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RESEARCH ARTICLE

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Comparative primate obstetrics: Observations of 15 diurnal births in wild gelada monkeys (*Theropithecus gelada*) and their implications for understanding human and nonhuman primate birth evolution

Nga Nguyen[1,2]* | Laura M. Lee[3]* | Peter J. Fashing[1,2]* | Niina O. Nurmi[4] |
Kathrine M. Stewart[5] | Taylor J. Turner[6] | Tyler S. Barry[7] | Kadie R. Callingham[8] |
C. Barret Goodale[9] | Bryce S. Kellogg[10] | Ryan J. Burke[11] | Emily K. Bechtold[12] |
Megan J. Claase[13] | G. Anita Eriksen[2] | Sorrel C.Z. Jones[14] | Jeffrey T. Kerby[15] |
Jacob B. Kraus[16] | Carrie M. Miller[17] | Thomas H. Trew[8] | Yi Zhao[18] |
Evan C. Beierschmitt[19] | Malcolm S. Ramsay[20] | Jason D. Reynolds[21] |
Vivek V. Venkataraman[22]

[1]Department of Anthropology & Environmental Studies Program, California State University, Fullerton, Fullerton, California

[2]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway

[3]School of Veterinary Medicine, University of Wisconsin, Madison, Wisconsin

[4]Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, University of Göttingen, Göttingen, Germany

[5]Department of Biology, University of Saskatchewan, Saskatoon, Canada

[6]908 Willowrock Drive, Loveland, Colorado

[7]85 S Fair Oaks Ave, Madison, Wisconsin

[8]Guassa Gelada Research Project

[9]School of Natural Resources and Extension, University of Alaska Fairbanks, Fairbanks, Alaska

[10]Forest Restoration Program, The Nature Conservancy, Bend, Oregon

[11]Department of Zoology, University of Oxford, Oxford, England, UK

[12]Department of Microbiology, University of Massachusetts, Amherst, Massachusetts

[13]Windy Ridge, Spring Hill, Little Staughton, Bedford, Bedfordshire, England, UK

[14]School of Biological Sciences, Royal Holloway, University of London, England, UK

[15]Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire

[16]Smithsonian Conservation Biology Institute, Front Royal, Virginia

[17]Department of Anthropology, University of Minnesota, Minneapolis, Minnesota

[18]Environmental Studies Program California State University Fullerton, Fullerton, California

[19]Department of Anthropology, University of California, Santa Barbara, Santa Barbara, California

[20]Department of Anthropology, University of Toronto, Toronto, Ontario, Canada

[21]Nova Consulting, New York, New York

[22]Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts

*These authors contributed equally to this study.

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Correspondence
Nga Nguyen, Department of Anthropology,
California State University Fullerton,
800 N. State College Blvd., Fullerton,
California 92834.
Email: nganguyen@fullerton.edu

Abstract

Objectives: The birth process has been studied extensively in many human societies, yet little is known about this essential life history event in other primates. Here, we provide the most detailed account of behaviors surrounding birth for any wild nonhuman primate to date.

Materials and Methods: Over a recent ∼10-year period, we directly observed 15 diurnal births (13 live births and 2 stillbirths) among geladas (*Theropithecus gelada*) at Guassa, Ethiopia. During each birth, we recorded the occurrence (or absence) of 16 periparturitional events, chosen for their potential to provide comparative evolutionary insights into the factors that shaped birth behaviors in humans and other primates.

Results: We found that several events (e.g., adopting standing crouched positions, delivering infants headfirst) occurred during all births, while other events (e.g., aiding the infant from the birth canal, licking infants following delivery, placentophagy) occurred during, or immediately after, most births. Moreover, multiparas ($n = 9$) were more likely than primiparas ($n = 6$) to (a) give birth later in the day, (b) isolate themselves from nearby conspecifics while giving birth, (c) aid the infant from the birth canal, and (d) consume the placenta.

Discussion: Our results suggest that prior maternal experience may contribute to greater competence or efficiency during the birth process. Moreover, face presentations (in which infants are born with their neck extended and their face appearing first, facing the mother) appear to be the norm for geladas. Lastly, malpresentations (in which infants are born in the occiput anterior position more typical of human infants) may be associated with increased mortality in this species. We compare the birth process in geladas to those in other primates (including humans) and discuss several key implications of our study for advancing understanding of obstetrics and the mechanism of labor in humans and nonhuman primates.

KEYWORDS
fetal emergence pattern, labor, parity, parturition, placentophagy

1 | INTRODUCTION

Birth—or parturition—is one of the most important life history events for eutherian mammals, yet little is known of the birth process for most species (Rosenberg & Trevathan, 2001; Trevathan, 2015). Birth occurs through the pelvis, a complex structure whose morphology can vary widely among mammals depending on the specific demands of locomotion, thermoregulation, support of the viscera, and parturition (for females) for each species (Hogervorst, Bouma, & de Vos, 2009). Regardless of mode of locomotion, a strong and stable pelvis is essential for efficient walking but can restrict the size and shape of the birth canal, a concern for mammals with large brains relative to body size as adults (Gruss & Schmitt, 2015). In humans and many nonhuman primates, neonates must squeeze through a birth canal barely larger than the size of their head in order to be born (Trevathan, 2010, 2015). Documenting the sequence of events before, at the time of, and immediately after birth offers important insights into the selective pressures that have shaped the anatomy and biology of mammalian females and those of their offspring.

Observations of live births in wild nonhuman animals also provide unique opportunities to revisit explanations for why some attributes of human births are unusual or unique among mammals (Trevathan,

2015). Here we provide accounts of 15 complete birth events—an unprecedented number for a wild mammal—observed in a population of gelada monkeys (*Theropithecus gelada*) at Guassa, Ethiopia, over a recent ∼10-year period. We capitalize on this uniquely rich dataset to evaluate the impact of prior maternal experience on the birth process in geladas, compare births in geladas to those in other primates, and discuss several key implications of our study for advancing understanding of obstetrics and the mechanism of labor in humans and other primates.

