Birth in Free-ranging *Macaca fuscata*

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Abstract The birth process is an integral part of reproductive success in mammals, yet detailed, quantitative descriptions of parturition in nonhuman primates are still rare. Observations of free-ranging births can help to elucidate factors involved in this critical event, to contribute to our understanding of how maternal and infant behaviors during parturition affect infant survival and to explain the evolution of human birth. We provide data on the parturition behavior of 4 multiparous Japanese

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macaques: 2 daytime live births that we photographed and video recorded at the Awajishima Monkey Center (AMC), Awaji Island, Japan in 2006; a daytime live birth video recorded in 1993 at the AMC; and a nocturnal breech stillbirth of a captive *Macaca fuscata*, video recorded at the Kyoto Primate Research Institute in 2006. Certain behaviors were similar among the females, such as touching of the vulva followed by licking of fingers, squatting during contractions, and average contraction durations. Parturient females facilitated the birth manually by guiding the emerging infant. There were also dissimilarities in the duration of the labor and birth stages, condition of the infant at birth, and the mother's behavior immediately postpartum. The mother's postpartum behavior ranged from almost entirely infant-focused to predominantly related to the consumption of the placenta. The 3 free-ranging females all showed considerable social tolerance during labor and birth. We argue that social proximity at parturition is more common in nonhuman primates than previously emphasized, and has potential adaptive advantages.

Introduction

Birth is a complex process that increases the vulnerability of both mother and neonate to mortality from birth-related complications or predation (Nowak *et al.* 2000). Given both the involved and crucial nature of parturition, particularly for slow-reproducing mammals, we would expect the birth process and birth-related behaviors to be shaped by strong selective pressures. There are several reports on births in wild and free-ranging nonhuman primates, e.g., *Alouatta caraya* (Peker *et al.* 2009), *A. palliata* (Dias 2005), *Macaca fuscata* (Nakamichi *et al.* 1992), *M. mulatta*: (Rawlins 1979), *M. nigra* (Duboscq *et al.* 2008), *M. sinica* (Ratnayeke and Dittus 1989), *M. sylvanus* (Hammerschmidt and Ansorge 1989), *Nasalis larvatus* (Gorzitze 1996), and *Saguinus imperator* (Windfelder 2000). There are also some reviews (Brandt and Mitchell 1971; Caine and Mitchell 1979; Hammerschmidt and Ansorge 1989; Trevathan 1987) and captive studies on parturitional behavior with larger sample sizes, e.g., *Macaca fascicularis* (Kemps and Timmermans 1982; Timmermans and Vossen 1996), *M. fuscata* (Kanazawa and Nakamichi 1991; Negayama *et al.* 1986), and *Saimiri sciureus* (Bowden *et al.* 1967). However, because the timing of parturition is difficult to predict, and because most diurnal primates, including macaques, tend to give birth at night (Jolly 1972; Suzuki *et al.* 1990), detailed, quantitative descriptions of parturition in free-ranging nonhuman primates are still rare. Such data are necessary for clarifying the factors involved in this critical reproductive event; understanding how social, maternal, and infant-related variables at birth influence infant survival; and learning about the evolution of parturitional behaviors in human and nonhuman primates (Rosenberg and Trevathan 2002; Trevathan 1987).

In examining the evolution of social human birth behaviors, nonhuman primates are often set in contrast: "Unlike non-human primates, which seek solitude at this

time, human mothers actively seek assistance in childbirth" (Rosenberg and Trevathan 2002, p. 1201). Similarly, Brandt and Mitchell (1973) assumed that "primate births in the wild apparently happen at night away from the main troop" (p. 520). The assumption that isolation during parturition would be the usual pattern for nonhuman primates is not unreasonable; many mammalian females do isolate themselves during parturition (Nowak *et al.* 2000). There are a number of potential evolutionary benefits to such isolation during birth, including preventing confusion around neonate-mother identity (Nowak *et al.* 2000), a reduced risk of postnatal infection (Trevathan 1987), and a reduced risk of infanticide (Pusey *et al.* 2008) as well as other negative attention from intragroup conspecifics (Takahata *et al.* 2001). For instance, chimpanzees seclude themselves during the periparituritional period, a behavior that is suggested as a mechanism to reduce infanticide risk posed by unrelated females in the community that may reduce future feeding competition by killing a neonate (Pusey *et al.* 2008). However, in a report on a free-ranging labor and birth of *Macaca fuscata*, Nakamichi *et al.* (1992) observed considerable social contact and proximity and noted that the female appeared to be "strongly motivated to remain within the group" (p. 418), and a photo sequence of another free-ranging Japanese macaque birth shows other individuals within a few meters of the parturient female (Nigi 1982). These examples suggested to us a more diverse social context for birth behaviors in wild and free-ranging nonhuman primates than researchers have previously emphasized.

We here provide quantitative data on 4 Japanese macaque births: 2 free-ranging daytime live births that we observed, photographed, and video recorded at the Awajishima Monkey Center (AMC), Japan, in 2006; a free-ranging daytime live birth, video recorded at the AMC in 1993 (Nobuhara and Nobuhara, *unpub. video*); and a captive breech stillbirth video recorded at the Kyoto University Primate Research Institute (PRI) in 2006 (Shimizu, *unpub. video*). Edited recordings of the 2 AMC births from 2006 are available as electronic supplementary material.

We address the following questions: 1) How does a free-ranging Japanese macaque behave during labor, birth, and immediately after the birth of her infant? 2) How similar are these behaviors among females and how do they compare to other observed births? 3) How do mothers behave in the minutes immediately after the birth of the infant and the delivery of the placenta? and 4) What is the social context of parturition in Japanese macaques and what are the implications of social tolerance during nonhuman primate parturition for understanding the evolution of birth in humans?

