule: (1) 1st week: 20 hours/day; (2) 2nd–8th week: 20 hours/week; (3) 9th–16th week: 20 hours/2 weeks; (4) 17th–52nd week: 20 hours/3 weeks. Observation times were counterbalanced to

equate, as much as possible, the representation of the different days (within each week/weeks) and of the different times of day (within each day). However, a restricted portion of the night phase (02:00–06:00 h) was excluded from the analysis, because in that period the animals were resting most of the time.

Suckling was defined as being apparently successful (successful suckling episodes, SS) when the calf inserted its lower jaw into the mother's urogenital groove and placed the upper jaw in contact with the skin immediately lateral to the mammary gland; the calf immediately stopped its own swimming movements to ride in the vortex created through the dam's momentum, and this posture was taken as an indication of milk intake. A little cloud of milk only sometimes disseminated into the water as the infant relinquished its hold (McBride & Kritzler, 1951), so that, also for a matter of visibility, the observation of the milk cloud was not considered as a valid criterion to discriminate between successful and unsuccessful suckling episodes. Suckling was considered concluded when the calf separated from the teat (Peddemors *et al.*, 1992). Unsuccessful or attempted suckling episodes (AS) were scored when the infant, approaching the mammary area, did not succeed in inserting the rostral and mandibular tips into either of the mammary slits; in this case, no cessation of body movements was observed (Peddemors *et al.*, 1992).

By means of a chronometer and a checklist, the following parameters were scored for each calf: (a) mean AS frequency per day/week/weeks; (b) mean SS frequency per day/week/weeks; (c) mean SS duration per day/week/weeks; (d) suckling lateralization or teat preference, i.e. total frequency of left vs right teat choice per day/week/weeks, scored for both AS and SS; (e) finally, the mean frequencies and durations recorded during the first six sessions (06:00–18:00 h) were averaged, and the same was done for those scored during the last three (20.00–02:00 h), to obtain, for both AS and SS, a day and a nighttime suckling estimate per day/week/weeks.

Design and statistical analysis

Mean frequencies and durations per day/week/weeks were analysed by a mixed-model factorial ANOVA, with Tabo and Golia as the levels of the first factor (animal), and age as the repeated measures factor. The design used the error estimated from intra-day repeated measures. Multiple comparisons with orthogonal and non-orthogonal coefficients were performed when necessary. A separate ANOVA was used to compare night and day data. Left vs right teat comparisons were performed by means of a Student's *t*-test for correlated measures.

Results

Attempted suckling frequency

A total number of 496 and 572 attempted suckling episodes was recorded throughout the studied year, respectively for Tabo and Golia. No attempted suckles (AS) were seen in the immediate time after birth. Tabo's first episode occurred 3.5 h after birth, while Golia's was observed 1.5 h after parturition.

As can be seen in Fig. 1, the mean AS frequency markedly decreased during the first week of life in both calves (day: $F=12.24$; $df=6,54$; $P<0.001$; day 1 vs 2, 3, 4, 5, 6, 7: $PS<0.001$; day 2 vs 4, 5, 6, 7: $PS<0.01$). A further, although slighter, decrease was recorded in the immediately following weeks (Fig. 2; week: $F=7.03$; $df=6,54$; $P<0.001$; week 2 vs 3, 4, 5, 6, 7, 8: $PS<0.01$), after which very low levels were maintained. However, from weeks 26–28 to 50–52, the calves showed a slightly increased AS frequency, which reached higher levels around weeks 44–46 and then tended to decrease again (week: $F=4.01$; $df=11,99$; $P<0.001$; weeks 17–19, 20–22, and 23–25 vs weeks 29–31: $PS<0.01$; vs the groups of weeks from 35 to 49: $PS<0.05$; weeks 44–46 vs all the other periods from week 17 except weeks 29–31 and 35–37: $PS<0.05$).

A rather similar developmental trend characterized the two calves during the whole study. However, some differences between them were found when looking at the period ranging from week 17 to the end of the observations, and in particular at the last months (animal × week: $F=1.93$; $df=11,99$; $P<0.05$). Although Golia had shown a higher AS frequency than Tabo on weeks 26–28 ($P<0.01$), the opposite difference occurred on weeks 44–46 and 47–49 ($PS<0.05$).

Successful suckling frequency

A total number of 1774 successful suckling (SS) episodes for Tabo and 1687 SS for Golia was recorded throughout the study. The first episode was observed 11 and 20 h after birth, respectively for the two calves, so that recordings of the first day of life show an SS frequency near to zero.