An entire field of medicine, obstetrics, is devoted to understanding the birth process in humans (Beckmann et al., 2009; Cunningham et al., 2009) and anthropologists have documented birth practices in many of the world's societies (Kay, 1982; Mead & Newton, 1967; Trevathan, 1987). Still, rising medical or surgical interventions in the birth process in many industrialized countries (Healy, Humphreys, & Kennedy, 2016)—including in many instances where interventions are later found to be unnecessary or harmful (Lothian, 2009)—suggest that our understanding of the biology of pregnancy and childbirth are far from complete (Wray, 2016). Comparative data from observations of live births in our closest living relatives (the nonhuman primates) are not only essential for advancing knowledge of childbirth, but also the obstetric consequences of bipedalism for

hominins (living and extinct), and the evolution of sexual dimorphism (Stoller, 1995; Trevathan, 2010).

Despite their importance, the events surrounding parturition remain poorly understood in wild nonhuman primates (Caine & Mitchell, 1979; Rosenberg & Trevathan, 2002; Trevathan, 2015). Behaviors surrounding birth have been well documented in a few captive primates (e.g., patas monkeys: Chism, Rowell, & Richards, 1978; chimpanzees: Elder & Yerkes, 1936; Nissen & Yerkes, 1943; cynomolgus monkeys: Timmermans & Vossen, 1996) and reports from captivity have provided important insights into the evolutionary mechanics of the birth process (e.g., Hirata, Fuwa, Sugama, Kusunoki, & Takeshita, 2011; Stoller, 1995). However, captivity and provisioning can alter animal behavior and bodily functions (reviewed in Costa & Sinervo, 2004; Fusani, Canoine, Goymann, Wikelski, & Hau, 2005), so studies of the birth process from a greater diversity of wild primate populations are needed to advance our knowledge of the social and ecological factors that have shaped primate births.

The paucity of published reports on live births in the wild is due largely to the fact that, being diurnal, most primates give birth at night (Dunn, 2012; Jolly, 1972, 1973). Nocturnal births are thought to be adaptive in diurnal species because they enable females to give birth when their group mates are at rest, thereby preventing females from being left behind and reducing their vulnerability to predation and agonism from conspecifics (Duboscq, Neumann, Perwitasari-Farajallah, & Engelhardt, 2008; Jolly, 1972). For species that build sleeping nests, like chimpanzees, there is the added benefit that a nest can act as a safety net if the infant falls during delivery (Hirata et al., 2011).

Even in the rare instances when births have been observed in the wild, poor visibility in the arboreal environments where most primates live often prevents researchers from observing one or more phases of the birth process (e.g., the moment of delivery: Brogan & Cords, 2010; Douglas, 2014; Martins, Chaves, Neves, & Bicca-Marques, 2015). Thus, the behaviors common to primates during the entire birth process have been difficult to identify (Rosenberg & Trevathan, 2002). Preliminary evidence from studies of captive primates suggests that prior maternal experience may influence the birth process, with experienced mothers generally exhibiting more competence at delivery than inexperienced mothers (Kemps & Timmermans, 1984; Timmermans & Vossen, 1996; Tinklepaugh & Hartman, 1931, 1932). However, to date, no comparable study of wild primates has provided data on a sufficiently large number of births to allow useful comparisons between mothers of differing levels of prior parturitional experience. If differences in delivery patterns do exist among wild primate mothers of varying prior experience, it may be supposed that humans, with their near-universal tendency towards assisted delivery (Trevathan, 2010), may be able to circumvent some of the common delivery-related blunders of inexperienced nonhuman primate mothers.

Human births are unusual (some argue "unique") among primates for at least five reasons: (a) neonates undergo internal and external rotation to deliver the head and shoulders, respectively, (b) infants are most commonly born facing the mother's spine, (c) mothers rarely, if ever, eat the afterbirth, (d) mothers almost never lick the infant but

almost always touch the infant after birth, and (e) mothers almost always have help from conspecifics during delivery (reviewed in Trevathan, 2010, 2015). Despite the importance of the birth process, we know surprisingly little of the factors that have shaped the evolution of these five defining attributes of human births. Unfortunately, few studies have compared patterns of birth among nonhuman primates to those of humans in key areas of evolutionary interest, including infants' orientation when emerging from the birth canal, maternal or conspecific aid to infants during delivery, or maternal consumption of the afterbirth (Hirata et al., 2011; Rosenberg & Trevathan, 2002; Trevathan, 2015; Turner et al., 2010). Comparative data from studies of wild nonhuman primate births can potentially shed light on the extent to which the unusual features of human births were outcomes of the hominin shift to habitual bipedalism and big brains (Trevathan, 2010).

During a recent ∼10-year period of research on gelada monkeys (T. gelada) at Guassa, Ethiopia (from 2007 to 2016), we directly observed 15 births, including 13 live births and two stillbirths. Here, we describe the behaviors surrounding birth among geladas at Guassa using 16 periparturitional events involving the mother, infant, or other group members during the birth process. In addition, we compare the behaviors surrounding birth in six first-time mothers to those in nine mothers with prior experience giving birth to at least one other infant and document several notable differences in the birth process between these groups of females. To help achieve a comparative evolutionary perspective towards parturition across primates, we also compare the behaviors associated with the births we witnessed among geladas to those from published accounts of the birth process in other nonhuman primate and human populations.