Methods

Study Site

The 3 births of free-ranging *Macaca fuscata* occurred at the AMC, a tourist destination on Awaji Island, Japan, that is frequented by a free-ranging group of *ca.* 200 Japanese monkeys for *ca.* 10 mo of the year. The monkeys are systematically provisioned twice daily, and they are also fed peanuts by tourists from within a caged enclosure (Nakamichi *et al.* 1997; Turner *et al.* 2008). The captive Japanese

macaque birth occurred at the Kyoto University Primate Research Institute in Inuyama, Japan.

Focal Subjects, Data Collection, and Analysis

There are 4 subjects in our study. Moko (birth 1), Cake (birth 2), and Mama (birth 3) were all free-ranging, multiparous adult females at the AMC. Moko was born in 1996, and we observed her parturition on July 21, 2006. Cake was born in the early 1990s, and was *ca.* 15 yr old at the time of the observed parturition on July 30, 2006. Mama was born in 1974, and the birth reported here occurred on July 31, 1993. Mff1549 (birth 4) was an individually caged, multiparous female used for research at the Kyoto University Primate Research Institute. She was captive-born in 1994 and birthed a stillborn infant in breech presentation at night on May 18, 2006. For each of births 1 and 2, we collected, transcribed, and amalgamated data from 2 video cameras, a digital SLR for still images, and notes taken *ad libitum* on a Palm. For births 3 and 4, we transcribed behavioral data from videos that were taken during the births.

We describe the parturition in terms of 3 phases (Timmermans and Vossen 1996): 1) a prepartum or labor phase, beginning when we first observed the female in labor and ending when the infant was first visible emerging from the birth canal; 2) a partum or birth phase, from the time the infant was first visible until it had entirely emerged from the mother's body; and 3) a postpartum phase, up to and including the delivery and consumption of the placenta (observations permitting). Out-of-sight time was not consistent among the cases, and the interval between the birth of the infant and the delivery of the placenta varied among females. Also, the emergence of the placenta provided a new behavioral possibility for the females: placentophagia. Therefore, we further divided the postpartum phase according to the emergence of the placenta. We examined the percentage of time a mother spent licking and handling the neonate separately for the interval before the emergence of the placenta and after the placenta was birthed until the placenta was consumed (birth 2) or data collection ended (births 1 and 3).

Our data on the births are not consistent in terms of the stages of parturition observed, the duration of observations, or the continuity of observations (Fig. 1). For birth 1, there is a gap between the first observed contraction and the beginning of detailed data recording that included contraction durations. We observed the complete consumption of the placenta only in birth 2. For birth 3, prepartum data were insufficient for quantitative analysis, and very little data were available after the delivery of the placenta. The recording of birth 4 extends to 4 min and 33 s after the birth and does not include the emergence of the placenta. The beginning of data collection for birth 4 (*ca.* 4 h before birth) is not included on Fig. 1, and in addition absolute times are not available for birth 4.

We defined a contraction bout as beginning when the female showed bearing down, lifted tail, straining, visible contraction of abdominal muscles, or squatting, rolling, or abrupt change of position, and continued until cessation of these behaviors. We defined handling the infant in the postpartum context as the mother physically inspecting and manipulating the infant's body with her hands without concurrent licking of the neonate, not simply holding the infant in physical contact.
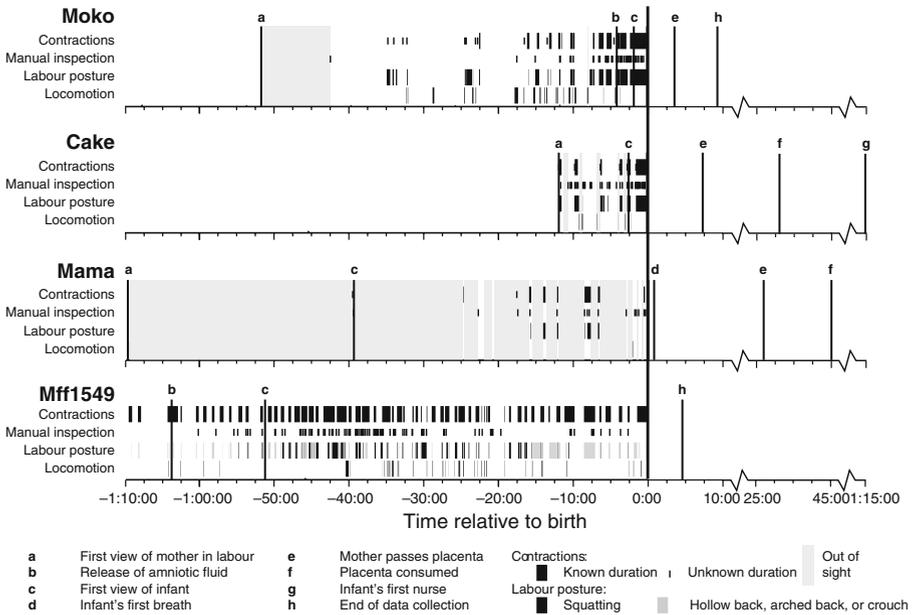
Fig. 1 Timeline of parturitions of *Macaca fuscata* observed in this study (after Nakamichi *et al.* 1992). Timing of major events and details of labor behavior—contraction frequency and duration, manual inspection of the vulva, labor posture, and locomotion—are shown up until the birth of the infant, with only the timing of major events indicated thereafter.

Results

AMC Birth 1: Moko

Prepartus

> 16:18: We identified Moko's labor from her squatting posture with lifted tail, and her manual inspection of the vulva, often followed by oral investigation of fingers.
> 16:27: Start of systematic data collection, including timed contractions (Fig. 1)
> 16:47: Start of video data collection
> 16:57: Provision feeding started for the group. Moko fed in between contractions.
> 17:02: Moko moved away from the provision feeding area and climbed onto a window bench behind the tourist enclosure. She paused during locomotion for contractions.
> 17:00: External vaginal dilation of 1.5–2 cm diameter
> 17:08: While touching her vaginal area, there was a gush of amniotic fluid; she continued to investigate her vulva manually and to move her hands from vagina to mouth.