A sharp increase in SS frequency was observed in both calves on days 2 and 3 (Fig. 1; days: $F=11.56$; $df=6,54$; $P<0.001$; day 1 vs 2, 3, 4, 5, 6, 7: $PS<0.001$). However, this measure readily returned to intermediate levels during the first week of life (day 5 vs 2, 3, 6, and day 7 vs 2: $PS<0.05$), and a further decrease went on for nearly two months (Fig. 2; week: $F=8.72$; $df=6,54$; $P<0.001$; week 2 vs 3, 4, 5, 6, 7, 8: $PS<0.01$; week 3 and 4 vs 5, 6, 7: $PS<0.05$; week 6 vs 8: $P<0.05$). Thereafter, SS frequency slightly but steadily increased again, so that each animal regained, by approximately its eighth–tenth month of life, values very similar to those of its first week (week: $F=5.54$; $df=11,99$;

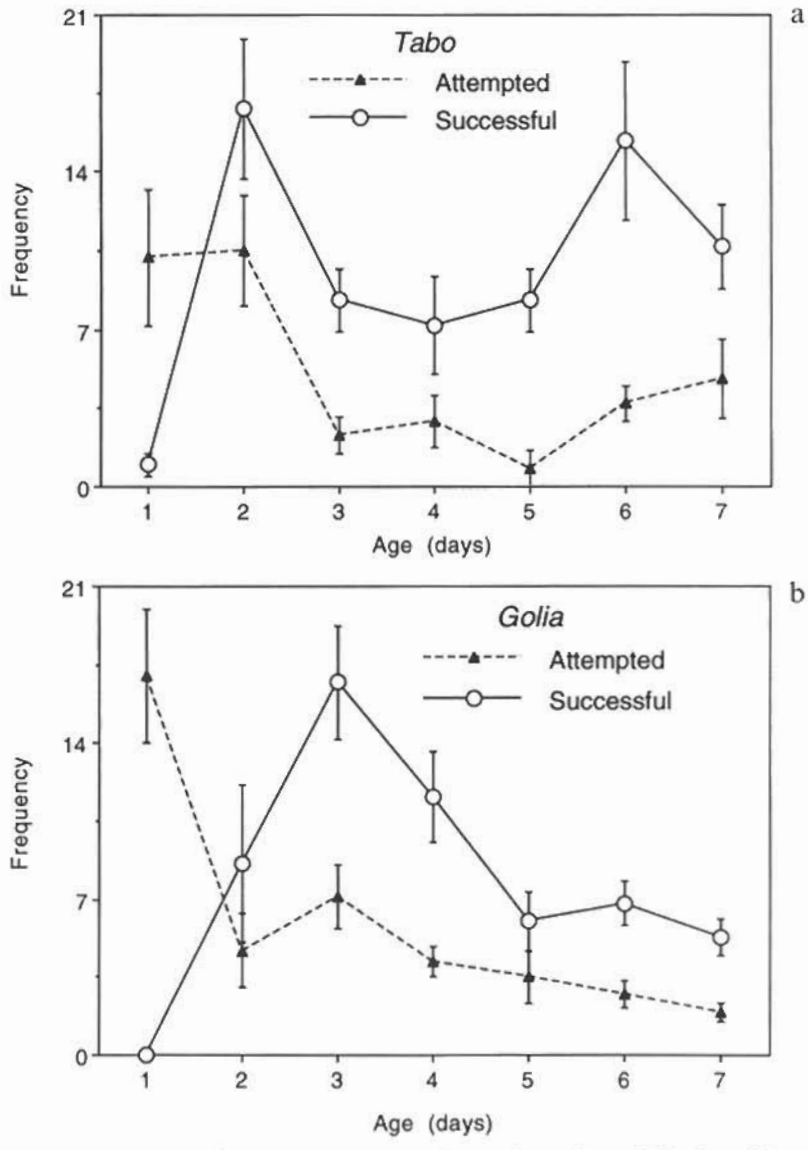

Figure 1. Mean (± SE) frequency (based on 10 observation sessions of 120 min each) of attempted (AS) and successful (SS) suckling episodes during the first week of life in the two calves.

$P<0.001$; week 44–46 vs all other groups of weeks from 17–19 onwards: $PS<0.05$). Both calves decreased their SS frequency again during the last month of observation.