2 | METHODS

2.1 | Study subjects and site

The subjects of this study are part of a larger population of wild, free-ranging geladas inhabiting the Guassa Plateau, an unusually ecologically intact Afroalpine grassland measuring 111 km² in size at elevations ranging from 3200 to 3600 m above sea level in north-central Ethiopia (Fashing, Nguyen, Venkataraman, & Kerby, 2014). Geladas are large, terrestrial, sexually dimorphic monkeys found only in the Ethiopian Highlands (Bergman & Beehner, 2013) where they subsist on a mixed diet of mostly graminoids and forbs (Fashing et al., 2014). Geladas form complex, multilevel societies which consist of a dynamic assemblage of one-male social units (Kawai, M., Ohsawa, H., Mori, U., & Dunbar, 1983; Snyder-Mackler, Beehner, & Bergman, 2012). Unlike most of the Ethiopian Highlands, which have been degraded by livestock grazing and agriculture (Williams, Pol, Spawls, Shimelis, & Kelbessa, 2005), our study site, Guassa, has remained largely ecologically intact due to a locally-enforced 400-year-old indigenous conservation system (Ashenafi & Leader-Williams, 2005). Guassa is characterized by a rich array of flowering plants and forbs as well as many tall graminoids rare or absent in other more degraded gelada habitats (Fashing et al., 2014). Owing to its ecological integrity, Guassa supports a diverse community of large carnivores rare or absent from many other gelada habitats

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including Ethiopian wolves (*Canis simensis*), African wolves (*Canis aureus lupaster*), servals (*Leptailurus serval*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*) (Rueness et al., 2011; Venkataraman, Kerby, Nguyen, Ashenafi, & Fashing, 2015). Guassa is thus an ideal site in which to study gelada behavior under conditions resembling those in which the species likely evolved.

The subset of the gelada population at Guassa that is under intensive study (i.e., the study population) has been monitored continuously since January 2007 when data first began to be collected on a near-daily basis by PJF, NN, and their students and collaborators (Nguyen et al., 2015). The study population currently consists of ∼200 extant individuals, though demographic and behavioral data on ∼200 additional animals that have died or dispersed are also available. Data for this study were collected from Jan 2007—November 2016 on the members of 16 one-male units that share a common home range (and thus belong to the same *band* of geladas—Steelers Band) at Guassa. As is typical of geladas elsewhere (Dunbar, 1986), additional one-male units were often seen traveling with units belonging to the Steelers Band (in daily ranging aggregations called *herds* that can include several hundred individuals). During our study, daily observed herd size ranged from 50 to >700 individuals (Nguyen & Fashing, unpublished data). One-male units were composed of 1–3 adult males, 1–9 adult females, and their dependent offspring (Nguyen et al., 2015). Members of these units are individually recognized from natural markings or parasitic swellings on their bodies (Nguyen et al., 2015). Like baboons, gestation in geladas lasts ∼6 months (McCann, 1995) and pregnant females possess a "pregnancy sign" [the skin around the ischial callosities changes from dark grey to deep pink (Altmann, 1970) (Nguyen & Fashing, unpublished data], making it possible for researchers to identify and monitor pregnant females. Data were collected on handheld electronic devices (Palm® m500) using a custom software program.

2.2 | Behavioral data

Upon detecting a pregnant female exhibiting periparturitional behavior (e.g., adopting a standing crouched posture, see Figure 1), we terminated other forms of data collection to focus on documenting as many details of the behaviors and events surrounding the birth process as possible using *ad libitum* sampling (Altmann, 1974). In our study, 12 birth events were witnessed for females belonging to Steelers Band and three additional births were observed involving non-Steelers females traveling in herds containing Steelers units. Reproductive histories of the 12 Steelers females who gave birth were known from near-daily, long-term monitoring, while the non-Steelers females could be classified as primiparous or multiparous based on their morphology. In particular, one non-Steelers female was classified as primiparous due to her small body size and the small size of her nipples [nulliparous female geladas possess tiny round nipples which develop into pendulous nipples after females nurse their first offspring (Dunbar & Dunbar, 1974; Nguyen & Fashing, personal observation), while the other two females were classified as multiparous on account of their large body size and pendulous nipples.

During each birth we recorded the presence or absence of 16 periparturitional events (Table 1 and Supplementary Information). These behaviors were chosen for both their conspicuousness and their potential to provide comparative evolutionary insights into the factors that shaped birth behaviors across nonhuman primates and humans (Rosenberg & Trevathan, 2002; Trevathan, 1987, 1988). Detailed accounts of the events surrounding 6 of the 15 births can be found in Lee (2011). Births were divided into four stages following Brandt and Mitchell (1971) that correspond roughly to clinically defined stages (in parentheses):

1. Prepartus (active labor)—phase just before the actual birth, during which observable uterine contractions occur,
2. Partus (second stage)—the birth itself, beginning with the first appearance of the infant's head and ending when the infant is completely expelled from the vaginal opening,
3. Postpartus I (third stage)—phase immediately after birth, during which the severing of the umbilical cord and expulsion of the placenta occur, and
4. Postpartus II—phase consisting of the period after the placenta is expelled through the mother's final efforts to consume it.

Though ours is the largest dataset of detailed observations on wild primate births to date, sample sizes were still too small in our study to enable statistical analysis. As a result, all comparisons between multiparous and primiparous females presented here are descriptive in nature. We chose to include the two stillbirths in our dataset along with the 13 live births because there was no variable for which the stillbirths differed from the births of all of the other females in our study (Table 1).