Fig. 2 Digital photos of the birth of a free-ranging Japanese macaque. Birth 1: Moko. (a) 17:10 The head ▶
emerges. (b) 17:12 Moko pulls on the infant. (c) 17:12 She bends and licks the neonate's face. (d) 17:14
The umbilicus is visible across Moko's leg and the placental membrane is visible emerging from her
vagina. (e) 17:16 Moko eats a bite of placental membrane. (f) 17:18 At the edge of the forest, Moko holds
and licks the infant. (Photos a, b, c, d, and e are located in front of a fence; Moko is not inside a cage.
Photos by S. E. Turner.).

Partus

17:10: Infant's head first visible; Moko in a bipedal squat posture. As the head
began to emerge, Moko grasped at it with her right hand. As she pushed the
infant out, she also used her left hand to pull on its head. There appeared to be a
tear in the tissue of the perineum (Fig. 2a).

17:12: The male infant was born in occiput posterior position (1 min and 55 s
after the head was first visible). She used both hands, then only her left hand to
pull the head out of the birth canal and up across her left hip and up the left side
of her body (Fig. 2b). The infant's body was birthed rapidly. Moko twisted
toward the emerging infant and immediately licked his face (Fig. 2c). During
and after the birth, she made 25 chirrup/clucking vocalizations as she licked the
neonate's head, neck, back, and anogenital area (Fig. 2d).

Postpartus

17:15: Placenta birthed. She pulled it with her right hand, while holding the
infant with her left. She consumed a small portion of the exterior membrane,
holding the infant ventrally (Fig. 2e).

17:22. She followed the group into the forest and licked the infant (Fig. 2f). She
carried the infant and placenta bipedally, then carried the infant by supporting
him with her arm, the placenta dragging behind.

Social Context

Moko labored within the group; she groomed a juvenile for 4 min 11 s between
contractions and fed briefly in contact with an adult female, then an adult male, and was
also within 1 m of an infant and 4 young monkeys during provision feeding. When she
moved behind the feeding enclosure, she was within visual range of the main group and
was ≤10 m of the nearest individual. During the birth, a young monkey leaned down
from a branch 3 m above and appeared to be watching the birth. When the group left the
feeding area for the night, Moko left with them.

AMC Birth 2: Cake

Prepartus

10:36: We first observed Cake sitting in a squat with her tail out, with a slight
white bulge at her vaginal opening, touching her vulva and then inspecting and
licking her hand (Fig. 1).

10:39: She moved to a sheltered area beneath a ramp, and vocalized 10 times toward tourists.

10:41: She climbed to the feeding enclosure roof. During contractions, she paused in her locomotion and squatted, periodically manually inspecting her vaginal area and then bringing her hand to her mouth. Contractions appeared to grow stronger as birth approached; in the last few minutes before birth the movement of her abdominal muscles was apparent during contractions.

Partus

10:46: Cake squatted and the top of the infant's head was first visible. The head retreated into the birth canal, then was visible again with the next contraction. Cake repeatedly touched her vaginal area, pulling at the top of the head and bringing her hands to her mouth in between.

10:48: The infant's head, shoulder, and right arm emerged with a strong contraction. She cupped the infant's head in her left hand and pulled the infant forward toward her ventrum. She grasped the infant's right arm as it was birthed, then supported the infant's emerging body, which was born in a gush of amniotic fluid 13 s after the head fully emerged. The female neonate appeared to cling with her arms during the birth; ventral-ventral contact was maintained.

Postpartus

10:49: Cake squatted on all 4 limbs, then bent forward and sniffed and briefly licked the infant. The neonate lay with its back on the roof, and Cake licked amniotic fluid; she then retrieved the infant in a dorsal-ventral orientation, and repeatedly licked the infant's head and back, licked her own hand, and licked some amniotic fluid from the roof. Her range of movement appeared constrained by the shortness of the exposed umbilical cord.

10:51: The placenta began to emerge. She raised her body into a tripedal squat, holding the infant's arm in her hand, and pulled out a piece of placental membrane and ate it. Squatting, she pulled on the umbilical cord and began to consume a portion of the partially emerged placenta.

10:56: She birthed the entire placenta with a final contraction and adjusted the infant in a ventral-ventral position. Then she began eating the placenta avidly, and nearly continuously, until the major portion was consumed, licking blood also from her own hand and from the roof.

11:19. Placenta completely consumed. She licked her hands and arms, nibbled the end of the umbilicus, and licked the neonate. She then moved into the forest, where she held her neonate.

12:02: First nurse 1 h and 14 min after the birth, then periodically all afternoon

17:27: Cake left with the group after provisioning, supporting the neonate with her arm during locomotion.

Social Context

Cake labored and birthed her infant within the group on a busy tourist day at the AMC. Early in our recording of her labor *ca.* 30 monkeys moved to within a *ca.* 5–7 m radius of her in the partially enclosed space under a ramp. During this group interaction, she was approached by one of the highest ranking females, who leaned in and sniffed Cake's nose and hand. Three young monkeys and an adult female approached within a meter. Cake investigated her vulva with her hand, and one of the young monkeys then bent forward and apparently sniffed her hand, while another sat in contact with her. Cake licked her hand, while one of the young monkeys sat with her face right at Cake's hand, then right at her nose, then her anogenital area. More young monkeys approached Cake until there were 11 monkeys at ≤1 m, with many more near and looking in her direction. She then moved rapidly away from the convergence. During the birth and as she consumed the placenta, most other monkeys remained ≥3 m away. However, a young monkey stood looking from 2 m away after the infant was born, 2 young monkeys watched her deliver the placenta from ≤3 m, and ≥5 young individuals watched her in the minutes after the birth. Cake appeared to ignore them.

AMC Birth 3: Mama

Prepartus

11:29: H. Nobuhara identified Mama's labor in the forest near the AMC feeding area; Mama walked with a stiff-legged gait, then rolled down to lie on her side (Fig. 1).
12:01: She squatted, arching her back during a contraction, then reached back to manually investigate her vulva. Her labor appeared to be progressing slowly: contractions did not appear intense and appeared to have relatively long intercontraction intervals.

