Aquatic Mammals 2009, *35*(4), 473-480, DOI 10.1578/AM.35.4.2009.473

First Observation of the Parturition and Peripartum Events in a Harbor Porpoise (*Phocoena phocoena*)

Marie-Anne Blanchet, Magnus Wahlberg, and Tomoko Ishigami

Fjord & Bælt, Margrethes Plads 1, 5300 Kerteminde, Denmark
Corresponding Author's E-mail: marie_blanchet@yahoo.fr
Current Addresses: Idrettsveien 40 B, 9009 Tromsø, Norway (M-AB)
206, 1-25-17 Obiyama, Kumamotocity 862-0924, Japan (TI)

Abstract

Parturition events in cetaceans are difficult to observe in nature and scarcely described in detail. Observations from animals in captivity offer the possibility to follow complete gestations and to obtain a precise description of the series of events pertaining to pregnancy and parturition. After a gestation period of 11 mo, the parturition of a harbor porpoise (*Phocoena phocoena*) was observed for the first time at the Danish research facility Fjord & Bœlt on 8 August 2007. Five prepartum signs useful to predict the onset of parturition were identified: (1) decrease in appetite (from 5,064 Kcal/d to 907 Kcal/d at 2 d before birth [B-2]), (2) unusual behavior (disinterest in training sessions, seeking of physical contact with the trainers, restlessness), (3) decrease in body temperature of 1.6º C at B-1, (4) swollenness in the genital area, and (5) increase in the inter-mammary distance (from 5 to 8 cm at B-1).

During labor, three stages described for other mammals in literature were observed and each stage's duration recorded: Stage 1 was characterized by uterine contractions and dilation of the cervix (between 2 h 19 min and 7 h 39 min), Stage 2 started with the rupture of fetal membranes (1 h 42 min at least), and Stage 3 comprised the expulsion of the fetus and its membranes (7 h). The total duration of the parturition was at least 16 h 21 min as there is an uncertainty in regards to the exact beginning of the labor.

The sequence of visible events occurring during parturition was as follows: apparition of the amniotic sac, apparition of the calf's flukes, apparition of the peduncle, delivery of the calf, and expulsion of the left horn of the placenta followed by the right horn. As described for other cetaceans, the delivery was caudal.

Contractions seemed to be longer and more frequent during the first stage and during the beginning of the second stage of labor. The contractions then shortened and became more regular during the expulsion of the calf. We observed that the expulsion of the calf was not provoked only by contractions but helped at the end by a violent rotational movement of the mother that broke the umbilical cord. The female's breathing rate increased dramatically towards the end of the expulsion of the calf.

Key Words: cetacean, reproduction, parturition stages, labor, contractions pattern, harbor porpoise, *Phocoena phocoena*

Introduction

There is little information on the reproduction of the harbor porpoise (*Phocoena phocoena*) (Desportes et al., 2003; Blanchet et al., 2008), and most of the data obtained come from by-caught, hunted, stranded, or captive animals (Lockyer, 2003; Lockyer & Kinze, 2003; Lockyer et al., 2003).

Parturition (i.e., the process by which the fetus is expulsed from the uterus to the extra-uterine environment [Challis et al., 2000]) and peripartum events are generally difficult to observe among wild animals because they generally tend to hide or move away from potential disturbances (Fedak et al., 2009). In some cases, females can even voluntarily delay parturition if environmental conditions are not favorable (Rock, 2006). Parturition in some marine mammals species has been documented, but mostly for pinnipeds that usually give birth on land (Ronald & Thomson, 1981; Stewart et al., 1981; Frank et al., 1985; Lawson & Renouf, 1985; Eliason et al., 1990; Layna et al., 1999; Blanchet et al., 2006; Acevedo et al., 2008). However, observing and documenting parturition is more difficult for cetaceans that give birth at sea with reports limited to scarce events that include strandings (Hückstadt & Antezana, 2001) or opportunistic observations at sea (Gambell et al., 1973; Balcomb, 1974; Weilgart & Whitehead, 1986; Notarbartolo di Sciara et al., 1997; Stacey & Baird, 1997). Harbor porpoises, as one of the smallest cetaceans, are especially difficult to spot at sea. A complete birth, from prepartum to peripartum events, has never been documented in the wild, except the opportunistic observation made by Graner (2003) in Sognefjord, Norway. In nature, detailed and accurate observations of parturition are practically impossible to obtain. Having animals in controlled environments offers more opportunity to witness these events. For example, cetaceans' pregnancies and births have been witnessed in zoological settings for the few species commonly hosted by aquaria such as beluga whales (*Delphinapterus leucas*) (Dalton et al., 1991; Robeck et al., 2005), bottlenose dolphins (*Tursiops truncatus*) (McBride & Kritzler, 1951; Essapian, 1963), and killer whales (*Orcinus orca*) (Katsumata et al., 1998).

