

Nursing behavior in captive false killer whales (*Pseudorca crassidens*)

Steven T. Clark and Daniel K. Odell

SeaWorld, Inc., 7007 SeaWorld Drive, Orlando, FL 32821-8097 USA

Abstract

The nursing behavior of two false killer whale (*Pseudorca crassidens*) calves born at SeaWorld Florida was observed continually during the first 13 weeks of life. Nursing parameters, including total nursing time (mins/week), time spent nursing (mins/hour), suckles/hour, bouts/hour, suckles/bout, suckle duration (secs) and bout duration (secs), peaked during the first week of life then slowly diminished. Mean nursing amount (mins) per week could be separated into three blocks. Nursing was most intense during week 1, followed by lesser amounts in the 2–8 week block, dropping further in the final 9–13 weeks. Though calves exhibited similar nursing patterns, there were significant differences between them among the parameters examined, perhaps as a result of individual variations in calves and mothers. Calf nursing was most intense in the afternoon (1300–1600h) and early morning (0300–0500h) and least during evening and overnight (1800–0200h) and mid-morning (0800–1000h). The amounts of time spent nursing at the left and right mammaries were equal. Change in the amount of nursing time (mins) from hour to hour could be predicted accurately from the number of suckles in a given hour in combination with the nursing time amount and number of suckles in the previous hour.

Introduction

Some of the basic questions about life history of any species deal with aspects of reproductive behavior. Among cetaceans, the bottlenose dolphin (*Tursiops truncatus*) has received most of the attention in this regard (McBride and Kritzler, 1951; Eastcott and Dickinson, 1987; Cockcroft and Ross, 1990; Peddemors *et al.*, 1992; Reid *et al.*, 1995).

Killer whales (*Orcinus orca*) have also received considerable attention (Bigg, 1982; Christensen, 1984; Walker *et al.*, 1988; Robeck *et al.*, 1993; Duffield *et al.*, 1995). More specifically, reproductive questions dealing with nursing behaviors have been examined in bottlenose dolphins (Reid *et al.*, 1995), beluga whales (*Delphinapterus leucas*) (Drinnan and Sadleir, 1981; Russell *et al.*, 1997) and killer whales (Asper *et al.*, 1988; Clark and Odell, SeaWorld, Inc., unpublished data). In the literature, there is a scarcity of information dealing with nursing behaviors of false killer whales (*Pseudorca crassidens*). Much of what is known about the reproductive biology of these animals has been gathered from mass strandings (Purves and Pilleri, 1978; Odell and McClune, 1999). Consequently, very few details are known about aspects of nursing behavior in these animals and may be related to the obvious difficulties in gathering accurate behavioral information from wild animals. Even though false killer whales are by no means the most common species in oceanaria, the few captive specimens can yield a wealth of life history information.

This study documents nursing behaviors of two false killer whales born in captivity. Our intention is to provide some information about calf nursing, thereby contributing to our knowledge of false killer whale reproductive life history parameters which, in turn, may be beneficial to field researchers and oceanarium caretakers [e.g., Kasuya *et al.* 1986, Duffield and Miller 1988].

Methods

The two female calves in this study were born at SeaWorld Florida (no. 9301 on 24 December 1993 and no. 9401 on 3 September 1994). Both calves were sired by the same male (no. 8526), but had different dams (no. 8327 and no. 8527). All parents had been at this park since 1984 and were wild caught in the Western Pacific (Japan). Both mother-calf pairs were housed in the same pool throughout the duration of data collection. Pool dimensions were 18.3 m in diameter, 3.7 m deep, with a surface

Correspondence to: Steven T. Clark, Corporate Zoological Operations, SeaWorld, Inc., 7007 SeaWorld Drive, Orlando, FL 32821-8097, (407)363-2663, fax (407)345-5397, e-mail: steve.clark@anheuser-busch.com

area of 262 m² and total volume of 972 m³. Water temperature was maintained between 23.0 and 23.5°C. The husbandry program included 24-hour observations of nursing from birth until a calf was 13 weeks old. In order to optimize accuracy of nursing data and minimize inter-observer variability, only observers with considerable previous experience with nursing behavior on cetaceans (i.e., killer whale calves born at SeaWorld) were used during the first few days following birth at which time training of future observers was conducted. This procedure minimized errors resulting from lack of discrimination between actual nursing, bumping and/or searching activities of the calf. Indicators of nursing are also well documented in the literature and were used to differentiate actual from false nursing events (McBride and Kritzler, 1951; Tavalga and Essapian, 1957; Logan and Robson, 1971; Drinnan and Sadlier, 1981; Cockcroft and Ross, 1990). These indicators include fluke movements of the calf prior to, during, and after presumed teat 'lock-on' in conjunction with the presence of milk in the water when the tongue/nipple seal was broken at the cessation of a nursing event. All data were scored on written ethograms which included entries for time of day, duration of suckle in seconds and an indication of either left or right mammary gland. Observers were stationed above the pool and communicated via walkie-talkies for consultation and confirmation of nursing events. One observer held the ethogram datasheet and recorded information for both observers.