Partus

12:02: The top of the infant's head was visible. Lying on her side, she periodically inspected her vaginal area and then slowly licked her hand.
12:28: Her vaginal opening was visibly 2–3 cm dilated.
12:43: Mama sat on her left hip with her right leg raised. She slowly reached down ventrally and ran her hand over her vulva, pulling at the hairs on the infant's head.
12:44: She raised herself to a crouching, squatting position, and reached back and cupped the emerging infant's head in her hand 20 s later. There appeared to be a *ca.* 1 cm tear in her perineum as the head was birthed. A second after the head emerged, she pulled on the infant's head from a tripedal squat position, and the body emerged. The neonate's head looked compressed and narrow, not wider than the shoulders. The male infant appeared dead; he was not breathing and his skin was purple.

Postpartus

12:44: Mama lifted and sniffed the limp neonate, licked him, and gently bit his head. She turned him over and looked at his anogenital region, sniffed him again, licked his face once, then put the infant on the ground and moved her hand on his face. The neonate's limbs moved in a slight tremor. Mama pressed the side of his head into the ground with her right hand. She then grabbed and manipulated the legs, and sniffed and licked the infant. The infant was limp as she manipulated it slowly with her hands.

12:45: The infant took his first breath (37 s after birth), his mouth opening audibly. Mama continued to lick his anogenital area, feet, and face, with the infant held or on the ground.

12:46: Mama pulled on the umbilical cord. She picked up the neonate and licked his head. She licked, looked at, and manipulated the infant, and licked her own hands, all in a slow manner.

12:48: The infant opened his mouth in a gasp, then took another breath again 9 s later.

12:54: The infant's body jerked, and had gained a more pink color.

13:01: The placenta began to emerge. Mama lifted the infant and he stretched his arms straight out and up and wrapped his arms around her.

13:09: She held him upside-down and licked his anogenital area; he moved and vocalized.

13:12: Placenta birthed; she pulled it out from behind and began eating it. The infant was moving a little, and his eyes were open.

13:29: She appeared to be finished with the placenta, although there was still some remaining attached to the umbilical cord. She held the infant, who was clinging to her, pink and alert.

Social Context

During Mama's labor there were ≥2 adult females and their infant and juvenile offspring within a few meters; 1 adult female sniffed Mama's anogential area, then sat *ca.* 2 m away. Mama was watched intently by an adult female from 2–3 m away during contractions, then from ≤1 m as she investigated her vaginal area. When she rolled down into a lying position, the other monkey brought her face close to Mama's anogenital area. Just before birth, a juvenile approached and appeared to sniff her face and anogenital area intently while in contact with her. During the birth itself, an infant approached and leaned against Mama's hip. Mama did not respond to the infant, as her own infant's head emerged. The other infant vocalized and departed. After the birth, 2 infants, which she appeared to ignore, approached and sat in contact with her while she handled her neonate.

Birth 4: Mff1549

Times are given relative to birth because absolute times were not available.

Prepartus

–3h49m13: Video data collection began. Bouts of contractions were identifiable by the monkey's behavior; during contractions she moved, squatted, or moved into and out of a hollow-backed posture with her head on the cage floor and her hindquarters in the air, or in quadrupedal arched-back position. Between contractions, she sat or lay on her side or front. As labor progressed, she spent more time crouching on all fours, contraction bouts became less distinct, and she investigated her vulva manually with increasing frequency (Fig. 1).
–1h4m39s: Release of amniotic fluid

Partus

–51m16s: The infant's feet were first visible. There was possibly some independent movement from the infant; however, there were no subsequent independent movements.
–43m54s: The mother was able to grasp the infant's leg and began pulling; she pulled up ventrally from between her own legs with apparent great effort during her contractions, and held the legs nearly continuously until the infant was born. She also occasionally rubbed her bottom and the emerging infant along the floor bars of the cage. During the intercontraction intervals, she sometimes rested or handled the emerging infant, licking her fingers vigorously after, and once it was possible, bending down to lick or nibble at the infant directly with her mouth.
0m0s: The infant was born, with a gush of fluid and with the mother crouched in a quadrupedal squat. When the infant was born, it was limp and showed no sign of life.

Postpartus

+0m13s: The mother pulled the neonate up from under the bars of the cage where it had fallen during the birth and was hanging from the umbilical cord.
+0m24s: The mother licked the infant, continuing until the end of the video recording.
+4m33s: End of video data collection. The infant's body was retrieved the next morning, with all the fingers of the left hand, the toes of the right food, and the little finger of the right hand absent, and likely consumed by the mother. She had also consumed the placenta.

Parturition Variables in the Context of Birth in Macaques

Quantitative information about these births is summarized in comparison to available data from other labors of *Macaca fuscata* in Table I and more widely available birth and postpartum data for *Macaca* spp. in Table II.