To our knowledge, only two cases of the birth of a phocoenid species have been described, which were for the Yangtze finless porpoise (*Neophocoena phocaenoides asiaorientalis*) (Wang et al., 2005) and a harbor porpoise (James, 1914). In these cases, however, no detailed description of the mother's behavior or the events occurring during parturition were presented.

This report details the first complete birth (from prepartum events through the delivery of the placenta) of a harbor porpoise under human care and provides detailed information on both the parturition and peripartum events.

Materials and Methods

The Fjord & Bælt in Denmark keeps three adult harbor porpoises (one male and two females) together on a permanent basis in an outdoor, semi-open enclosure. All three animals were wild-caught in pound nets set in the inner Danish waters. The two oldest animals, Eigil (E) and Freja (F), a male and a female, respectively, arrived together in 1997 and were estimated to be between 1 to 2 y of age, immature at that time (Desportes et al., 2003; Lockyer et al., 2003). The third animal, Sif (S), a female, arrived at the center in 2004 and was estimated to be approximately 1 y old. Harbor porpoises are known to become sexually mature between 3 to 4 y of age (Lockyer et al., 2003). Nevertheless, mating and copulation was observed between E and F since 1997 (Desportes et al., 2003). To our knowledge, F did not conceive until 2003 when she suffered a miscarriage at an early stage in gestation. In 2005-2006, F carried out a full-term pregnancy that resulted in a stillborn fetus in July 2006; the description of this pregnancy is reported in Blanchet et al. (2008). F then became pregnant again in September 2006 and gave birth to a healthy female calf on 8 August 2007 at 0200 h.

During the last weeks of the successful pregnancy, F was separated from the other animals in a maternity pool (8×13×2 m). This enclosure was made of an underwater "cage" composed of aluminum frames holding small mesh nets (1×1 cm) attached to the edges of the floating pontoons surrounding the pool. The corners of the pools were rounded with wooden boards, and all edges were padded with a foam material. F was still in acoustic and visual contact with the two other animals, but no physical contact was possible.

Unusual events (e.g., behavioral and physical changes) were recorded by the trainers during working hours (0800 through 1700 h) and by trained volunteers during evening hours (1700 through 0800 h). Observations during parturition were made from a balcony overlooking the maternity pool lit by two floodlights. The behavior of the parturient animal was not disturbed as movements around the pool were very limited, and she had been desensitized over the precedent months to the presence of staff and the light during dark hours. F's body was smeared with white zinc ointment (applied the day before the delivery through voluntary medical behavior [Ramirez, 1999; Desportes et al., 2007]) to be able to spot her easily underwater to track and record her contractions and the behavior more precisely. The measurement of the inter-mammary distance and the body temperature were collected voluntarily during the pregnancy (see Blanchet et al., 2008).

When labor started, observations were recorded *ad libitum* (Altmann, 1974) by two independent observers on an observation sheet and with a video camera (Phillips LTC 0600/10). We defined a contraction on the basis of observations made of bottlenose dolphins (McBride & Kritzler, 1951; Essapian, 1963) and from videos of births provided by Kolmården Djurpark in Sweden.

Results

Table 1 summarizes the physical, physiological, and behavioral changes that occurred for F before parturition. Physically, we observed an increase in the inter-mammary distance from 5 cm normally to 8 cm 1 d before birth (B-1) and a general swollenness in the genital and mammary areas (from B-20) as well as occasional secretions from the tip of the nipples (from B-64). Physiologically, from B-3, F's body temperature started to drop below her average of 36.7º C (SD = 0.4) during the pregnancy to reach 35.1º C at B-1. Her food intake became irregular from B-8 and went from a daily diet of 5,064 Kcal/d (equivalent to 6.4 kg of fish) during the last 2 wks of pregnancy to 907 Kcal/d (1.3 kg) at B-2 and 3,231 Kcal/d (3.2 kg) at B-1. The female's behavior also changed previous to parturition. Along with a general disinterest in training sessions, F was seeking physical contact with the trainers, offering her ventral side, peduncle, and flukes for rubbing from B-8. Movements from the calf were often recorded from B-49 during daily physical examinations and were noticed until B-5. False labor characterized by contractions and flexions on B-23 was observed in the early morning but stopped after 4 h.