In accordance with Reid *et al.* (1995), the following terminology was used to describe the various nursing behaviors: suckle—when the calf is actually locked-on to the nipple. Presumably the calf is obtaining milk during this time, although it is impossible to tell for certain (however, milk is frequently expelled into the water when the calf releases from the nipple, suggesting milk transfer was occurring); suckle duration—amount of time spent locked-on to the nipple; bout—a suckle or series of suckles with intersuckle intervals of <5 minutes (Drinnan and Sadlier, 1981) (this 5-minute demarcation does not have any biological significance, yet it was kept consistent throughout the study when establishing patterns of nursing, as well as when making comparisons between the two calves); bout duration—total time of suckle duration(s) in a given bout.

The amount of time spent nursing exhibited autocorrelation (runs test for trend data, $t_s = -2.78$; $P < 0.01$). Therefore, non-parametric statistical techniques were employed for some of the analyses (Sokal and Rohlf, 1995). All data analyses were done using the SYSTAT statistical package (version 6.1 for Windows, SPSS, Inc., 1996).

Results

Overall nursing patterns

The overall weekly patterns for the combined dataset of both animals were characterized by peaks in total nursing time (mins)/week, mean time spent nursing (mins)/hour, mean suckles/hour, mean bouts/hour, mean suckles/bout, mean suckle duration (secs) and mean bout duration (secs) in the first week of life followed by a slowly diminishing trend throughout the remainder of the study period (Tables 1 and 2). Intersuckle interval (mins) tended to increase throughout the 13 weeks.

Examination of the plot of mean nursing time (mins) with calf age suggested the presence of three distinct time periods (Fig. 1). It appeared week 1 was a period of the most intense nursing, followed by decreased nursing in weeks 2 through 8 with further decrease in the weeks 9 through 13.

Differences between calves

Both calves exhibited similar patterns in nursing in which nursing parameters peaked quickly within the first two weeks following birth and then decreased slowly throughout the rest of the 13 week observation period (Fig. 2).

Mann-Whitney U tests indicated, with the exception of intersuckle interval, calf no. 9301's nursing parameters exceeded those of calf no. 9401 throughout the 13 weeks of the study (Table 3).

Temporal nursing patterns

Circadian variations in nursing were calculated from a combined dataset of both calves and plotted as mean time (mins) spent nursing against time of day (Fig. 3). A LOWESS (locally weighted regression and smoothing scatterplot) curve (tension=0.2) was fitted to the data and revealed two peaks in nursing time. The LOWESS curve fitting technique forms a nonparametric regression of dependent variable upon independent variable and can be used to smooth time series plots in order to examine functional relationships between the variables (Cleveland, 1979, 1994; SYSTAT 8.0 Statistics, 1996) There was a small peak in the early morning hours (0300–0500h), a large peak during the afternoon (1300–1600h). Nursing time was least during the evening and overnight (1800–0200h) and mid-morning hours (0800–1000h). Differences in nursing time between hours were significant (Kruskal-Wallis test, $H = 76.48$; $P < 0.01$).

Mammary preference

There was no statistically significant difference between mean time spent nursing on either the left or right mammary (mean \pm SD: left = 7.66 \pm 4.05 mins., right = 7.54 \pm 3.78 mins.; Mann-Whitney test, $U = 7\ 439\ 298.5$; $P = 0.72$).

Table 1. Nursing parameters for a female false killer whale calf (no. 9301) born at SeaWorld Florida. Except for sums of observation time and total nursing time, all data are listed as mean or mean (standard deviation)