Although such an ontogenetic profile was rather similar in the two calves, some slight differences appeared between them. In particular, it has to be mentioned that the final decrease in SS frequency appeared to be more pronounced in Golia, whose score was in fact overtaken by Tabo from weeks 44–46 to the end of the study (animal × week: $F=3.18$; $df=11,99$; $P<0.001$; all comparisons: $P<0.01$).

Successful suckling duration

Tabo spent a total of 10.385 s suckling, the corresponding time for Golia being 9.313. A clear-cut developmental profile, which was markedly similar in the two calves, emerged for the mean duration of

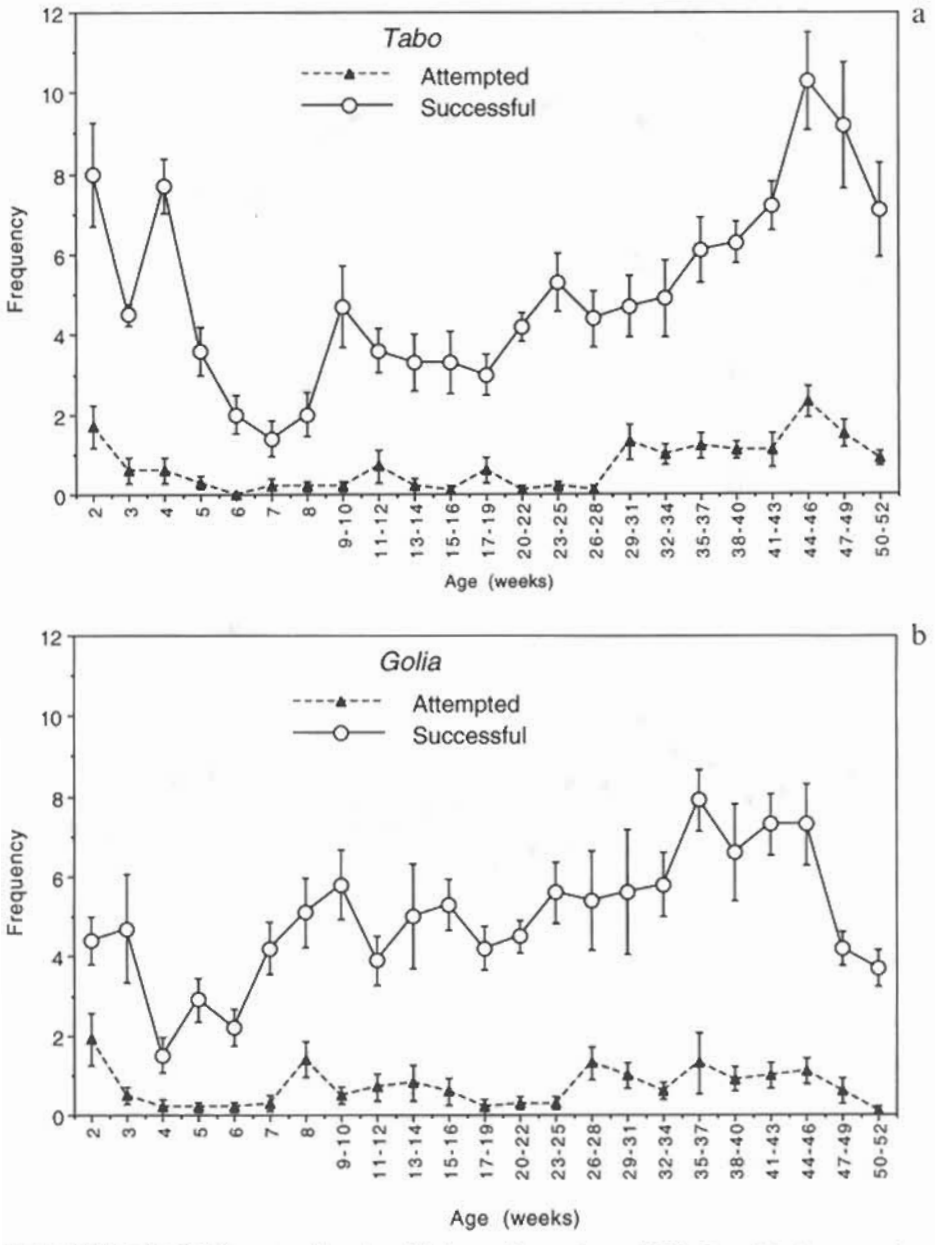

Figure 2. Mean (± SE) frequency (based on 10 observation sessions of 120 min each) of attempted (AS) and successful suckling (SS) episodes from week 2 to week 52 in the two calves.

successful suckling. As for the first week of life (Fig. 3a), SS duration was very low on day 1, while a threefold increase was observed during the following two days (day: $F=57.76$; $df=6,54$; $P<0.001$). Thereafter, it remained nearly constant, so that all comparisons between day 1 and the other days yielded significance ($PS<0.001$).