Table I Prepartum labor data for *Macaca fuscata*

Reference	Duration of labor[1,2] (in sight)	Contraction rate/min (n)	Mean contraction duration (range)	Mean intercontraction interval (range)	Vulva investigation rate/min (n)	% investigations with hand lick (n)	Labor postures[3]
Births observed in this study							
Birth 1: Moko	51:45 (43:30) video only: 22:44 (12:10)	0.55[4] (25)	0:33 (0:05–2:26)	0:46 (0:02–2:38)	2.77[4,5] (43)	60.5 (26)	a–d
Birth 2: Cake	10:58 (7:45)	0.57[4] (6) (7)	0:36 (0:14–1:37)	1:49 (0:42–3:13)	3.39[4] (36) (15)	72.2 (26)	a,b,e
Birth 3: Mama	32:28 (0:34)	—	—	—	—	33.3 (5)	a–d
Birth 4: Mff1549	3:02:57	Final 30 min[6]: 0.84 (25) Total: (134)	0:30 (0:04–1:35)	0:53 (0:05–4:33)	Final 30 min: 0.70 (21) total: 0.39 (90)	Final 30 min: 90.5 (19) Total: 74.4 (67)	a–g
Births observed in other studies							
Itoigawa and Tanaka 1963	a: 44:00 b: 51:00	—	—	—	a: (46 in 5 d leading up to birth) b: –	–	a,c,f,g
Kanazawa and Nakamichi 1991	~1:30:00–~3:00:00	Final 30 min: ~0.60–~0.90 (~18–~27)	20.2–26.9	1:09–1:34	(frequent)	–	a,e,f
Nakamichi et al. 1992	~35:00	0.51 (18)	0:30 (0:06–1:21)	1:36 (0:09–5:00)	0.29 (10)	100 (10)	a,e,g
Nakamichi et al. 2004	~2:00:00	Final 30 min: 0.44 (13) Total: (39)	Final 30 min: 0:28	—	Final 30 min: 0.54 (16) Total: 0.16 (19)	52.6 (10)	a,c,e,g
Total ranges (all studies):	–	0.26–~0.90	0:20–0:36	46–109	0.16–2.84	33.3–100	a–g

*Captive; ***free ranging.

[1] Time data are in units of m:s or h:m:s.

[2] This duration is the minimum possible length for labor, from the first observation of labor behaviors (births 1 and 2) or the beginning of the video record (births 3 and 4) to the first view of the emerging infant.

[3] a = squat; b = sit; c = lie; d = roll; e = arch back; f = hollow back/stretched back; g = crouch.

[4] Contraction and investigation rates calculated using the in-sight time up to the birth of the infant (Moko: 45:25; Cake: 10:37).

[5] We calculated the rate of vulvar investigation for Moko using the video data only (42 observed over 14 min and 25 s).

[6] For MMf1549, we report values calculated over the final 30 min of labor (in addition to over the total duration) so as to compare better with other reported births in this paper and in the literature.

Table II Birth and postpartum data for macaques

Reference	Species (n births)	Maternal parity (age)	Duration[1] of birth stage	Posture during birth	Infant position at birth	Infant latency: i: grasp ii: eyes open	Latency to ventral-ventral contact	% time licking infant[2] (duration)	% time handling infant[2] (duration)	% time eating the placenta (duration)
Births observed in this study										
Birth 1: Moko	Macaca fuscata (1)***	Multi (10)	1:55	Squat (mostly bipedal)	VOP[3]	i: 0:08 ii: 1:44	3:00	a: 84.5 (2:16) b: 33.3 (2:01)	a: 0.0 b: 1.7 (0:06)	13.2 (0:48)
Birth 2: Cake	M. fuscata (1)***	Multi (~15)	2:52	Squat (mostly tripedal)	VOP	i: 0:00 ii: <12:13	0:00 (at birth)	a: 12.2 (0:35) b: 3.1 (0:41)	a: 4.5 (0:13) b: 2.1 (0:27)	52.6 (11:25)
Birth 3: Mama	M. fuscata 7 (19)***	7 (19)	42:16	Tripedal squat	VOP	i: 18:21 ii: <45:24	2:34 (brief ventral contact)	a: 34.6 (7:30) b: 0.0	a: 9.5 (2:04) b: 0.9 (0:03)	65.5 (3:40)
Birth 4: Mff1549	M. fuscata 2 (12)*	2 (12)	51:16	Quadrupedal squat	Breech	–	–	a: 88.3 (4:01) b:—	a: 0.4 (0:01) b:—	–
Births observed in other studies										
Gouzoules 1974	M. arctoides (1)*	2 (12)	~8 min	–	Vertex	–	~25:00	licked briefly, put infant on the ground	held and handled after consuming placenta	exclusively ate placenta for ~22:00
Kemps and Timmermans 1982	M. fascicularis (5)*	4–8 (>9)	Vertex births: 1:02, 2:13, 0:06, 0:34	Squat	4 VOP 1 breech	Vertex births: i: 0:00 ii: 0:00	–	a+b: 7, 8, 12, 13	a+b: 2, 2, 6, 11	21, 29, 71
Timmermans and Vossen 1996	M. fascicularis (21)*	10 primi (4.5–6), 11 multi 3–9 (8–~20)	0:03–1:53[4] Mean: 0:25.6	Squat	Vertex	i: 0:00	Primi mean: 4:43.10 Multi mean: 0:40.67	Primi mean a and b: 15.1 Multi mean a and b: 9.7	–	Primi mean: (27:30) Multi mean: (16:22.5)

Table II (continued)

Reference	Species (n births)	Maternal parity (age)	Duration[1] of birth stage	Posture during birth	Infant position at birth	Infant latency: i: grasp ii: eyes open	Latency to ventral–ventral contact	% time licking infant[2] (duration)	% time handling infant[2] (duration)	% time eating the placenta (duration)
Itoigawa and Tanaka 1963	M. fuscata (2)*	1 primi 1 multi	1: 5:00 2: 0:30	–	Vertex	i1:10:00 i2: 0:02 ii1:— ii2:4:00	1: 0:05 2: 0:03	–	–	–
Kanazawa and Nakamichi 1991	M. fuscata (6)*	1 primi 5 multi (8–21)	Breech births: 7:00 1:25:00	–	4 vertex 2 breech	–	–	–	–	–
Nakamichi et al. 1992	M. fuscata (1)***	1 (8)	~2 min	Quadrupedal stand	VOP	–	Within seconds	Intermittent lick	–	–
Negayama et al. 1986	M. fuscata (12)*	4 primi (5–9) 8 multi 1–5 (8–20)	–	–	8 vertex 1 breech 3?	i: "Commonly seen immediately"	"Commonly seen immediately" (multi)	C[5]. a: 22.3 b: 1.1 I. a: 18.9 b: 2.8 N. a: 2.6 b: 2.4	–	C. 66.8 I. 9.3 N. 0
Brandt and Mitchell 1973	M. mulatta (14)*	Primi and multi	"A few seconds to a few minutes"	Squat or sit	13 vertex 1 breech	i: 0:00 ii: "At or soon after birth"	–	Most intently licked infant	–	85% of mothers ate it
Rawlins 1979	M. mulatta (1)***	Multi (18)	~1:00	Squat	Vertex	i: seconds ii: ~20:00	Within seconds	Licked for ~15:00	–	Did not pass placenta >8:38:00
Duboscq et al. 2008	M. nigra (1)****	Multi	~1:00	Quadrupedal stand then sit	VOP face first	–	<1:00	Licked herself and neonate	–	–
Ratnayeke and	M. sinica 1 (7.6)		<2:00	Bipedal stand	Vertex	i: 0:00	Within seconds	"Frequent"	–	Ate a portion, as