Table 2 shows the successive events occurring during parturition. The time scale is normalized in h:min—0.00 is the time of birth (0200 h on 8 August); the negative times are those before the delivery, and the positive times are after the delivery. The sequence of events was as follows: a part of the amniotic pouch was first visible under the pressure of the contractions at -7:02 h; at -1:42 h, the calf's tail flukes appeared followed at -1:14 h by the rest of the peduncle. Complete expulsion occurred 9 h 21 min after the visible start of labor. The placenta was retrieved in two pieces at +5:00 h (left horn) and +7:00 h (right horn). If we divide the labor into the three stages of parturition documented for mammals, the duration of the following stages was:

Stage 1 – between 2 h 19 min and 7 h 39 min
Stage 2 – at least 1 h 42 min
Stage 3 – 7 h

The total duration of this parturition was 16 h 21 min. It is important to note that a first nursing attempt was observed 2 h after birth, and a successful nursing occurred 4 h after birth even though the placenta had not yet been expulsed.

Figure 1 shows the evolution of F's breathing rate during the different phases of labor. Her average breathing rate during pregnancy was 2.7 breaths/min (SD = 0.5), and during the first part of labor it stayed within that range. However, from the moment the fluke was exposed, F's breathing rate increased up to 4.7 breaths/min during the expulsion.

The frequency of the contractions increased as labor progressed, reached a maximum at mid-labor (6 h before the expulsion), and then started to decrease to reach a minimum when the tail flukes were exposed as shown in Figure 2. The same pattern was then repeated over a shorter time until expulsion.

The duration of the contractions also followed the same tendency, with a progressive increase until mid-labor and a decrease through the expulsion (Figure 3). The longest contractions occurred before the tail flukes were exposed.

Table 1. Prepartum events with time scale in days; B is the birth day (8 August 2007)

Days before birth (B-d)	Events
B-64	Dry yellow secretion seen at the tip of nipples.
B-49	Movements of the calf perceived through abdominal wall.
B-40	Movements of the calf perceived through abdominal wall.
B-32	Movements of the calf perceived through abdominal wall.
B-23	False labor observed for 4 h in early morning.
	White mucus/liquid expulsed during a contraction.
B-22	Movements of the calf perceived through abdominal wall.
B-20	Nipples and mammary slits swollen.
B-19	Movements of the calf perceived through abdominal wall.
B-18	Nipples and genital slit swollen; cervix looks distended.
B-15	Increases of the inter-mammary distance from 5 to 7 cm.
B-8	Change in behavior towards the trainers; F is seeking tactile contact especially around the abdomen, the peduncle, and the tail fluke; irregular food intake.
B-7	Same as B-8.
B-5	Movements of the calf perceived through abdominal wall.
B-4	Apparent discomfort throughout the day marked by slower swimming, unusual postures, and poor interest in formal training sessions.
B-3	Drop in body temperature to 35.6º C from the normal body temperature of 36.7º C.
B-1	Drop in body temperature to 35.1º C.
	Drop in appetite; ate 3.6 kg.
	Increases in inter-mammary distance to 8 cm.
	Apparent discomfort throughout the day; eyes sunken inside head; tactile contacts the whole day.
	Labor started at 1640 h.
B	Birth at 0200 h.

Table 2. Events occurring during parturition; the time scale is normalized in h:min. 0:00 is the time of birth (0200 h on 8 August); the negative times are before the birth and the positive times are after the birth. The nursing, though not typically part of the parturition, is mentioned as it unusually occurred during the last parturition stage.

Time during labor (h:min)	Events	Stages of parturition
- 9:21	Start of contractions	Stage 1
- 7:02	Amniotic pouch visible for the first time	Stages 1 & 2
- 1:42	Fluke visible	Stage 2
- 1:14	Peduncle visible	Stage 2
- 0:01	Dorsal visible	Stage 2
0:00	Calf expulsed	Stage 2
+2:00	First nursing attempt	
+4:00	First successful nursing	
+5:00	Left horn of placenta expulsed	Stage 3
+7:00	Right horn of placenta expulsed	Stage 3

Discussion

Prepartum Signs

Prepartum signs are well-known and documented for many mammal species, but the literature is scarce regarding details for births in fully aquatic marine mammals (Blanchet et al., 2008). A change in behavior is usually noted prior to parturition such as separation from the social group and increase in aggressiveness and restlessness (Trevathan et al., 1996). In captive odontocetes, future mothers seem to seek the company of other pregnant females or females with young (McBride & Kritzler, 1951; Stacey & Baird, 1997). As F was separated from the rest of the group before the birth, it is not known if she would have displayed a similar behavior. However, harbor porpoises are considered to be solitary animals (Lockyer & Kinze, 2003), not belonging to social groups with an elaborate social organization like many other odontocetes and are believed to give birth alone in a sheltered location (Graner, 2003). The change of behavior towards the trainers was interpreted as a prepartum sign and was already observed during the previous pregnancy of the same individual (Blanchet, unpub. data).