Week	Observation time (h)	Total nursing time (min)	Nursing time/hour (min)	Intersuckle interval (min)	Suckles/hour	Bouts/hour	Suckles/bout	Suckle duration (sec)	Bout duration (sec)
1	168	164.45	0.98	45.11	5.51 (7.43)	1.33 (1.26)	4.17 (5.57)	10.67 (5.65)	44.54 (72.87)
2	167	59.95	0.36	66.67	2.75 (3.31)	0.90 (0.97)	3.03 (2.54)	7.84 (4.37)	23.71 (20.45)
3	168	71.47	0.43	47.24	3.76 (3.41)	1.27 (0.88)	2.81 (1.46)	7.11 (2.89)	20.04 (12.58)
4	168	34.05	0.20	109.09	1.81 (5.35)	0.55 (0.67)	2.65 (1.48)	8.20 (3.45)	21.79 (14.23)
5	168	30.60	0.18	101.69	1.40 (1.94)	0.59 (0.70)	2.35 (1.53)	7.78 (3.08)	18.54 (11.51)
6	168	34.07	0.20	109.09	1.49 (2.23)	0.55 (1.02)	2.99 (1.97)	8.02 (3.02)	24.63 (17.08)
7	168	40.07	0.24	120.00	1.73 (2.56)	0.50 (0.60)	3.45 (2.39)	8.29 (3.20)	28.62 (20.38)
8	168	34.83	0.21	103.45	1.44 (1.96)	0.58 (1.00)	2.67 (1.61)	8.64 (4.14)	23.22 (17.47)
9	168	27.28	0.16	120.00	1.33 (1.87)	0.50 (0.60)	2.65 (1.60)	7.34 (3.51)	19.49 (14.59)
10	168	21.12	0.13	133.33	1.18 (1.83)	0.45 (0.63)	2.62 (1.56)	6.37 (2.92)	16.67 (11.90)
11	168	29.02	0.17	100.00	1.60 (2.36)	0.60 (0.79)	2.66 (1.70)	6.47 (2.79)	17.24 (11.52)
12	168	37.58	0.22	100.00	1.81 (2.58)	0.60 (0.74)	3.01 (1.71)	7.42 (3.38)	22.36 (14.83)
13	168	35.42	0.21	100.00	1.80 (2.40)	0.60 (0.69)	3.03 (1.87)	7.04 (2.83)	21.15 (15.02)
Σ	2183	619.90							
All 13 weeks			0:28 (0.22)	96.59 (27.15)	2.12 (1.23)	0.69 (0.29)	3.03 (2.77)	8.16 (4.16)	24.82 (32.56)

Table 2. Nursing parameters for a female false killer whale calf (no. 9401) born at SeaWorld Florida. Except for sums of observation time and total nursing time, all data are listed as mean or mean (standard deviation)

Week	Observation time (h)	Total nursing time (min)	Nursing time/hour (min)	Intersuckle interval (min)	Suckles/hour	Bouts/hour	Suckles/bout	Suckle duration (sec)	Bout duration (sec)
1	168	123.65	0.74	43.48	5.20 (5.65)	1.38 (1.23)	3.73 (2.87)	8.46 (4.08)	31.47 (27.05)
2	168	44.32	0.26	80.00	2.31 (2.57)	0.75 (0.74)	3.31 (3.24)	6.93 (3.40)	21.51 (15.41)
3	168	24.77	0.15	95.24	1.36 (1.71)	0.63 (0.65)	2.41 (2.98)	6.49 (2.58)	13.81 (8.52)
4	168	25.25	0.15	101.69	1.39 (1.82)	0.59 (0.65)	2.30 (1.31)	6.47 (2.78)	15.30 (8.92)
5	168	18.90	0.11	130.43	1.01 (1.55)	0.46 (0.68)	2.19 (1.12)	6.71 (2.89)	14.73 (7.67)
6	168	19.08	0.11	111.11	1.06 (1.53)	0.54 (0.72)	1.99 (1.07)	6.43 (2.74)	12.74 (9.11)
7	168	23.02	0.14	103.45	1.36 (1.72)	0.58 (0.64)	2.34 (1.37)	6.02 (2.59)	14.09 (9.79)
8	168	12.07	0.07	130.43	0.80 (1.31)	0.46 (0.66)	1.74 (1.06)	5.40 (2.10)	9.40 (6.04)
9	168	14.25	0.08	122.45	0.92 (1.39)	0.49 (0.66)	1.81 (0.93)	5.55 (2.33)	10.34 (6.05)
10	140	13.67	0.10	157.89	0.81 (1.48)	0.38 (0.65)	2.13 (1.21)	6.03 (2.29)	12.81 (7.58)
11	168	10.28	0.06	146.34	0.81 (1.30)	0.41 (0.59)	1.97 (1.09)	5.23 (2.09)	10.11 (6.43)
12	168	16.15	0.10	146.34	1.00 (1.63)	0.41 (0.59)	2.43 (1.30)	5.77 (2.57)	14.04 (8.81)
13	160	9.77	0.06	127.66	0.80 (1.30)	0.47 (1.08)	1.97 (0.95)	4.58 (2.26)	9.08 (6.68)
Σ	2148	355.72	0.16 (0.18)	115.12 (31.03)	1.46 (2.51)	0.58 (0.80)	2.55 (2.15)	6.79 (3.36)	17.02 (16.19)