								did α female
Dittus 1989 (1)****								
Hammerschmidt and Ansorge 1989	M. sylvanus (1)**	Multi (9) "One single rapid event"	Squat or quadrupedal arched back	Vertex, infant did not touch the ground	ii: –	–	8 min "Intensive" licking" prior to placenta	Totally consumed in 4 min
Summary:	–	~1:00–~8:00 for vertex	Usually squat	Usually VOP[6]	Usually almost immediate	0:00–~25:00	a: 2.6–88.3 b: 0.0–33.3	a: 0.0–9.5 b: 0.0–2.1	9.3–66.8% for mothers who ate the placenta.

*Captive; **semi-free-ranging; ***free ranging; **** wild.

[1] Time data are in units of m:s, m:s.decimal, or h:m:s.

[2] a = the time period from the birth of the infant to the delivery of the placenta and b = the time period from the birth of the placenta to the complete consumption of the placenta, the mother's last efforts to eat it, or the end of data collection in the cases in which we did not observe the complete consumption of the placenta.

[3] VOP = vertex occiput posterior.

[4] From the time the head fully emerged until the birth of the entire body.

[5] Negayama et al. 1986 divided their sample into 3 groups for postpartum data analysis and presentation: type C mothers that consumed the entire placenta, type I mothers that partially consumed the placenta, and type N mothers that did not consume the placenta at all.

[6] Breech births were stillborn.

Discussion

We have described 4 Japanese macaque births, 3 of which were in a free-ranging context, and 1, a breech stillbirth in captivity. The labor and birthing positions and behaviors we observed were consistent with other published accounts of macaque parturition (Adachi *et al.* 1982 and Tables I and II).

Kanazawa and Nakamichi (1991) noted a marked convergence in length of contractions and intercontraction intervals among captive female *Macaca fuscata* in the last 30 min of labor; Nakamichi *et al.* (1992) reported comparable results for a free-ranging *M. fuscata*. Despite dissimilarities in the durations of the birth stages, and the outcomes of the births, mean contraction durations were very similar among the 3 females for which we had sufficient quantitative labor data and also similar to those in other studies (Table I). Further, during the final stages of labor in these and other observed births of *Macaca fuscata*, the average length of contractions seems to be restricted to a fairly limited range, suggesting that there may be a narrow optimum for the progression of late labor and birth (Table I).

The rate of contractions per minute and the mean intercontraction intervals ranged somewhat more, with our observations widening the previously reported ranges for these variables. Touching the vulva, often followed by licking the fingers, occurred in all Japanese macaque labors; however, the frequency of manual-vulva contact and subsequent hand licking was idiosyncratic and did not appear to correspond with other labor variables. All females assumed a squatting posture during some contractions; we also observed rolling and arching of the back for free-ranging females, and captive females used additional postures (Table I), perhaps in response to reduced potential for mobility.

Macaque infants tend to be born in vertex occiput posterior position—head first with the infant facing the mother's front—with the mother usually in a squatting position at the time of birth (Table II). The birthing stage itself tends to be very rapid, ranging from a few seconds to a few minutes (Table II). Selection pressure for fairly rapid birth in nonhuman primates is likely strong, in terms of both maternal and infant survival. During labor, macaque females are able to move around, eat, drink, and climb (Kemps and Timmermans 1982; Nakamichi *et al.* 1992), whereas the mother is most restricted in locomotion and self-defense during the birth stage. Thus, rapidity in birth minimizes the point of greatest vulnerability to the mother. In humans, pigs, and mink, extended labor tends to be associated with complications and fetal and neonatal death (Fraser *et al.* 1997; Malmkvist *et al.* 2007; Trevathan 1987), and it seems likely that the same is true in macaques; of the births reported here, the 2 infants born quickly were in better condition than those whose births were more protracted. For Mff1549, breech presentation of the infant (feet or bottom emerging first) explained the relatively slow birth stage, and this infant was stillborn. For Mama, there was no apparent cause for the slow progression to the birth stage, and although the infant did survive, his survival was clearly marginal for the first few hours, so this birth also supports the suggestion that a rapid birth is optimal for macaques.

In humans, breech births are associated with increased maternal and infant mortality and morbidity (Hannah *et al.* 2000). Although specially trained and experienced midwives and physicians can safely assist in vaginal breech birth,

breech babies tend to be delivered by cesarean section in most parts of the world where such health care is available (Chinnock and Robson 2007). Breech births in monkeys are also associated with reduced infant survival. Bowden *et al.* (1967) reported an infant mortality rate for breech births without veterinary assistance in monkeys as *ca.* 90%, and a number of subsequent papers have reported examples of breech stillbirths in nonhuman primates (Brandt and Mitchell 1971, 1973; Kanazawa and Nakamichi 1991; Kemps and Timmermans 1982; Nash 1974; Negayama *et al.* 1986; Price 1990). In all of these instances, breech birth was associated with a prolonged birth phase during parturition (Table II). In 1 wild breech birth that resulted in a live born infant, the birth phase was described as relatively long, at 5 min (Moreno *et al.* 1991) versus the usual 1–2 min (Sekulic 1982); however, this birth was still rapid compared to the breech birth we observed and others reported in the literature. In the nonhuman primate examples, the longer birth phase associated with breech presentations, in which the infant is often partially outside the mother, likely creates the same circumstances for hypoxia and stillbirth described in humans (Tunde-Byass and Hannah 2003), emphasizing the selection for a short birth phase.