A loss of appetite is often documented in relation with the imminence of parturition (McBride & Kritzler, 1951) but is highly individual (Robeck et al., 2005) and can also depend on the pregnancy. For the precedent pregnancy documented on the same animal, food intake was null on the day of the delivery (Blanchet et al., 2008) in contrast with this present parturition when food intake was only reduced. A loss of appetite is a sign of the imminence of the delivery but cannot be considered as a precise indicator of the start of the parturition itself.

A drop in body temperature of at least 1º C is known to announce the imminence of birth in many mammal species from cattle (Porterfield & Olson, 1957) to dogs (Tsutsui & Murata, 1982) and marine mammals (Katsumata et al., 1998; Terasawa et al., 1999). This drop is associated with a decreased level of circulating progesterone (Katsumata et al., 1998; Concannon, 2000)

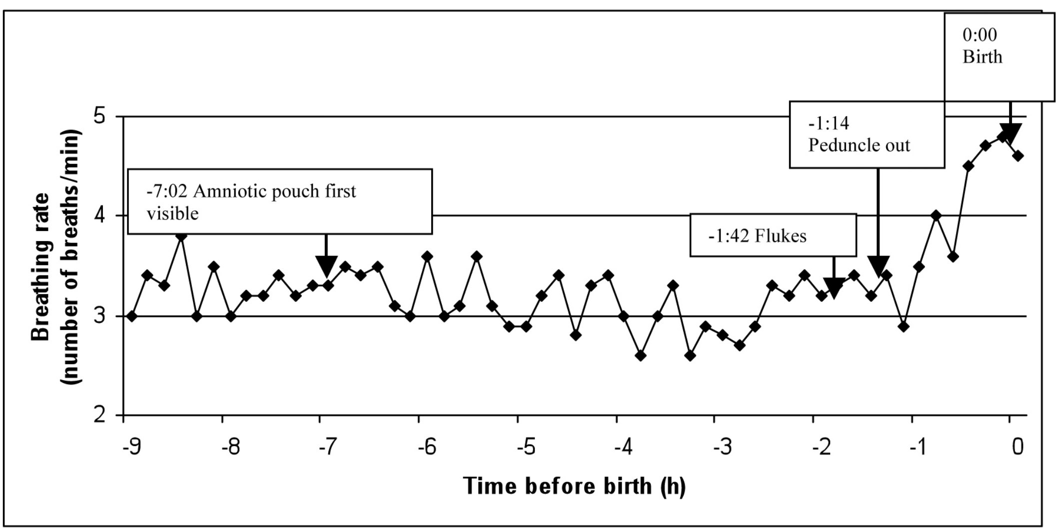

Figure 1. F's breathing rate during labor; the x-axis represents the time before the birth in hours: -9 being the beginning of labor (1640 h on 7 August) and 0 the time of expulsion (0200 h on 8 August).

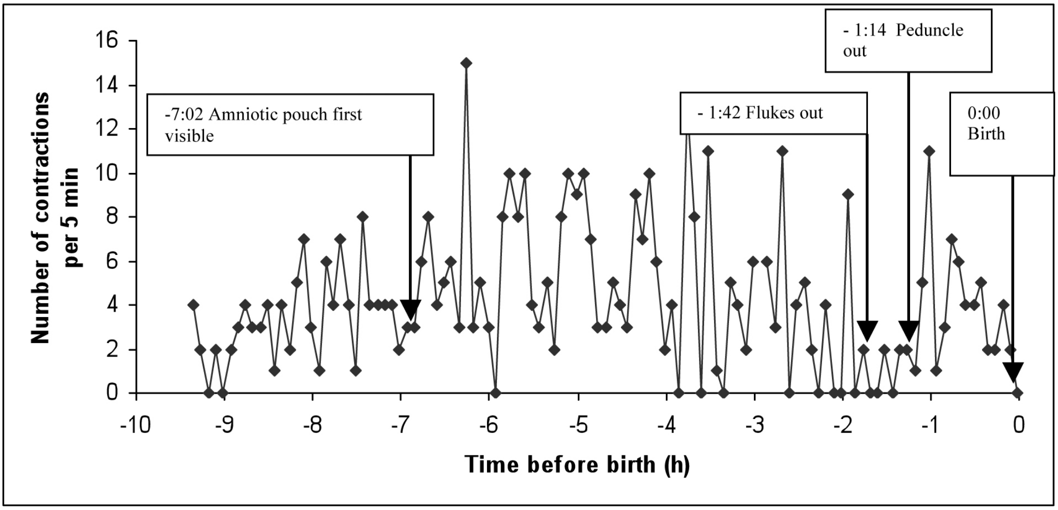

Figure 2. Frequency of F's contractions during labor; the x-axis represents the time before the birth in hours: -9 being the beginning of labor (1640 h on 7 August) and 0 the time of expulsion (0200 h on 8 August).