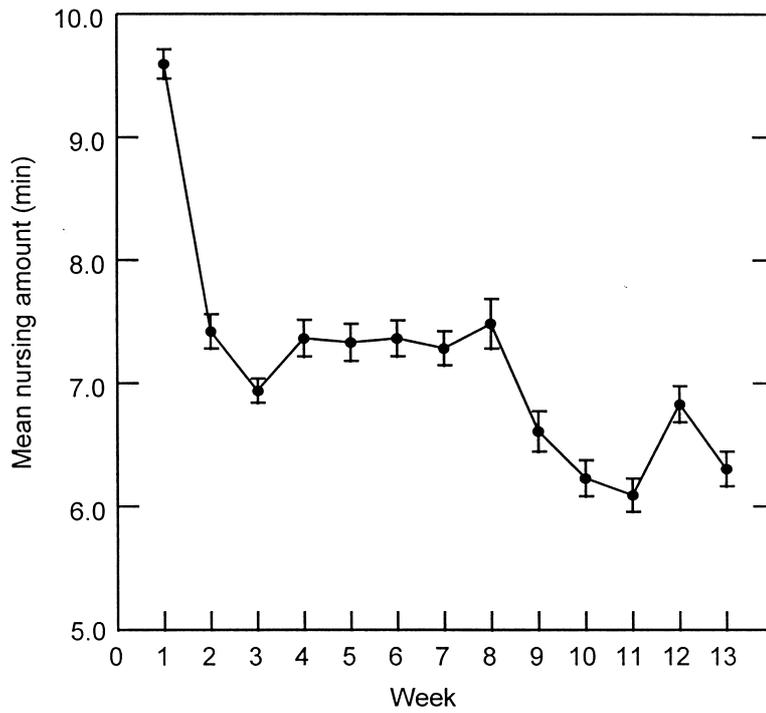


Figure 1. Mean nursing time (mins) by week since birth for two captive-born false killer whale calves (no. 9301 and no. 9401) at SeaWorld Florida. Bars represent ± 1 standard error.

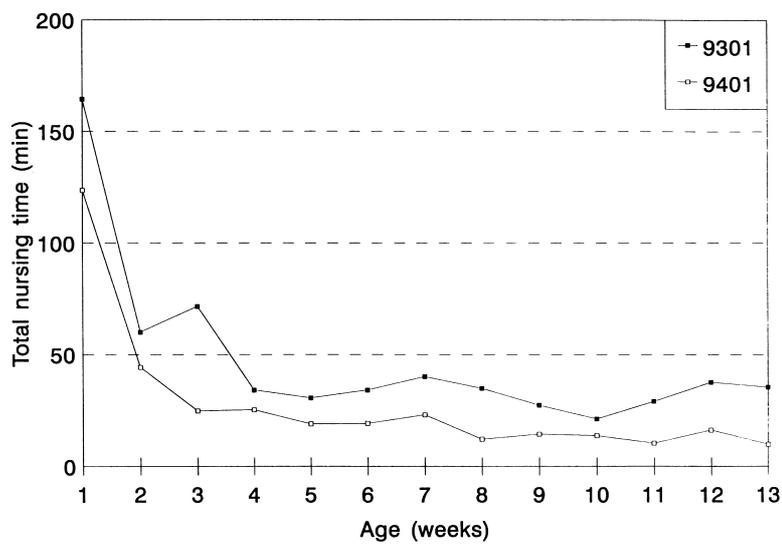


Figure 2. Total daily nursing time (mins) by week since birth for two female captive-born false killer whale calves (no. 9301 and no. 9401) at SeaWorld Florida. Data begin with first full day of nursing following birth (i.e., day 1=second day of life).

Table 3. Comparisons of nursing parameters between two female false killer whale calves born at SeaWorld Florida. Results are presented for the first 13 weeks of life. Values for 'P' were derived from Mann-Whitney U tests and were considered significant at $\alpha=0.05$

Parameter	E	No. 9301 mean	SD	E	No. 9401 mean	SD	P
Total nursing time (min)	619.90			355.72			
Nursing time/hour (min)		0.28	0.23		0.16	0.18	0.002
Intersuckle interval (min)		96.59	27.15		115.12	31.03	0.095
Suckles/hour		2.12	1.23		1.46	2.51	<0.001
Bouts/hour		0.69	0.29		0.58	0.80	<0.001
Suckles/bout		3.03	2.77		2.55	2.15	<0.001
Suckle duration (sec)		8.16	4.16		6.79	3.36	<0.001
Bout duration (sec)		24.82	32.56		17.02	16.19	<0.001