3 | RESULTS

3.1 | Gelada birth behaviors

We observed births to 12 females (10 live and two stillbirths) in the 16 gelada study units belonging to Steelers Band and 3 live births by females in units not belonging to our study band. Together, the 12 births we observed among Steelers Band females represented 4.9% of the 247 births to 106 focal females in 16 one-male units in this band during the ∼10-year study period (Nguyen & Fashing, unpublished data). The majority of births at Guassa probably took place at night, on or near the sleeping cliffs, where observers cannot follow the animals. However, diurnal births certainly make up more than 5% of all births at Guassa since on several occasions, we obtained circumstantial evidence of diurnal births that were not directly witnessed (e.g., late morning or afternoon observations of freshly born, bloody and wet, neonates, often still attached to the umbilical cord). Of the 15 total births we observed, six involved primiparous (first-time) mothers while nine involved multiparous females with experience delivering at least one other offspring. The number of prior pregnancies, including the present offspring, among the multiparas ranged from 2 to ≥6 (some focal females were already multipara at the onset of our study in 2007). A summary of 16 key periparturitional events surrounding the 15 births in our study can be found in Table 1 and Supplementary Information.
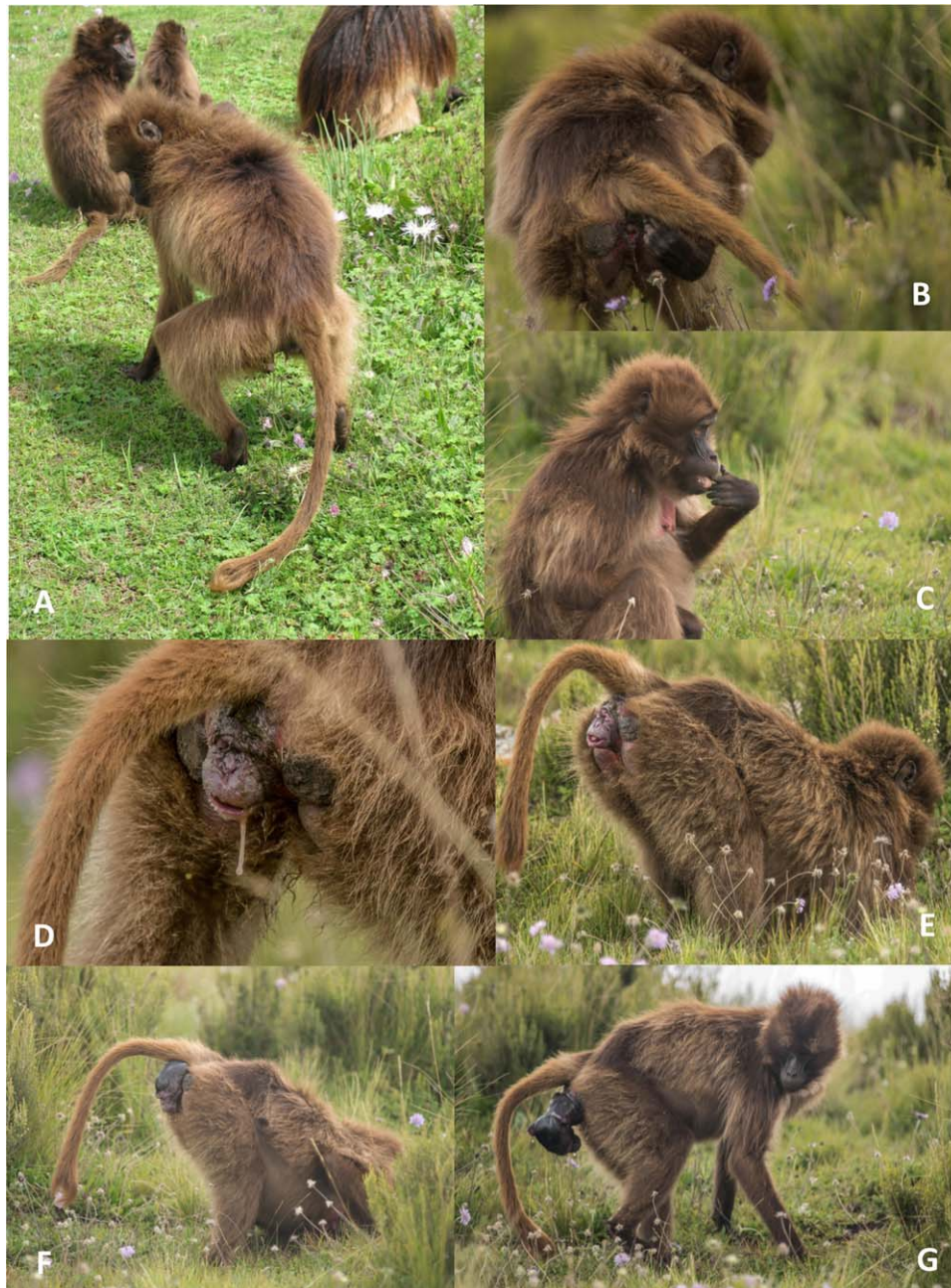
FIGURE 1 Typical behaviors exhibited by female gelada monkeys during the birth process at Guassa, Ethiopia: (A) adopting a standing, crouched posture during early labor, in close proximity to several conspecifics; (B) touching perineal zone and vulva; (C) licking fingers after touching perineal zone and vulva; (D) infant emerges face first (face presentation) from the birth canal; (E) mother pushing the remainder of the infant's face out of the birth canal; (F) delivering the rest of the infant's head; (G) delivering the infant's shoulders; (H) mother reaches back to manually guide the rest of the infant out of the birth canal; (I) mother reaches down to 'catch' infant as it exits the birth canal; (J) mother reaches back (while seated) to guide the delivered infant up towards her chest; (K) after successfully delivering both infant and placenta, mother ignores placenta; (L) mother consumes placenta; (M) mother licks infant clean following delivery; and (N) infant successfully emerging from the birth canal in the occipital anterior position typical of humans. Photos courtesy of Jeffrey T. Kerby, Ryan J. Burke, and Niina O. Nurmi. Additional photos and videos of many of the births are available upon request

3.1.1 | Prepartus

During the 30 min leading up to the beginning of the birth (or partus), all 15 females were seen within 5 m of other group members and assumed a standing, crouched position during contractions (Figure 1a). All but three females (all primiparas) touched their perineal zone and vulva (Figure 1b), often subsequently sniffing and licking their fingers (Figure 1c). Females frequently pulled at tufts of grass and yawned during contractions. All but three females remained silent during all stages of the birth—a primipara and two multiparous females—who each uttered one to several soft grunt vocalizations during labor or delivery.

FIGURE 1 Continued

Intriguingly, one of the two vocalizing multiparas (Belle) was the only female in this study to successfully deliver an infant with its face directed towards the mother's spine, as opposed to her face, which is more typical for this species.