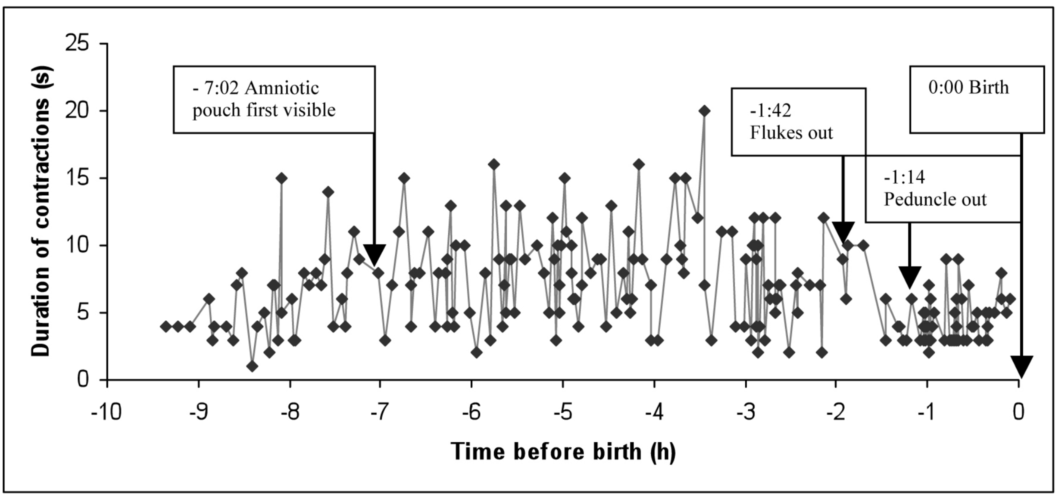

Figure 3. Duration of F's contractions during labor; the x-axis represents the time before the birth in hours: -9 being the beginning of labor (1640 h on 7 August) and 0 the time of expulsion (0200 h on 8 August).

and an acute rise of prolactin (Verstegen-Onclin & Verstegen, 2008). However the delay between temperature drop and delivery can vary according to species (Katsumata et al., 2006; Blanchet et al., 2008); it can go from 5 d prior to parturition in killer whales (Katsumata et al., 2006) to 12 to 24 h in bottlenose dolphins (Terasawa et al., 1999). In our observations, F's temperature began to decrease at B-3 and reached its minimum at B-1, which is consistent with observations conducted during the previous gestation for the same animal (Blanchet et al., 2008).

Other physical signs, such as the enlargement of the mammary glands and secretion of pre-colostrum, are also indicative of parturition and have been used to assess the reproductive stage of dead whales like bowhead whales (*Balaena mysticetus*) (Harms, 1993). An increase of the inter-mammary distance can be a valuable indicator of the onset of parturition in several species of odontocetes (Dalton et al., 1991; Blanchet et al., 2008); however, this increase can begin several weeks before birth and is not an absolute sign itself of birth. The inter-mammary distance also varies individually but seems to be consistent from one pregnancy to another as recorded in our case.

False labor occurs commonly during the last stages of a pregnancy in various mammals and has been documented for bottlenose dolphins (McBride & Kritzler, 1951). False labor is thought to be a preparation of the muscles from the uterine wall to true labor (Woods, 1962; Lye & Freitag, 1982; Lye, 1994). The increase of the uterine muscle activity is stimulated by a combination of maternal and fetal signals and occurs frequently toward term (Challis et al., 2000). However, false labor is not accompanied by any other signs preceding true labor such as loss of appetite, drop of body temperature, or increase of inter-mammary distance.

Parturition

The three stages of parturition are well-described in a number of mammals (Trevathan, 1996; Girotti & Zingg, 2003): **Stage 1** is characterized by uterine contractions, dilation of the cervix, and the allantochorion pushed in the birth canal; **Stage 2** begins with the rupture of the membranes and ends when the fetus is delivered; and **Stage 3** involves the expulsion of the fetal membranes (Kahn & Line, 2005). When considering a bicornuate uterus, like in odontocetes, both horns of the placenta are expulsed one after the other. Stages of parturition described in several species of odontocetes, such as bottlenose dolphins (Joseph et al., 2000), killer whales (Robeck et al., 2001), and beluga whales (Robeck et al., 2005), follow the ones described in other mammalian species. However, there are differences in the timing and duration of these events between species, among individuals, and between pregnancies (Robeck et al., 2005). Our observations are in accordance with the above described sequence, but the duration of each stage was difficult to estimate precisely as the rupture of the fetal membranes that characterize the passage from Stage 1 to Stage 2 was impossible to observe.