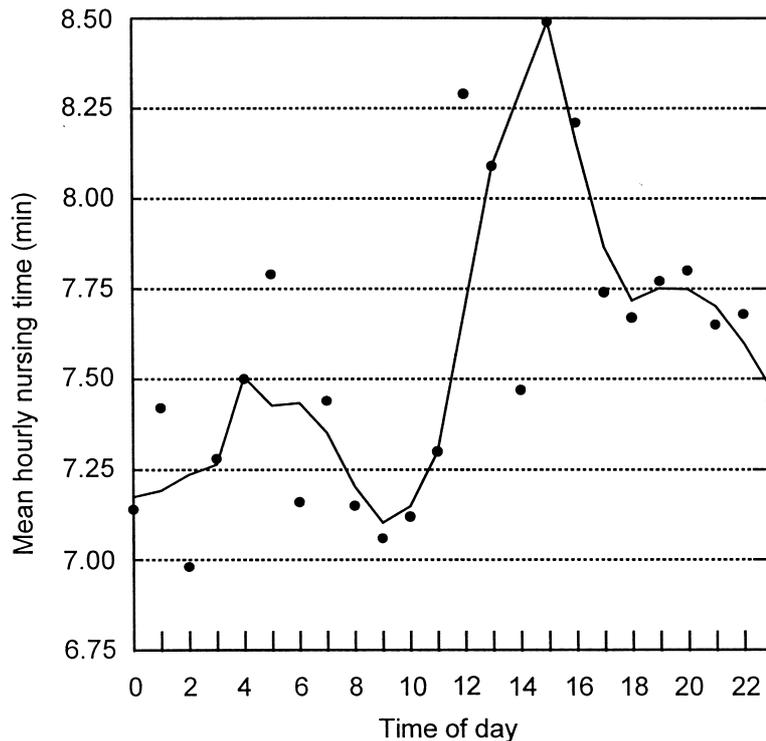


Figure 3. Mean nursing time per hour for two female captive-born false killer whale calves (no. 9301 and no. 9401) at SeaWorld Florida. A LOWESS curve (tension=0.2) fitted to the data suggested one peak in early morning (0300–0500h) and afternoon (1300–1600h) and least nursing in evening and overnight (1800–0200h) and mid-morning hours (0800–1000h).

Prediction of amount of nursing

A multivariate regression analysis was conducted in order to assess the possibility that the change in nursing time in a given hour could be predicted from other nursing parameters (Russell *et al.*, 1997). Stepwise multivariate linear regression indicated that change in nursing time (secs) in a given

hour could be predicted from two variables, the number of suckles in the given hour and the nursing time (secs) in the hour previous. An ANOVA demonstrated that these two predictor variables were significant ($F=9769.97$; $P<0.001$). The model described the data well ($r^2=0.90$) and was as follows

$$\Delta N = -5.55 + 8.07 * PS - 2.01 * PrS - 0.88 * PrN$$

where ΔN = change in nursing time (secs) in a given hour versus previous hour, PS = number of suckles in a given hour, PrS = number of suckles in previous hour, PrN = nursing time (secs) in previous hour. Examination of the coefficients indicated an increase in nursing time with a greater number of suckles (the positive PS coefficient) and decrease in nursing time as the nursing time and number of suckles in the previous hour increased (the negative PrS and PrN coefficients).

Discussion

The lack of information on *Pseudorca* nursing requires us to make comparisons with other odontocetes, as well as with other marine and terrestrial mammals.

Much like bottlenose dolphins (McBride and Kritzler, 1951; Cockcroft and Ross, 1990; Peddemors *et al.*, 1992; Reid *et al.*, 1995) and killer whales (Clark and Odell, SeaWorld, Inc., unpublished data), our false killer whales exhibited nursing patterns characterized by overall decreasing time (total nursing time, nursing time/hour, suckle duration, bout duration) and number of events (suckles/hour, bouts/hour, suckles/bout) during the first 13 weeks of life. This pattern of decreasing nursing time and decreasing number of nursing events also occurs in a variety of terrestrial mammals (Clutton-Brock *et al.*, 1982 in red deer [*Cervus elaphus*]; Gauthier and Barrette, 1985 in white-tailed deer [*Odocoileus virginianus*] and fallow deer [*Dama dama*]; Byers and Moodie, 1990 in pronghorn [*Antilocarpa americana*]; Birgersoon and Ekvall, 1994 in fallow deer). The fact that nursing activity from false killer whales in this study could be categorized into three separate periods was interesting. Intense nursing in week 1 may be attributable to several physiological and behavioral factors. The requirement for rapid growth during this period of early development may have an affect. As documented in Harrison (1969), cetaceans grow quite rapidly during the first few weeks of life and throughout the first year. Since information about calf growth and the quantity of milk could not be collected, we can only speculate about the biological significance of the observations. Perhaps thermoregulatory considerations played a role in this high level of nursing soon after birth. Since cetaceans must develop an adequate layer of blubber to provide insulation, the increased feeding may be attributable to this requirement for rapid deposition of insulation. On a behavioral level, the instinctual necessity for maintenance of mother-calf contact (e.g. to minimize risk of predation [Mann & Smuts, 1998]) may also have influenced the amount