3.1.2 | Partus

While giving birth, primiparous females (4 of 6) were more likely to remain near (i.e., within 5 m of) conspecifics than multiparous females (0 of 9) (Figure 2a). All infants emerged headfirst (i.e., fetal presentation was cephalic). Eleven of the 15 infants emerged with their face directed toward their mother's face. Of these 11 births, the fetal face was foremost in the birth canal and the first part of the head to emerge in all 8 cases in which fetal attitude or posture could be determined (i.e., not obscured by vegetation or the mother's position relative to observers), indicating that the fetal head and neck were extended—instead of flexed which is more typical of human births—during delivery (Figure 1d–f). Three of the 15 infants emerged from the birth canal in the occiput anterior position typical of human infants, though only one

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TABLE 1 Behaviors during 15 births observed among geladas at Guassa, Ethiopia between 2007 and 2016 in order from earliest to most recent, with multiparas listed above primiparas and stillbirths (indicated by [r]) listed last in each grouping.

Mother		Birth details						Near conspecifics? (≤5 m)			Received aggression?	
Name	Multipara?	One-Male Unit	Infant Name	Infant Sex	Date	Time	Observed By	Before[a]	During[b]	After[c]	From ♂♂[d]	From ♀♀[e]
LAKER	+	L	LEROY	♂	07NOV08	1730	LML	+	–	+	–	+
WENDY	+	W	WASABI	♀	24NOV08	1654	LML, NON	+	–	+	–	–
SUMMER	+	S	SIEGFRIED	♂	07APR09	1747	LML, NON	+	–	+	+	–
BELLE	+	B	BEAST	♂	16OCT09	1640	CBG, TSB	+		+	+	–
AMBROSIA	+	A	ALMUERZA	♀	03OCT12	1248	BSK, CMM	+	–	–	–	–
HESTER	+	D	HAVANA	♂	13FEB16	1828	JBK	+	–	–	+	–
ADF1[q]	+			♂	06OCT14	1256	EKB, MJC, JTK	+	–	–	–	–
ADF2	+			♂	12SEP16	1129	GAE, KRC	+	–	+	+	–
WEEZER[r]	+	W	WE1	♂	11JAN13	1303	BSK	+	–	–	–	–
TOPANGA	–	T	TALISMAN	♂	24APR09	1335	NON	+	+	+	–	–
RHEA	–	R	RAMPAGE	♀	09APR10	1347	CBG, TSB	+	–	+	–	–
ADF3[s]	–				13JUN11	1708	RJB, SCZJ, KMS, TJT, YZ	+	+	+	–	–
THRASHER	–	T	TYKO	♀	10AUG11	1012	KMS, TJT	+	+	–	–	–
RAMPAGE[t]	–	R	REGINALD	♂	23NOV16	1039	KRC, THT	+	–	–	–	–
ATHENA[r]	–	A	AT1	♀	17AUG11	0912	KMS, TJT	+	+	–	–	–

Mother		Infant birth details			Maternal behavior before birth			Maternal behavior during/after birth				
Name	Multipara?	Amniotic sac intact[f]	Emerged head first[g]	Emerged facing the mother's face[h]	Assumed standing, crouched position[i]	Touched perineal zone and vulva[j]	Vocalized[k]	Aided infant[l]	Licked newborn[m]	Consumed amniotic sac[n]	Placentophagy[o]	Licked blood from surrounding area[p]
LAKER	+	+	+	+	+	+	–	+	+	–	–	–
WENDY	+	+	+	+	+	+	–	+	+	+	+	+
SUMMER	+	–	+	(+)	+	+	–	+	+	+	+	+
BELLE	+	–	+	–	+	+	+	+	+	+	+	–
AMBROSIA	+	–	+	(+)	+	+	–	+	+	+	+	+
HESTER	+	–	+	(+)	+	+	–	+	+	+	+	–

(continues)

TABLE 1 (continues)

Mother		Infant birth details			Maternal behavior before birth			Maternal behavior during/after birth				
Name	Multipara?	Amniotic sac intact[f]	Emerged head first[g]	Emerged facing the mother's face[h]	Assumed standing, crouched position[i]	Touched perineal zone and vulva[j]	Vocalized[k]	Aided infant[l]	Licked newborn[m]	Consumed amniotic sac[n]	Placentophagy[o]	Licked blood from surrounding area[p]
ADF1[q]	+	−	+	(+)	+	+	−	+	+	+	+	+
ADF2	+	−	+	(+)	+	+	+	+	+	−	+	+
WEEZER[r]	+	+	+	−	+	+	−	−	+	−	−	+
TOPANGA	−	+	+	(+)	+	+	−	−	+	+	−	−
RHEA	−	−	+	(+)	+	−	+	+	+	+	+	−
ADF3[s]	−	+	+	+	+	−	−	−	+	−	−	−
THRASHER	−	+	+	(+)	+	+	−	+	+	+	−	+
RAMPAGE[t]	−	+	+		+			−	−	+	+	+
ATHENA[r]	−	−	+	−	+	+	−	+	+	+	+	+

+ indicates that the behavior was observed; − indicates that the behavior was not observed; and blanks indicate that observers were unable to determine whether or not the behavior occurred.

[a]Before parturition (during 30 min prior to birth), female was within 5 m of another gelada.

[b]During parturition, female was within 5 m of another gelada.

[c]After parturition (during 30 min following birth), female was within 5 m of another gelada.

[d]During labor or soon thereafter (within 30 min of birth), female received aggressive signals from male group members.

[e]During labor or soon thereafter (within 30 min of birth), female received aggressive signals from female group members.

[f]Amniotic sac was intact (or not fully ruptured) at the time the infant's head emerged from the birth canal; in some cases, mothers punctured the sac covering the infant's face (with their hands or teeth) to clear the infant's airway during or after delivery.

[g]Infant emerged head first from the birth canal.

[h]Infant emerged from the birth canal with its face directed towards the mother's abdomen and face; the three infants that did not emerge this way emerged with their faces directed towards their mother's spine, in the occiput anterior position typical of human births; () indicates cases of confirmed face presentations.

[i]During labor, female assumed a standing position and hunched her back, via a temporary curvature of her spine.

[j]During labor, female touched her perineal zone and vulva, followed (in some cases) by licking or smelling of the fingers.

[k]Female uttered one or more soft grunt(s) during contractions.