As is expected for macaques, the 3 free-ranging infants all emerged in vertex occiput posterior position (Table II), a position that allows the mother to assist manually in the birth of her infant (Trevathan 1988), by pulling on, supporting, and guiding the infant head first out of the birth canal. Like many nonhuman primate females, all 4 mothers used their hands during the birth process. Some amount of manual self-assistance during birth seems to be nearly universal for macaques (Brandt and Mitchell 1973; Duboscq *et al.* 2008; Gouzoules 1974; Ratnayeke and Dittus 1989; Timmermans and Vossen 1996).

The ability to facilitate birth manually in nonhuman primates has potential advantages in terms of infant survival, particularly where births occur arboreally or on cliffs and the mother can potentially prevent the neonate from falling by holding the infant with 1 or both hands as it is born (Abegglen and Abegglen 1976; Moreno *et al.* 1991; Peker *et al.* 2009). Further, if manual self-assistance can speed or facilitate a stalled or difficult birth, it has the potential to impact both maternal and infant survival (Wittman and Wall 2007). Mama's infant was in very poor condition at birth, and it is certainly possible that her extraction of him from her body helped secure his survival. Moreno *et al.* (1991) suggested that experienced nonhuman primate mothers may be relatively more successful in dealing with potential life-threatening birthing situations, a suggestion that complements the finding that multiparous mothers behave more skillfully and efficiently during preparturient and postparturient periods than do primiparous mothers (Timmermans and Vossen 1996). The survival of Mama's neonate (her seventh) can be contrasted with the birth of an infant to a primiparous female *Macaca fuscata* at the Calgary Zoo. This female gave birth on a branch over the water, without manual self-assistance, and the infant fell to its death (L. Corewyn, *pers. comm.* to S. E. Turner).

Manual self-assistance is generally difficult for humans because human infants tend to be born in vertex occiput anterior position, the evolutionary result of encephalization and pelvic adaptations for bipedalism (Rosenberg 1992; Rosenberg and Trevathan 2002; Trevathan 1988). In this position, the mother cannot pull the infant forward until it has almost fully emerged without risking damage to the infant's neck and back (Trevathan 1987). Rosenberg and Trevathan (2002) argued

that, as a result, human birth in almost every culture and society around the world is attended by someone who can provide assistance and support to the mother (Rosenberg and Trevathan 2002; Trevathan 1987).

The overall postpartum behavioral repertoire—licking and handling the neonate, self-licking, and at least some placentophagia—was similar among the females we observed and similar to other reports in the literature (Table II). However, the females were dissimilar in terms of their postpartum allocation of time. The postpartum behaviors of the females we observed were notably divergent in terms of the percentage of time the mothers spent licking and handling the neonate before and after the emergence of the placenta and consuming the placenta (Table II). In the interval before the placenta emerged, licking of the neonate in macaques ranged from a brief lick to near complete absorption with licking the neonate; where quantitative measures were available, they also reflect this range (Table II). Although some mothers do physically manipulate and inspect their neonate without concurrent licking, Mama handled her neonate considerably more than the other females we observed and more than others reported in the literature (although this variable is rarely quantified).

After the emergence of the placenta, most macaque mothers reduce their focus on the infant; however, a macaque mother's behavior toward the placenta ranges from ignoring it to the avid and rapid consumption often described in the literature on placentophagia (Kristal 1991). The avid consumption of the placenta, often while ignoring the neonate, appears to be a common behavior among macaque females (Gouzoules 1974; Hammerschmidt and Ansorge 1989; Kemps and Timmermans 1982; Negayama *et al.* 1986), particularly multiparous females (Timmermans and Vossen 1996 and Table II). Placentophagia is a very common behavior in nearly all terrestrial mammals, and evidence suggests that placentophagia enhances opioid-mediated analgesia, in addition to providing protection from predators by removing the smell, and providing nutrition to the mother (Kristal 1991). However, not all nonhuman primate females consume the placenta (Brandt and Mitchell 1973; Negayama *et al.* 1986), humans nearly universally do not consume the placenta, and the factors that predict individual placental consumption in nonhuman primates are poorly understood (Hrdy 2009; Kristal 1991). Negayama *et al.* (1986) reported a positive relationship between a mother's postpartum licking behavior and placento-phagia in captive *Macaca fuscata* (Table II); however, our available data did not show this pattern. We did note that Cake, the female that consumed the placenta most consistently and avidly, also showed the highest rates of prepartum vaginal investigation and subsequent hand licking, data that support the idea of an overall connection between parturition orality and placentophagia (Kristal 1991; Negayama *et al.* 1986). However, Moko also engaged in substantial prepartum oral behavior and her near complete disregard for the placenta on its emergence stands out as unusual, especially compared to Cake's avid consumption of the placenta.

Although the specifics of their social involvement and tolerance at the time of birth varied among the females in the three free-ranging births reported here, a notable element of these births was that the mothers did not appear to seek solitude. A survey of the literature on wild and free-ranging nonhuman primate parturition shows that the social context of these births is not so unusual. Free-ranging and wild nonhuman primate births occur in a variety of social contexts, and as more

observations of such births have accrued, a more varied picture than the posited contrast between the social parturient human woman and the isolated nonhuman primate female emerges. Some nonhuman primate females gave birth in isolation from their group (Chivers and Chivers 1975; Duboscq *et al.* 2008; Goodall and Athumani 1980; Ratnayeke and Dittus 1989; Rawlins 1979; Takahata *et al.* 2001); others gave birth within the social group (Gorzitze 1996; Kumar *et al.* 2005; Moreno *et al.* 1991; Nakamichi *et al.* 1992; Nash 1974; Nigi 1982; Peker *et al.* 2009; Stewart 1984; Takahata *et al.* 2001); and still others gave birth within the group, but with some amount of spatial separation from most or all conspecifics (Abegglen and Abegglen 1976; Condit and Smith 1994; Hammerschmidt and Ansorge 1989; Kinnaird 1990; Peker *et al.* 2009; Sekulic 1982; Windfelder 2000). Of course, we cannot assume that every nonhuman primate female that has been observed to give birth did so in the optimal location from the perspective of the mother or infant (Sekulic 1982). However, the diversity of the observed locations of wild and free-ranging parturient female nonhuman primates in relation to other group members suggests that the potential evolutionary benefits of isolation during birth, e.g., avoidance of negative attention from intragroup conspecifics, and reducing the risk of infection, infanticide or mother-neonate identity confusion, may be sometimes outweighed by the potential evolutionary benefits of being in or near the group during parturition.