The following months were characterized by slight but significant variations in SS duration, which remained throughout the study period in the range of 4–8 s (Fig. 3b). A slight increase was observed around the end of the second month of age, which was however immediately followed by a decreasing trend (week: $F=5.44$; $df=3,27$; $P<0.01$;

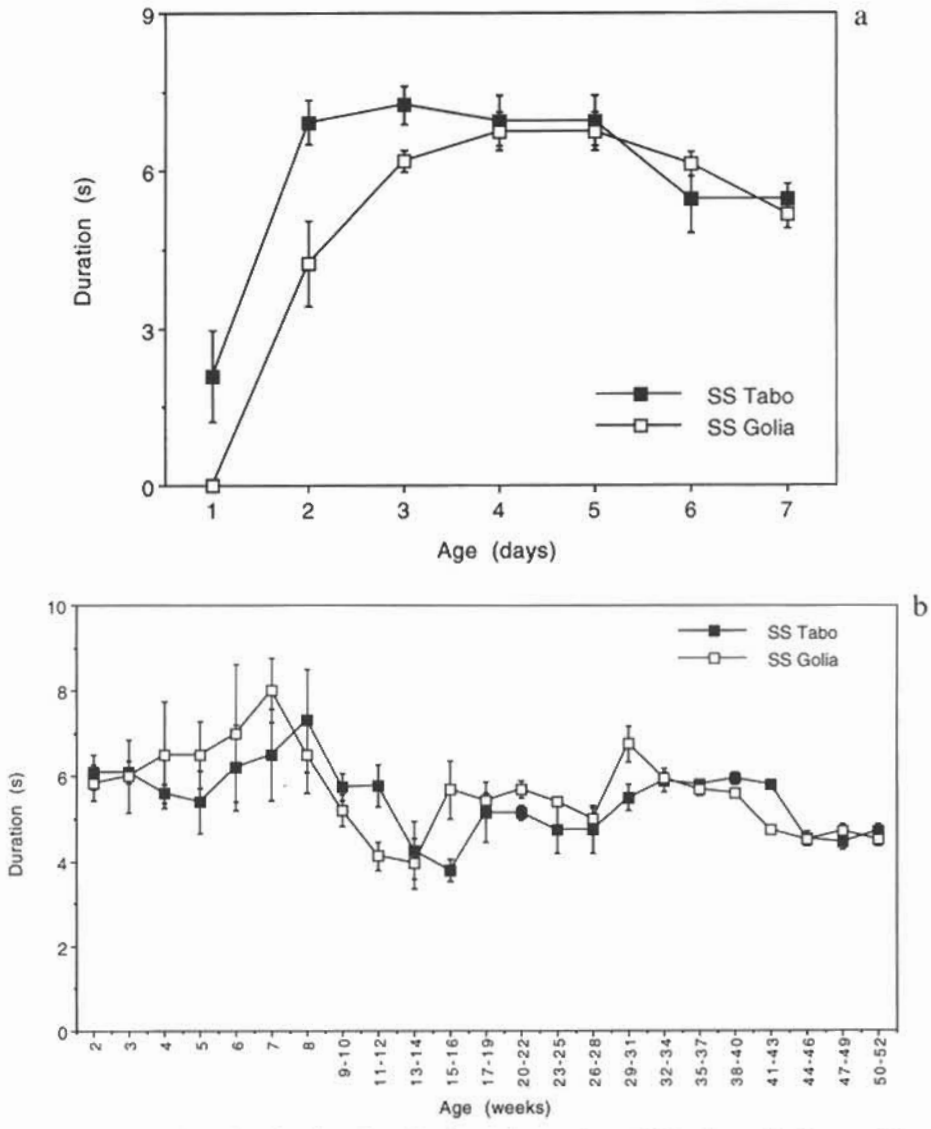

Figure 3. Mean (± SE) duration (based on 10 observation sessions of 120 min each) of successful suckling episodes (SS) in the two calves: (a) during the first week of life; (b) from week 2 to week 52.

weeks 9–10 vs 13–14 and 15–16: $PS<0.05$; weeks 11–12 vs 13–14: $PS<0.05$). By the end of the fourth month of age, intermediate levels were regained and maintained throughout the study, although some minor fluctuation was still significant (week: $F=7.65$; $df=11,99$; $P<0.001$; weeks 26–28 vs 29–31: $P<0.001$; weeks 38–40 vs 44–46: $P<0.001$; weeks 41–43 vs 44–46: $P<0.01$).