of nursing during this first week or weeks. Reid *et al.* (1995) found bottlenose dolphin mothers were responsible for maintaining contact early on in the calf's life; yet, this responsibility reversed as the calf aged. Indeed, as our calves matured, perhaps these behavioral factors continued to affect nursing causing frequencies and amounts to decrease. Trivers (1974) speculates about the presence of a parent-offspring conflict. Mother and calf have differing 'ideas' on how long and intense nursing should be maintained. In particular, while the calf attempts to nurse as long as possible to increase its own fitness, Trivers' theory suggests the mother should decrease the amount of nursing time as the calf matures culminating in weaning. This is necessary in order for her to sustain her present fitness, as well as preserving her fitness necessary for future calving events. Weaning of our study animals was not officially recorded by the staff. Behavioral records indicated calves began consuming solid food between 6 and 8 months of age; although, one animal continued to nurse sporadically for over 2 years. Although this conflict may start to arise in our false killer whale calves, the length of this study (only 13 weeks) precluded of from making any definitive statements about these particular behavioral aspects. Even though not officially recorded in this study, anecdotal accounts of increases observed in the mother-calf spatial distances as the calves age by the SeaWorld Florida staff, similar to those observed by Reid *et al.* (1995), may have been subtle indicators of the beginnings of this conflict. The influence of captivity (e.g. feeding and show schedules, veterinary examinations, confines of the pools, etc.), although difficult to precisely ascertain, may be another factor and cannot be ignored when examining mother and calf behavior. Changes in milk quality throughout lactation could also account for the nursing patterns observed. If milk quality increased during lactation, presumably the amount of nursing time may decrease. However, investigations of milk quality changes during lactation have not yielded definite results as considerable variability exists among mammals (Arvy, 1973; Oftedal, 1997 in odontocetes; Reidman and Ortiz, 1979; Kretzmann *et al.*, 1991 in pinnipeds; Bachman and Irvine, 1979; Walsh *et al.* SeaWorld, Inc., unpublished data in manatees [*Trichechus manatus*]; Birgersoon and Ekvall, 1994 in fallow deer). Finally, perhaps the overall nursing patterns were due to an increased effectiveness in milk transfer as documented in bighorn sheep (*Ovis canadensis*) (Festa-Bianchet, 1988). As a matter of survival, calf and mother must develop effective nursing skills and strategies during the first few weeks of life. Primiparous mothers, as were the mothers in this study, may accomplish this at a rate slower than multiparous mothers. Since we do not

have data on multiparous mothers for comparison we cannot corroborate or refute this statement. Accounts on nursing behaviors in killer whale multiparous mothers indicate they, like primiparous mothers, also possess this initial peak in nursing times and frequencies (Clark and Odell, SeaWorld, Inc., unpublished data). Therefore, this more intense amount of nursing may not solely be indicative of physiological requirements, such as developing a sufficient thermoregulatory blubber layer, but may also represent calf knowledge acquisition on efficient nursing techniques (Gauthier and Barrette, 1985; Birgersson and Ekvall, 1994). Weeks 2 through 8 represent a period of decreasing nursing, perhaps as the calves acquired more blubber and/or became more skilled at nursing. The decrease seen in the third period (weeks 9–13) may reflect even continued advances along these lines of physiological and behavioral changes as the calf ages.

Russell *et al.* (1997) and Drinnan and Sadleir (1981) found that two beluga whale calves had consistent intersuckle intervals of about 36 minutes and 32–42 minutes, respectively. Other investigators have found that intersuckle intervals remained consistent throughout the first few weeks following birth of bottlenose dolphins (McBride and Kritzler, 1951; Eastcott and Dickinson, 1987). In contrast, our animals increased intersuckle interval times which was similar to what Logan and Robson (1971) found in common dolphins (*Delphinus delphis*). As they develop, false killer whale calves nurse less in regards to amounts and frequencies of nursing times and events (suckles, bouts, suckles/bout) and spend more time between nursing events.