One potential benefit of birthing in a social context is reduced predation risk associated with being in a group in which the vigilance of other group members and vocalizations can alert the parturient female to predation threats. Also, the presence of conspecifics may divert the attention of potential predators, diffuse predation risk, and may dissuade the predator from preying upon members of the group at all (Coss *et al.* 2007; Nowak *et al.* 2000; Ramakrishnan and Coss 2001; Windfelder 2000). Usually, the presence of potential predators is not mentioned in reports on birth. At AMC, there is low risk of predation; however, feral dogs occasionally hunt in the forest, suggesting that predation avoidance might help explain the social tolerance we observed. Also, in some species, threats from extragroup conspecifics may help explain intragroup birth (Duboscq *et al.* 2008).

Socially tolerant parturient females may also benefit through kin selection. If a primiparous female has witnessed a birth, she might be more likely to respond well to the birth of her first infant, and therefore improve that infant's chance of survival, her own reproductive success, and the inclusive fitness of female relatives in the group. Birth and the first few days of life are a vulnerable time and mammalian infant survival is highly dependent on adequate maternal care (Malmkvist *et al.* 2007). Further, primiparous mothers have a higher rate of infant mortality than do multiparous females (Sunderland *et al.* 2008), but young females with infant handling experience are more effective primiparous mothers than those without (Fairbanks 1990).

If kin selection were indeed a driving aspect of socially tolerant behavior in parturient females, we would expect that young female relatives would be the ones most likely to be tolerated and would be likely to show interest in the birth process. Young females are often noted to be close observers of at least part of the birth process (Abegglen and Abegglen 1976; Kinnaird 1990; Nakamichi *et al.* 1992; Sekulic 1982; Stewart 1984). However, the response of group members to parturition is extremely varied (Caine and Mitchell 1979). In some instances,

conspecifics that are nearby during parturition appear to pay little or no attention (Moreno *et al.* 1991), and it is not always young females that approach or watch the parturient female (Goodall and Athumani 1980; Kumar *et al.* 2005; Nash 1974). Also, a somewhat isolated parturition does not exclude the possibility of kin selection benefits; in some instances, even females that were isolated from most group members during parturition tolerated their own offspring nearby (Goodall and Athumani 1980; Hammerschmidt and Ansorge 1989; Pusey *et al.* 2008).

Finally, although nonhuman primates do not show anywhere near the degree of midwifery and birth assistance that is virtually ubiquitous in human societies (Trevathan 1987), in some species, the presence of conspecifics may assist the parturient female (Caine and Mitchell 1979; Trevathan 1987). In captivity, orangutan, cotton-top tamarin, and common marmoset fathers have been reported directly touching and gently pulling on the emerging neonate (cited in Caine and Mitchell 1979; cited in Price 1990). There are also some less direct free-ranging examples. For instance, a primiparous wild hamadryas baboon gave birth in such a way that the infant fell over the edge of a cliff and hung from the umbilicus as it was born, and the α-male "attempt[ed] to catch the falling infant" (Abegglen and Abegglen 1976, p. 55). A capped langur female that was vocalizing in a distressed manner during labor and parturition was groomed by other females that approached during her vocalizations (Kumar *et al.* 2005). In humans, parturition is more likely to require fewer medical interventions when a woman has emotional support during her labor (Trevathan 1987). In addition to the rare reports of more direct assistance, most nonhuman primates are very social animals and may maintain social proximity if affiliative social interactions during labor helped reduce labor pain and stress, which could facilitate smoother labor and birth and therefore neonate survival.

Although the degree of social behavior, involvement, and assistance during human birth is indeed unique, as more observations of wild and free-ranging nonhuman primate births have accrued, the contrast of the solitary birthing nonhuman primate female no longer appears so marked. In addition to the tight maternal-pelvic opening size to fetal cranial size ratio, resulting from adaptations for bipedalism and encephalization, which likely selected for a social birthing environment in humans (Rosenberg and Trevathan 2002), we need to consider how predator avoidance, kin selection, and general sociality may also select for more socially tolerant parturition behavior in nonhuman primates: factors that may also have influenced the evolution of human social birth behaviors.

Conclusions

We draw conclusions from this small sample with caution. There are many consistencies in behaviors throughout parturition, and particularly during labor, where females are similar especially in terms of posture and contraction duration. The duration of the birth stage appears to be related to infant position and to affect infant condition, and it is likely that there is selection pressure for a relatively short birth stage. Although the overall behaviors we observed were similar among females, the allocation of time, particularly in terms of postpartum behavior and placentophagia, appeared idiosyncratic. However, we can report considerable

variation in adequate postpartum maternal care behaviors because all 3 of the free-ranging infants survived to ≥1 yr, despite variation in behaviors of the mothers in the minutes after birth. Further, we observed that mothers will care for unresponsive infants in the minutes after birth, so infant behavior is not always necessary for prompting maternal care of neonates. Finally, all 3 free-ranging labors and births occurred within the social group and were observed by other individuals. We found that there is considerable variation across published reports in the relative sociality of females during parturition, and we suggest that social tolerance during parturition may be adaptive for many nonhuman primate females.

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