Besides other minor differences between the two calves, Golia was higher than Tabo on weeks 29–31, whereas the opposite difference occurred on weeks 41–43 (animal × week: $F=2.03$; $df=11,99$; $P<0.05$).

Day/night differences

No significant differences in the frequency of attempted suckling were observed when comparing the day to the night time. As for successful suckling, both frequency and duration measures showed some significant day/night differences during the first week. On days 2 and 3, the infants suckled

Table 1. Total frequency of left vs right teat choice per day (based on 10 observation sessions of 120 min each), for attempted (AS) and successful (SS) suckling episodes in the two calves during the first week of life

	Days of age						
	1	2	3	4	5	6	7
AS Tabo							
Right	39	34	6	14	2	3*	8†
Left	63	71	17	15	6	34	40
AS Golia							
Right	87	13	22‡	17	17	16	9
Left	83	34	49	25	18	11	10
SS Tabo							
Right	4	43	40	32	9	69	55
Left	6	82	43	40	12	85	52
SS Golia							
Right	0	40	87	42	28	37	34
Left	0	46	80	74	32	31	19

*AS Tabo RI vs LE, $P<0.001$.
†AS Tabo RI vs LE, $P<0.05$;
‡AS Golia RI vs LE, $P<0.01$.

more frequently during the night ($P<0.0001$ and $P<0.05$, respectively; means for day vs night: 6.25 vs 23.3 and 8.25 vs 9.33, respectively), whereas this difference was reversed on day 5 ($P<0.05$; means for day vs night: 8.83 vs 3.33). In addition, both animals reached higher SS durations during the night compared to the day all over the first week ($P<0.0001$; means for day vs night: 5.03 vs 6.17; in particular, $P<0.0003$ for Tabo and $P<0.001$ for Golia; means for day vs night: 5.36 vs 6.60 and 4.05 vs 5.75, respectively for the two calves).

Nipple preference

A difference in the mean AS frequencies between the left and the right teat emerged only during the first week (see Table 1; Student's t-test: $t(69)=4.63$ and 2.04, $P<0.001$ and 0.05, respectively for Tabo and Golia), when both infants tried to suckle more frequently on the left nipple (Golia, day 3: $P<0.01$; Tabo, day 6: $P<0.001$; Tabo, day 7: $P<0.05$). In addition, the t-test showed that the two calves exhibited no preference for successful suckling on either the left or the right teat during the whole year studied (totals: 810 right and 964 left for Tabo; 809 right and 878 left for Golia).

Discussion

The present study describes the development of suckling behavior during the first year of life of two calves of *Tursiops truncatus*. A high frequency of attempted or unsuccessful suckling episodes (AS) was observed during the first postpartum phase. However, AS episodes were more frequent than successful ones (SS) only during the first day of life. In fact, AS frequency readily decreased to very low levels when SS episodes appeared and sharply increased in their frequency, so that by the third day of life, the correct behavior had almost totally replaced the attempts. These data confirm and accurately describe the initial decrease in AS frequency observed by Eastcott & Dickinson (1987) and suggested by Peddemors *et al.* (1992). However, it is difficult to explain why a slight increase in AS frequency occurred in the present study after the sixth month of life, also because no data are reported in the literature about the development of this parameter beyond the first postpartum phase.

Both dam's postural presentation and calf's learning should play a role in the development of a correct suckling behavior in bottlenose dolphins (Cockroft & Ross, 1990). The present data on the initial decrease of AS coupled with the increase of SS frequency are likely to be explained by the dams' and calves' physiological and behavioral maturation. From a behavioral point of view, the development of successful suckling was preceded in our study by what may be considered as a brief 'training period', in which calves often attempted to suckle at incorrect parts of the dam's body. This kind of behavior was particularly evident for the Isa–Golia pair during the first hours of life, when the calf tried to suckle at nearly all the mother's skin folds. The dam did not help Golia to find the nipples and no display of the mammary area was seen during the whole first day—a behavior that might be attributed to Isa's primiparity.