[l]During labor, female used her hands to aid infant out of the birth canal.

[m]Mother licked newborn following delivery.

[n]Mother consumed at least a portion of the amniotic sac.

[o]Mother consumed at least a portion of the placenta.

[p]Mother licked blood from the surrounding vegetation after giving birth.

[q]Multiparous adult female (long, pendulous nipples, and large body size) who was not a member of our study band.

[r]Female gave birth to a stillborn infant.

[s]Primiparous adult female (small nipples and small body size) who was not a member of our study band; we were unable to ascertain the sex of her newborn infant at the time of birth because mothers often clutch newborns close to their bodies; the female was not known to us and her social unit was not with our study band on subsequent days.

[t]unusually swift birth; infant was delivered within seconds of crowning and with its head enclosed in the amniotic sac, so observers were unable to determine fetal attitude or posture; female did not lick her newborn infant following delivery, but was seen grooming it.
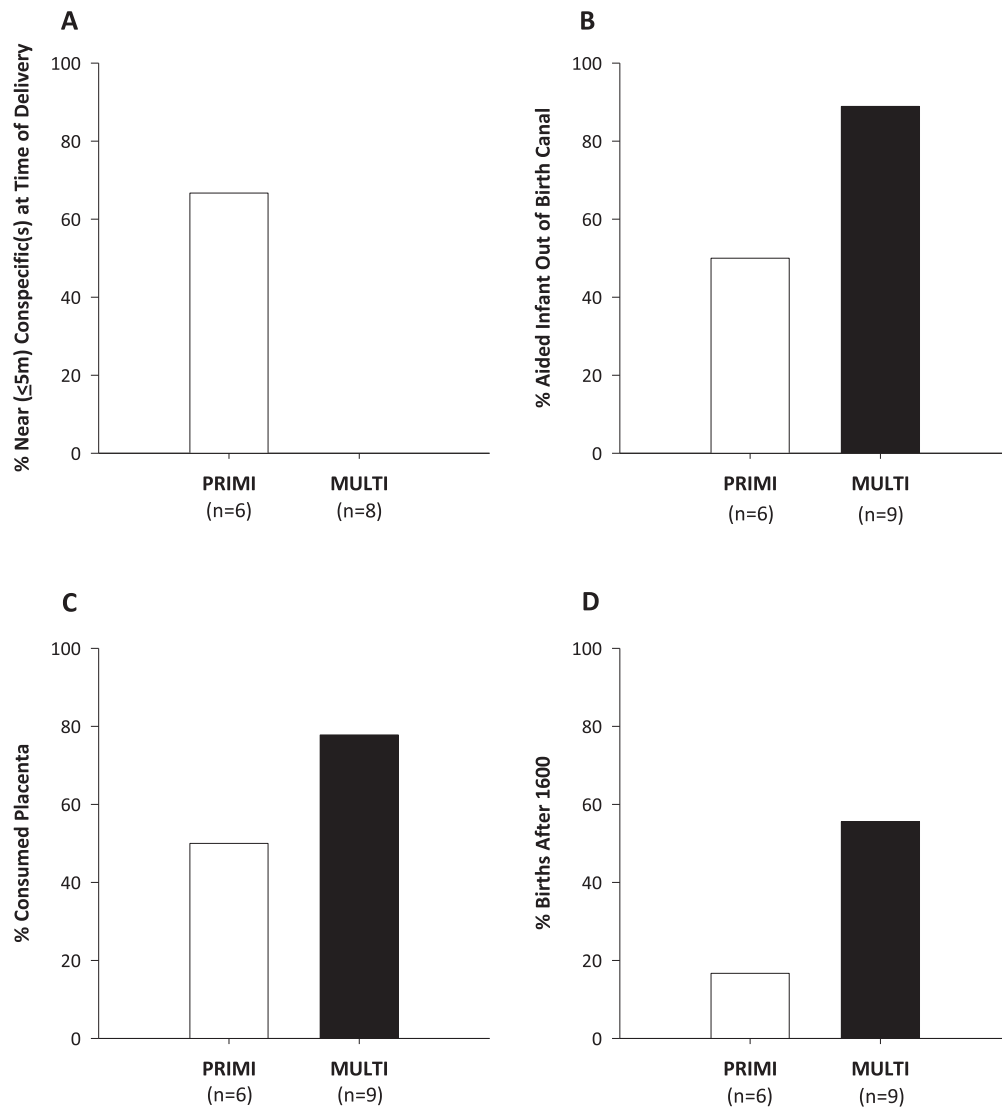
FIGURE 2 The four major differences between patterns of birth in primiparous and multiparous female geladas at Guassa: (a) percent of females that remained near (≤5 m away from) group mate(s) at time of delivery; (b) percent of females that aided their infants out of the birth canal; (c) percent of females that consumed the afterbirth following delivery; and (d) percent of births that occurred after 1600

of these infants (Belle's) was born alive (the other two were stillbirths) (Figure 1n). During one additional birth (Rampage's) the infant was delivered within seconds of crowning and with its head enclosed in the amniotic sac, so observers were unable to determine fetal attitude or posture. Most mothers manually assisted their infants out of the birth canal, though multiparas (8 of 9) were more likely to do so than primiparas (3 of 6) (Figure 2b). To help guide infants out of the birth canal, mothers used one (while standing crouched) or both hands (while partly seated or lying down), usually after the infant's head and shoulders had cleared the birth canal, to pull infants up along the mothers' abdomen and towards their chest (Figure 1h–j). Females other than the mother never helped to guide the infant out of the birth canal. In nearly half of all births, the amniotic sac had not fully ruptured when the infant's head emerged from the birth canal so mothers punctured the sac (with their hands or teeth) to clear the infant's airway during or after delivery (3 multipara, 4 primipara).

3.1.3 | Postpartus (I and II)

Upon emerging from the birth canal, infants appeared fragile, disoriented, and weak, but were able to grip slightly. Their grip was never strong enough to support themselves, however, and mothers had to periodically support their infants in the hours following birth until the sleeping cliff was reached.