In all instances, except for nursing periodicity, calf 9301's values exceeded those of calf 9401. The differences seen may have been due to individual variation in calves or mothers (both calves had different mothers). Other things being equal, it is reasonable to assume a calf that nursed longer and more frequently would exhibit a higher growth rate. Unfortunately, we do not have detailed growth data and cannot make any precise statements concerning the obvious nursing differences seen between the two calves.

Mean nursing time (mins) was greater during the afternoon (1300–1600h) and early morning hours (0300–0500h) than in the evening and overnight (1800–0200h) or mid-morning hours (0800–1000h). We believe that the trend observed may have been influenced by confounding variables such as visibility and/or the effect of performance show schedules (these animals were housed in area adjacent to where daily live performances occurred). However, the difference between peak nursing hour and least nursing hour was only 1.5 minutes. Our results

regarding temporal variation in nursing by these animals seem inconclusive. Indeed, Russell *et al.* (1997) found no circadian rhythm in beluga whale calf nursing.

The amount of time a calf spent nursing in any given hour was dependent upon the number of suckles in that hour, the amount of nursing (secs) in the previous hour, and the number of suckles in the previous hour. Specifically, the number of suckles in a given hour caused an increase in nursing time within that hour. An increased amount of nursing time and number of suckles in one was followed by a decreased amount of nursing in the given hour. These results indicated a carryover effect on nursing and were similar to that reported by Russell *et al.* (1997). As they postulated, we felt it was most likely attributable to feeding satiation by the calf. Further examination of this relationship may help to answer questions about digestion times of nursing calves as length of time between nursing events in conjunction with duration of nursing may give indications of amount and energy content of milk transferred.

Acknowledgments

The authors would like to extend their thanks and appreciation to all members of the SeaWorld Florida animal training and animal care staffs and two anonymous reviewers. We additionally thank A. Kordowski for providing husbandry and training records. This is SeaWorld Florida technical contribution No. 9807-F.

References

- Arvy, L. (1973) Mammary gland, milk and lactation in cetaceans. In: G. Pilleri (ed). *Investigations of Cetacea*, Volume 5. pp. 157–202. Institute of Brain Anatomy, University of Berne: Berne, Switzerland.
- Asper, E. D., Young, W. G. & Walsh, M. T. (1988) Observations on the birth and development of a captive-born whale. *International Zoo Yearbook* **27**, 295–304.
- Bachman, K. C. & Irvine, A. B. (1979) Composition of milk from the Florida manatee (*Trichechus manatus latirostris*). *Comparative Biochemistry and Physiology* **62A**, 873–878.
- Bigg, M. A. (1982) An assessment of killer whales (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Report of the International Whaling Commission* **32**, 641–650.
- Birgersson, B. & Ekvall, K. (1994) Suckling time and fawn growth in fallow deer (*Dama dama*). *Journal of Zoology, London* **232**, 641–650.
- Byers, J. A. & Moodie, J. D. (1990) Sex specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioral Ecology and Sociobiology* **26**, 157–164.