At birth, powerful and rhythmic contractions of the uterine muscles aided by the abdominal muscles expel the fetus (Stewart & Stewart, 2009). Contractions are described in bottlenose dolphins as "a spasmodic contraction of the abdominal musculature" with the animal's "tail drooping as much as it would if she were sleeping near the surface" (McBride & Kritzler, 1951, p. 254). Essapian (1963) describes the contractions as "a series of strains apparently intended to expel the fetus" and the "straining activity as arching their back both ways and dilating their genital opening" (p. 406). We observed the same type of behavior both during false labor and labor. Most of these contractions were paired with a "flexion" or arching of the back. We considered that both movements were part of the same action tending towards the expulsion, and we recorded it as the same sequence. In horses, the mare may roll during the first stage of labor to facilitate the rotation of the fetus into the birth canal (Kahn & Line, 2005). In monk seals (*Monachus schauinslandi*) and harbor seals (*Phoca vitulina*), the female often rolls on her back presumably for the same reason (Eliason et al., 1989; Layna et al., 1999; Blanchet et al., 2006). In dolphins and porpoises that are giving birth in water to a breeched neonate, the flexion part of a contraction might have the same action.

The contractions seemed to be the longest and the most frequent during the first stage and at the beginning of the second stage of labor. Once the fluke was out, the contractions became shorter and more regular in duration as well as less frequent. A similar pattern is commonly observed during delivery in terrestrial mammals when the myometrial contractions of the uterus increase in strength and frequency as the cervix dilates in Stage 1 and culminate in the delivery of a neonate (Kahn & Line, 2005). In our case, however, it seems that the most violent contractions ended when the fluke was exposed but the calf was not born yet. We observed that the expulsion of the calf was not provoked only by contractions but mainly by a violent, swirling movement of the mother as described in bottlenose dolphins and interpreted as an effort to sever the umbilical cord (McBride & Kritzler, 1951; Trevathan, 1996).

The breathing rate remained within F's normal range during most of the parturition. It started increasing dramatically during the end of Stage 2 and Stage 3 as the frequency and duration of contractions decreased. It seems rather counterintuitive as one would think that the most energy demanding efforts would be associated with a higher breathing rate.

During Stage 3, the left horn of the placenta was expulsed first, which is consistent with observations of other cetaceans wherein the left ovary and left horn are employed in reproduction (Slijper as cited in Silvers et al., 1997).

The start of nursing appeared to be rather quick in F's case as the first attempt was observed 2 h after birth, and the first successful attempt was 4 h after birth compared to beluga whales for which this time is much longer (between 19 and 51 h). However, in this species, there is a large inter-individual variation, and the experience of the cow plays an important role (Robeck et al., 2005). It is likely also to be the case in harbor porpoises.

These observations provide the first description of parturition and peripartum events in a harbor porpoise. They confirm that prepartum indicators exist also in this species (e.g., behavioral changes, decrease in appetite, enlargement of mammary glands, secretion of colostrum, increase in the inter-mammary distance, and decrease of body temperature). Being able to pinpoint the onset of parturition is essential to follow the process of labor and identify possible problems such as dystocia, stillbirth, weakening of contractions, or any abnormal behavior from the parturient animal. But as literature shows, there is a wide inter-individual variability in several odontocete species. More pregnancies from single animals and different individuals of the same species need to be observed to establish a reliable baseline essential for an efficient management of animals in zoological settings.

Studying the reproductive behavior of captive animals can help to gain a better understanding of the factors influencing reproduction of endangered species like harbor porpoises and to understand some of the population recovery factors.

Acknowledgments

This study was funded by Fjord & Bælt, University of Southern Denmark, and the Danish Forest and Nature Agency. The porpoises are held under a permit from the Danish Forest and Nature Agency, permit numbers J.nr. SN 343/FY-0014 and 1996-3446-0021. We thank all trainers at Fjord & Bælt and the volunteers who helped in collecting the data.

We particularly thank Dr. Mats Amundin from Kolmården Animal Park in Sweden for his advice in the design of the maternity pool and for the material on the birth of bottlenose dolphins.

Literature Cited

Acevedo, J., Aguayo-Lobo, A., & Torres, D. (2008). Fetus presentation and time taken for parturition in Antarctic fur seal, *Arctocephalus gazella*, at Cape Shirreff, Antarctica. *Polar Biology*, *31*, 1137-1141.

Altmann, G. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227-267.

Balcomb, K. C. (1974). The birth of a grey whale. *Pacific Discovery*, *27*, 28-31.

Blanchet, M-A., Desportes, G., Nance, T., & Vanman, C. (2006). The description of the pregnancies, labours and pre- and post-partum events of two harbour seals in a zoological environment. *Aquatic Mammals*, *32*(2), 145-151.

Blanchet, M-A., Nance, T., Ast, C., Wahlberg, M., & Acquarone, M. (2008). First case of monitoring a pregnancy in a harbour porpoise (*Phocoena phocoena*) under human care. *Aquatic Mammals*, *34*(1), 9-20.