As for the developmental trend of the frequency of SS episodes beyond the first three days of life, part of our data seems to agree with the scattered indications in the literature. In particular, a decrease in suckling frequency during the first week has been observed by Peddemors *et al.* (1992) and by Eastcott & Dickinson (1987). As for the following period, the decrease in SS frequency we found during the second month of life was recorded in a similar developmental phase by Peddemors *et al.* (1992) and by Eastcott & Dickinson (1987). Similar observations were also made by Cockroft & Ross (1990). It might therefore be concluded that at least the early ontogenetic trend of SS frequency is rather constant and determined in developing calves of bottlenose dolphin. However, in contrast to our and Peddemors' results, Gurevich (1977) and Cockroft & Ross (1990) reported that the increase in bouts frequency observed by the third month was followed by a highly variable decrease.

It seems most likely that the final decrease we recorded in SS frequency during the last two months can be attributed to weaning. It has been reported that captive bottlenose dolphin calves usually show their first interest in fish between 3 and 9 months of age. During this period, according to Leatherwood (1977), they obtain about 50% of their nourishment from nursing and 50% from fish-food. In the present study, the weaning process started spontaneously in both calves between 6 and 9 months, involving progressively greater amounts of solid food. Different authors (Cockroft & Ross, 1990; Peddemors *et al.*, 1992) suggested that a continuous decrease in suckling rates may be the result of weaning. In this frame, it has to be recalled that, although the overall developmental profile was grossly similar for the two calves, during the last two months Golia showed a more marked decrease in suckling frequency compared to his half-sibling. Such a difference can most likely be attributed to the different time-course of weaning in the two calves. In fact, the latter started spontaneously at 6 months of age for Golia, and only later, i.e. at 9 months of age, for Tabo. Each infant, during its first two months of weaning, occasionally consumed a small amount of fish (i.e. small herrings). After this period, solid food intake became more regular and both animals took a daily amount of fish of about 500 g. However, while Tabo presented an initial delay and was still showing a low level of fish intake, Golia markedly increased his consumption of solid food (up to 1 or 2 kilos/day) at 11 months of age. This was precisely the time when Golia's marked decrease in SS frequency appeared, being more evident than that of his half-sibling, who was still relying on suckling as a major food source. The analysis of the second year data, which is still in progress, will more thoroughly depict the relationship between the time-course of weaning and that of suckling behavior.

The assessment of the duration of suckling bouts in developing bottlenose dolphin calves has received scattered attention in the literature and although discrepancies are not big, different results have been reached. Moreover, whereas only a few studies measured this parameter over different developmental time-points, our longitudinal study was precisely aimed at such a characterization and provides an accurate picture of the time-course during the whole first year of the calves' life. When comparing the present results to literature data, both agreements and discrepancies can be found, but these are always a matter of a few seconds. In agreement with our findings, Kastelein *et al.* (1990) reported that, during the first month of life, suckling episodes lasted for a maximum of 10 s. In addition, for the first three months, Cockroft & Ross (1990) reported a 3–9 s range, with a mean of 5.6, which is very similar to our values. However, different authors obtained a slightly higher (Cockroft & Ross, 1990; Eastcott & Dickinson, 1987; Gurevich, 1977) or lower values (Peddemors *et al.*, 1992) than those shown by our calves.

As for the possible existence of a nipple preference or suckling lateralization, the only difference found was the attempted or unsuccessful episodes during the first week, when both calves tried to suckle more frequently on the left teat. However, they did not show any lateralization in either SS frequency or duration. Such findings provide a further confirmation of the apparent lack of teat preference that has been reported by the two dolphin studies that have previously dealt with this topic (Cockroft & Ross, 1990; Peddemors *et al.*, 1992).

The first week was also the only period in which a circadian suckling pattern appeared, with both SS duration and SS frequency being higher in the night compared to daytime. Although both the studies by Cockroft & Ross (1990) and Peddemors *et al.* (1992) found no circadian trend in dolphins' suckling, the data by Eastcott & Dickinson (1987) are similar to our findings. In fact, according to their observations, during the first two weeks of life, there is a difference between day and night in the duration of interval times between succeeding suckling episodes, with nighttime intervals shorter than those for the day. These authors also reported that the time spent at the nipple was biased in the same direction. Similarly, another author (Harrison, 1968), studying a later stage of the calf's development, found that suckling occurred more frequently at night than in the daytime. According to the suggestion by Eastcott & Dickinson (1987), such a day/night pattern might be attributed to the calves' tendency to preferably suckle when minimal interruption and disturbance from the general environment occurs.

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