- Christensen, I. (1984) Growth and reproduction of killer whales, (*Orcinus orca*), in Norwegian coastal waters. Report of the International Whaling Commission (Special Issue #6), 253–258.
- Cleveland, W. S. (1979). Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association* **74**, 829–836.
- Cleveland, W. S. (1994) The Elements of Graphing Data, Revised Edition. Hobart Press: Summit, NJ.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982) Red Deer. Behavior and Ecology of the Sexes. University Press: Chicago, IL.
- Cockcroft, V. G. & Ross, G. J. B. (1990) Observation on the early development of a captive bottlenose dolphin calf. In: S. Leatherwood & R. Reeves (eds). The Bottlenose Dolphin. pp. 461–478. Academic Press Inc.: San Diego, CA.
- Drinnan, R. L. & Sadleir, R. M. F. S. (1981) The suckling behavior of a captive beluga (*Delphinapterus leucas*) calf. *Applied Animal Ethology* **7**, 179–185.
- Duffield, D. A. & Miller, K. W. (1988) Demographic features of killer whales in oceanaria in the United States and Canada, 1965–1987. *Rit Fiskideildar* **11**, 297–306.
- Duffield, D. A., Odell, D. K., McBain, J. F. & Andrews, B. (1995) Killer whale (*Orcinus orca*) reproduction at SeaWorld. *Zoo Biology* **14**, 417–430.
- Eastcott, A. & Dickinson, T. (1987) Underwater observations of the suckling and social behavior of a newborn bottlenosed dolphin (*Tursiops truncatus*). *Aquatic Mammals* **13**, 51–56.
- Festa-Bianchet, M. (1988) Nursing behavior of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. *Animal Behavior* **36**, 1445–1454.
- Gauthier, D. & Barrette, C. (1985) Suckling and weaning in captive white-tailed and fallow deer. *Behaviour* **94**, 128–149.
- Harrison, R. J. (1969) Reproduction and reproductive organs. In: H. Anderson (ed). The Biology of Marine Mammals. pp. 253–345. Academic Press: New York.
- Kasuya, T., Tobayama, T., Saiga, T. & Kataoka, T. (1986) Perinatal growth of delphinoids: information from aquarium reared bottlenose dolphins and finless porpoises. *Scientific Report of the Whales Research Institute* **37**, 85–97.
- Kretzmann, M. B., Costa, D. P., Higgins, L. V. & Needham, D. J. (1991) Milk composition of Australian sea lions (*Neophoca cinerea*): variability in lipid content. *Canadian Journal of Zoology* **69**, 2556–2561.
- Logan, F. D. & Robson, F. D. (1971) On the birth of a common dolphin (*Delphinus delphis* L.) in captivity. *Zoologische Garten (Leipzig)* **40**, 115–124.
- Mann, J. & Smuts, B. B. (1998) Natal attraction: allo-maternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour* **55**, 1097–1113.
- McBride, A. F. & Kritzler, H. (1951) Observation on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. *Journal of Mammalogy* **32**, 251–266.
- Odell, D. K. & McClune, K. M. (1999) False killer whale *Pseudorca crassidens* (Owen, 1846). In: S. Ridgway (ed). Handbook of Marine Mammals, Volume 6. pp. 213–244. Academic Press, Ltd.: New York.
- Oftedal, O. T. (1997) Lactation in whales and dolphins: evidence of divergence between baleen- and toothed-species. *Journal of Mammary Gland Biology and Neoplasia* **2**, 205–230.
- Peddemors, V. M., Fothergill, M. & Cockcroft, V. G. (1992) Feeding and growth in a captive-born bottlenose dolphin *Tursiops truncatus*. *South African Journal of Zoology* **27**, 74–80.
- Purves, P. E. & Pilleri, G. (1978) The functional anatomy and general biology of *Pseudorca crassidens* (OWEN) with a review of the hydrodynamics and acoustics in Cetacea. In: G. Pilleri (ed). Investigations of Cetacea, Volume 5. pp. 67–227. Institute of Brain Anatomy, University of Berne: Berne, Switzerland.
- Reid, K., Mann, J., Weiner, J. & Hecker, N. (1995) Infant development in two aquarium bottlenose dolphins. *Zoo Biology* **14**, 135–147.
- Reidman, M. & Ortiz, C. L. (1979) Changes in milk composition during lactation in the northern elephant seal. *Physiological Zoology* **52**, 240–249.
- Robeck, T. R., Schneyer, A. L., McBain, J. F., Dalton, L. M., Walsh, M. T., Czekala, N. M. & Kraemer, D. C. (1993) Analysis of urinary immunoreactive steroid metabolites and gonadotropins for characterization of the estrous cycle, breeding period, and seasonal estrous activity of captive killer whales (*Orcinus orca*). *Zoo Biology* **12**, 173–187.
- Russell, J. M., Simonoff, J. S. & Nightingale, J. (1997) Nursing behavior of beluga calves (*Delphinapterus leucas*) born in captivity. *Zoo Biology* **16**, 247–262.
- Sokal, R. R. & Rohlf, F. J. (1995) Biometry, 3rd edition. W. H. Freeman and Company: New York.
- SPSS, Inc. (1998) SYSTAT 8.0 Statistics. Chicago: SPSS, Inc.
- Tavolga, M. C. & Essapian, F. S. (1957) The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): mating, pregnancy, parturition and mother-infant behavior. *Zoologica* **42**, 11–31.
- Trivers, R. L. (1974) Parent-offspring conflict. *American Zoologist*, **14**: 249–264.
- Walker, L. A., Cornell, L., Dahl, K. D., Czekala, N. M., Dargen, C. M., Joseph, B., Hseueh, A. J. W. & Lasley, B. L. (1988) Urinary concentrations of ovarian steroid hormone metabolites and bioactive follicle-stimulating hormone in killer whales (*Orcinus orca*) during ovarian cycles and pregnancy. *Biology of Reproduction* **39**, 1013–1020.