Challis, J. R. G., Matthews, S. G., Gibb, W., & Lye, S. J. (2000). Endocrine and paracrine regulation of birth at term and preterm. *Endocrine Reviews*, *21*, 514-550.

Concannon, P. W. (2000). Canine pregnancy: Predicting parturition and timing events of gestation in recent advances in small animal reproduction. In P. W. Concannon, G. England, J. Verstegen III, & C. Linde-Forsberg (Eds.), *Recent advances in small animal reproduction.* Ithaca, NY: International Veterinary Information Services. Retrieved November 13, 2009, from www.bakalo.com/health/canine_pregnancy.htm.

Dalton, L., Robeck, T. R., Calle, P., & Cook, R. A. (1991, May). *Observation at parturition of eight beluga whales (*Delphinapterus leucas*)*. Presented at the 24th Conference of the International Association for Aquatic Animals Medicine (IAAAM). Chicago, IL.

Desportes, G., Buholzer, L., Anderson-Hansen, K., Blanchet, M-A., Acquarone, M., Shephard, G., et al. (2007). Decrease stress; Train your animals: The effect of handling methods on cortisol levels in harbour porpoises (*Phocoena phocoena*) under human care. *Aquatic Mammals*, *33*(3), 286-292.

Desportes, G., Kristensen, J., Benham, D., Wilson, S., Jepsen, T., Korsgaard, B., et al. (2003). Multiple insights into the reproductive function of harbour porpoises (*Phocoena phocoena*): An ongoing study. *NAMMCO Scientific Publications*, *5*, 91-106.

Eliason, J. J., Johanos, T. C., & Werber, M. (1990). Parturition in the Hawaiian monk seal (*Monachus schauinslandi*). *Marine Mammal Science*, *6*, 146-151.

Essapian, F. S. (1963). Observation on abnormalities of parturition in captive bottlenose dolphins and concurrent behavior of other porpoises. *Journal of Mammalogy*, *44*, 405-414.

Fedak, M., Wilson, B., & Pomeroy, P. (2009). Reproductive behavior. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 943-955). Amsterdam, Elsevier.

Frank, R. J., Ronald, K., & Lightfoot, N. (1985). Parturition in the hooded seal (*Cristophora cristata*). *Journal of Mammalogy*, *66*, 558-559.

Gambell, R., Lockyer, C., & Ross, G. B. (1973). Observation of the birth of a sperm whale calf. *South African Journal of Science*, *69*, 147-148.

Girotti, M., & Zingg, H. (2003). Gene expression profiling of rat uterus at different stages of parturition. *Endocrinology*, *144*, 2254-2265.

Graner, F. (2003). *Group structure and behaviour of the harbour porpoise* Phocoena phocoena *in Indre Sognefjord, Norway*. Ph.D. thesis, University of Liverpool, Liverpool, England. 272 pp.

Harms, C. A. (1993). Composition of prepartum mammary secretions of two bowhead whales (*Balaena mysticetus*). *Journal of Wildlife Disease*, *29*, 94-97.

Hückstadt, L., & Antezana, T. (2001). An observation of parturition in a stranded *Kogia breviceps*. *Marine Mammal Science*, *17*, 362-365.

James, L. H. (1914). Birth of a porpoise at the Brighton Aquarium. *Proceedings of the Zoological Society of London*, 1061-1062.

Joseph, B. E., Duffield, D. A., & Robeck, T. R. (2000). Summary data on reproduction of bottlenose dolphins in controlled environments. In D. Duffield & T. R. Robeck (Eds.), *The Bottlenose Dolphin Breeding Workshop* (pp. 43-56). Silver Springs, MD: AZA Marine Mammal Taxon Advisory Group.

Kahn, C. M., & Line, S. (Eds.). (2005). *The Merck veterinary manual* (9th ed.). Whitehouse Station, NJ: Merck.

Katsumata, E., Katsumata, H., Tobayama, T., & Usuki, S. (1998, September 22-25). *Body temperature in reared killer whale (*Orcinus orca*): Useful predictive method of confinement in females?* Proceedings of the Third International Symposium of the Asia and Oceanic Society for Comparative Endocrinology, Kwangju, South Korea.

Katsumata, E., Jaroenporn, S., Katsumata, H., Konno, S., Maeda, Y., Watanabe, G., et al. (2006). Body temperature and circulating progesterones levels before and after parturition in killer whales (*Orcinus orca*). *Journal of Reproduction and Development*, *52*, 65-71.

Lawson, J. W., & Renouf, D. (1985). Parturition in the Atlantic harbor seal (*Phoca vitulina concolor*). *Journal of Mammalogy*, *66*, 395-398.