All but one of the 15 females licked their newborns clean shortly after giving birth (Figure 1m). We also observed 10 of the 15 mothers consuming their own placentas after expelling them from their bodies (Figure 1l cf. 1k). Intriguingly, multiparas (7 of 9) were more likely to engage in placentophagy than nulliparas (3 of 6) (Figure 2c). Mothers were never observed sharing their placentas with other group members and no geladas were ever seen stealing the placenta from a mother or eating another individual's discarded placenta.

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3.2 | Agonism surrounding births

Five females were the recipients of agonism during the birth process (labor or delivery). One of these females received threats from female group mates. The other four females received threats from their leader males when they lagged too far behind during labor or delivery. However, leader males also occasionally provided agonistic "support" to birthing mothers. On one occasion, a leader male directed threats towards female unit members who ventured within 1m of a birthing mother. On another occasion, a (different) leader male threatened males from outside his unit who came within 10m of a female as she was giving birth.

3.3 | Timing of births

The 15 births we observed were all diurnal (we do not follow the geladas after dark once they descend down to their sleeping cliffs), occurring between the hours of 0912 and 1828. Multiparas tended to give birth later in the day than primiparas; 5 of the 9 multiparas gave birth after 1600, while nearly all of the primiparas (5 of 6) gave birth before 1400 (Figure 2d). As a result of giving birth later in the day than primiparas, multiparous females had, compared to primiparas, fewer daylight hours to travel with their social units while simultaneously recovering from the birthing process and caring for a vulnerable newborn infant.

4 | DISCUSSION

The 15 diurnal births we witnessed among wild gelada monkeys at Guassa, Ethiopia represent the largest number of detailed observations of births reported for any wild primate population to date. Here, we discuss the birth process and periparturitional behaviors among geladas at Guassa, focusing especially on the differences we identified between first-time and experienced mothers. We compare our results with those from studies of parturition in other nonhuman primates and humans and discuss how observations from wild nonhuman primates can inform our understanding of the evolution of the birth process in humans.

4.1 | Behaviors surrounding birth

4.1.1 | Proximity to groupmates

In almost all human cultures, childbirth is a social event at which midwives, relatives or friends provide assistance or support to the expectant mother (Rosenberg & Trevathan, 2002; Trevathan, 1987). Although direct assistance with birth has rarely been reported in nonhuman primates (Trevathan, 2015), the presence of conspecifics nearby (<5 m) at birth have recently been reported in several species (DeLuycker, 2013; Douglas, 2014; Turner et al., 2010). These and earlier reports of female primates giving birth within sight of other group members (e.g., Gorzitze, 1996; Moreno, Salas, & Glander, 1991; Peker, Kowalewski, Pave, & Zunino, 2009; Stewart, 1984b) suggests that complete isolation from conspecifics during birth may not always be possible—or desirable—for female primates.

At Guassa, all 15 gelada females were within 5 m of their groupmates at some point during the half hour immediately before birth, but only 4 females remained within 5 m of conspecifics at the time of delivery. Nearby groupmates included immatures as well as adults, males and females, some of whom glanced occasionally at the laboring female, and, on a few occasions, approached to within a meter or less of her. Curiously, only inexperienced mothers remained in proximity to their groupmates during the delivery of the infant itself, while multiparas did not. Though not often physically far from their groupmates, multiparas were usually "out of sight" of other geladas, hidden by vegetation, rocks, or mima mounds (large mounds created by the resident rodent community). Moving away from other group members might help gelada females avoid agonistic interactions with other females, but places isolated females at increased risk of agonism from their unit's leader male for lagging behind the rest of their unit. In general, our results suggest geladas neither consistently seek seclusion nor companionship during birth, and that prior maternal experience appears to influence this decision.

4.1.2 | Vocalizations

Though vocalizations are emitted during the birth process in many primates (e.g., lemurs: Sauther, 1991; monkeys: Dias, 2005; Kumar, Solanki, & Sharma, 2005; Turner et al., 2010; Windfelder, 2000; apes: Goodall & Athumani, 1980; Stewart, 1977; and humans: Trevathan, 1987), gelada females were typically silent during labor at Guassa. This finding contrasts with the report of a single birth to a gelada female in the Simien Mountains, Ethiopia who emitted a loud "staccato cough" vocalization during an unusually swift delivery (Dunbar & Dunbar, 1974). Silence during parturition is likely beneficial to delivering mothers because it helps avoid detection by predators which may be especially important for geladas giving birth during the day in open alpine grasslands without nearby options for escape from predators, though vocalizations may be involuntary in some cases due to the probable painfulness of the birth process.

4.1.3 | Supporting infant emergence

Most females at Guassa used their hands to aid their infants out of the birth canal, guiding them up towards their breasts along the natural flexion of the infant's spine. Manual assistance from mothers is thought to be common among primates (Rosenberg & Trevathan, 2002), and reduces the risk of newly born infants falling to the ground before they can establish and maintain contact with the mother's body themselves with their own hands and feet. Given that a fall from the trees can be traumatic (Moreno et al., 1991), we might expect that arboreal primate mothers more consistently provide infants manual assistance during delivery than terrestrial primate mothers. At Guassa, manual assistance during delivery was indeed variable among mothers, with primiparas less likely to guide their infants out—which resulted in their infants falling short distances to the ground after birth—compared to experienced mothers. On the sleeping cliffs, where most gelada infants are probably born, the risk of falling long distances to the ground (sometimes 1 km below) are much greater, though it is possible that delivering mothers may adopt behaviors—orienting their perineums away from the edge of

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the sleeping cliffs, for example—to reduce the risk of neonates falling to their deaths.

4.1.4 | Licking

Nearly all gelada mothers licked their newborns clean soon after birth at Guassa. Evidence from the literature suggests that nearly all nonhuman mammals lick their infants after birth (Brandt & Mitchell, 1971, 1973; Gorzitze, 1996; Hemmalin & Loy, 1989; Stewart, 1977). Maternal licking has far-reaching consequences for the infant, including (a) promoting its breathing, heat retention, digestion, and waste elimination, (b) stimulating development of its respiratory and digestive systems, and (c) facilitating nursing and mother-infant bonding (reviewed in Trevathan, 2010). A specific example demonstrating the benefits of maternal licking can be found in a recent report of a Japanese macaque infant that emerged from the birth canal purple and not breathing. Shortly after its mother licked its face, the infant took its first breath and appeared to be revitalized (Turner et al., 2010).