Layna, J. F., Cedenilla, M. A., Afaricio, F., & Gonzalez, L. M. (1999). Observations of parturition in the Mediterranean monk seal (*Monachus monachus*). *Marine Mammal Science*, *15*, 879-882.

Lockyer, C. (2003). Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters. *NAMMCO Scientific Publications*, *5*, 71-89.

Lockyer, C., & Kinze, K. (2003). Status, ecology and life history of harbour porpoise (*Phocoena phocoena*) in Danish waters. *NAMMCO Scientific Publications*, *5*, 143-175.

Lockyer, C., Heide-Jøregnsen, M. P., Jensen, J., & Walton, M. J. (2003). Life history and ecology of harbour porpoises (*Phocoena phocoena*) from west Greenland. *NAMMCO Scientific Publications*, *5*, 177-194.

Lye, S. J. (1994). The initiation and inhibition of labour: Towards a molecular understanding. *Seminars in Reproductive Endocrinology, 12*, 284-294.

Lye, S. J., & Freitag, C. L. (1990). Local and systemic control of myometrial contractile activity during labour in the sheep. *Journal of Reproduction and Fertility*, *90*, 483-492.

McBride, A., & Kritzler, H. (1951). Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. *Journal of Mammalogy*, *32*, 251-266.

Notarbartolo di Sciara, G., Barbaccia, G., & Azzelino, A. (1997). Birth at sea of a false killer whale *Pseudorca crassidens. Marine Mammal Science*, *13*, 508-511.

Porterfield, I. D., & Olson, N. O. (1957). Vaginal temperature of dairy cows before and after calving. *Journal of the American Veterinary Medical Association*, *131*, 381-383.

Ramirez, K. (1999). *Animal training: Successful animal management through positive reinforcement.* Chicago: Shedd Aquarium Society. 578 pp.

Robeck, T. R., Atkinson, S., & Brook, F. (2001). *Reproduction*. In L. A. Dierauf & F. M. D. Gulland (Eds.), *CRC handbook in marine mammal medicine* (2nd ed., pp. 193-236). Boca Raton, FL: CRC Press.

Robeck, T. R., Montfort, S., Calle, P. P., Dunn, L. J., Jensen, E., Boehm, J. R., et al. (2005). Reproduction, growth and development in captive beluga (*Delphinapterus leucas*). *Zoo Biology*, *24*, 29-49.

Rock, J. (2006). Delayed parturition: Constraint or coping mechanism in a viviparous gekkonid? *Journal of Zoology*, *268*, 355-360.

Ronald, K., & Thomson, C. A. (1981). Parturition and postpartum behaviour of a captive harbour seal (*Phoca vitulina*). *Aquatic Mammals*, *8*, 79-90.

Silvers, L. E., Atkinson, S., Iwasa, M., Combelles, C., & Salden, D. R. (1997). A large placenta encountered in the Hawaiian winter grounds of the humpback whale, *Megaptera novaeangliae*. *Marine Mammal Science*, *13*, 711-716.

Stacey, P. J., & Baird, R. W. (1997). Birth of a "resident" killer whale off Victoria, British Columbia, Canada. *Marine Mammal Science*, *13*, 504-508.

Stewart, R. E. A., & Stewart, B. E. (2009). Female reproductive systems. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 423-428). Amsterdam: Elsevier.

Stewart, R. E. A., Lightfoot, N., & Innes, S. (1981). Parturition in harp seals (*Phoca groenlandica*). *Journal of Mammalogy*, *62*, 845-850.

Terasawa, F., Yokoyama, Y., & Kitamura, M. (1999). Rectal temperatures before and after parturition in bottlenose dolphins. *Zoo Biology*, *18*, 153-156.

Trevathan, W. (1996). An evolutionary perspective on authoritative knowledge about birth. In R. Davis-Floyd & C. Sargent (Eds.), *Childbirth and authoritative knowledge* (pp. 80-91). Berkeley: University of California Press.

Tsutsui, T., & Murata, Y. (1982). Variations in body temperature in the late stage of pregnancy and parturition in bitches. *Nippon Juigaku Zasshi*, *44*, 571-576.

Verstegen-Onclin, J., & Verstegen, J. (2008). Endocrinology of pregnancy in the dog: A review. *Theriogenology*, *70*, 291-299.

Wang, D., Hao, Y., Wang, K., Zhao, Z., Chen, D., Wei, Z., et al. (2005). The first Yangtze finless porpoise successfully born in captivity. *Environmental Sciences & Pollution Research*, *5*, 247-250.

Weilgart, L. S., & Whitehead, H. (1986). Observations of a sperm whale (*Physeter catodon*) birth. *Journal of Mammalogy*, *67*, 399-401.

Woods, E. C. (1962, June). Behaviour of the human myometrium *in vivo*. In *Proceedings of Society for the Study of Fertility Annual Conference*. London, England.