Curiously, licking of newborns appears to be absent in all human cultures. Among human mothers, touching appears to be the most common behavior directed towards newborns (Trevathan, 2010, 1987). In humans, skin-to-skin contact results in an increase in the hormone oxytocin which helps ensure successful nursing, promotes mother–infant bonding, and reduces anxiety (Bramson et al., 2010; Mikiel-Kostyra, Mazur, & Boltruszko, 2002; Uvnäs-Moberg, 1996). Another potential benefit of maternal touching of the infant in humans may be to rub the uniquely human fatty substance (vernix caseosa) coating the relatively hairless human neonate deeper into the skin to protect the infant from heat loss and prevent its skin from drying out (Hoath, Narendran, & Visscher, 2001; Hoath, Pickens, & Visscher, 2006).

4.1.5 | Placentophagy

Placentophagy (consuming all or part of the placenta, amniotic fluid and associated membranes) is considered a nearly universal behavior among peripartum mammalian females, occurring routinely (though not necessarily after every birth) in almost all species, with the notable exceptions of humans and marine mammals that deliver in the water (reviewed in Kristal, DiPirro, & Thompson, 2012). At Guassa, all mothers ingested some amniotic fluid from eating the anmiotic sac or licking their newborn infants or their fingers after touching their urogenital region. In addition, 10 of the 15 mothers consumed all or part of their placentas immediately after expelling them from their bodies. There are many hypotheses for the evolution of placentophagy (e.g., preventing discovery of the birth from predators, nourishing the exhausted mother, etc.; reviewed in Coe, 1990), though none have ever been tested empirically (Kristal et al., 2012).

Recent experimental research using laboratory rats demonstrated that placentophagy has analgesic effects on mothers and enhances mother-infant bonding in this species. In rats, placentophagy appears to (a) enhance opioid-mediated pain relief causing higher pain tolerance (to counter the pain of labor), (b) enhance maternal attraction to neonatal stimuli causing earlier and more frequent contact with infants, and (c) result in shorter delays to the onset of maternal caretaking behav-

iors (Apari & Rozsa, 2006; Blank & Friesen, 1980; DiPirro & Kristal, 2004; Grota & Eik-Nes, 1967; Kristal, 1991; Kristal et al., 2012). The generalizability of these findings to other eutherian mammals remains unclear, though given the near universality of placentophagy in peripartum mammals, it is possible that this behavior may have similarly positive effects on mothers and infants in other mammals as well.

At Guassa, consumption of the placenta was more common among multipara than among primipara. Only two of the nine multipara did not consume the placenta following delivery, while three of the six primipara discarded the placenta without eating it. As with other apparent differences in behavior surrounding birth at Guassa, placenta consumption may be at least partly learned through experience. Similarly, in a study of captive Japanese macaques, multipara more often consumed the placenta and finished eating it faster than primipara (Timmermans & Vossen, 1996). Geladas at Guassa showed no interest in other females' placentas. However, among macaques, higher-ranking females have been reported to sometimes steal and consume the placentas of lower-ranking females in captivity (Timmermans & Vossen, 1996) and in the wild (Ratnayeke & Dittus, 1989).

Surprisingly, placentophagy is rare or absent in humans, including in all preindustrial societies studied to date (Hrdy, 2009; Kristal, 1980; Kristal et al., 2012; Ober, 1979; Onuaguluchi & Ghasi, 1996; Trevathan, 1987; Young & Benyshek, 2010), though it is possible that the practice was more common in the past (Kristal et al., 2012; Young & Benyshek, 2010). The conspicuous absence of placentophagy in nearly all human cultures (Kristal, 1980; Trevathan, 1987; Young & Benyshek, 2010), despite the near-universal (and thus likely ancestral) placental mammalian habit of afterbirth consumption (Kristal et al., 2012) has prompted some researchers to argue that strong selective pressures against the behavior must have arisen at some point during human evolution, resulting in the behavior's elimination from our species' behavioral repertoire. What this selective force may be is a mystery. Young and colleagues have recently suggested that the advent of the controlled use of fire by *Homo erectus* ∼2 Mya (Wrangham, 2009) would have routinely exposed pregnant females to harmful toxins released from the burning of vegetation for the first time in hominin history, resulting in the sequestration and accumulation of these toxins in the placenta, which, if ingested, would expose mothers and newborn infants to the harmful substances contained therein (Young, Benyshek, & Lienard, 2012). Though intriguing, there is as yet little empirical support for the "fire hypothesis" explanation for the disappearance of routine placentophagy from the human lineage. Nonetheless, the deleterious health consequences of indoor and outdoor smoke inhalation, especially for women and children, are now well documented (Naeher et al., 2007; Torres-Duque, Maldonado, Pérez-Padilla, Ezzati, & Viegi, 2008). Similarly, growing evidence suggests a role for the placenta in keeping some toxicants away from the developing fetus until they are both expelled from the mother's body at birth (Myllynen, Pasanen, & Pelkonen, 2005). Additional research on the placentas of pregnant women who are routinely exposed to smoke from the burning of vegetation is needed to evaluate the role of fire in the enigmatic disappearance of placentophagy from the human lineage.

4.2 | Timing of birth

Our observations of 15 diurnal births over a recent ~10-year study period suggest that a small but considerable contingent of geladas give birth during the day. We do not know how representative the births we witnessed are for geladas, or if (and how) time of day affects the birth process in this and other diurnal primates. However, daytime births have now been observed multiple times in several other wild primate populations (e.g., Chism, Olson, & Rowell, 1983; Peker et al., 2009; Takahata, Koyama, Miyamoto, & Okamoto, 2001). These observations suggest that while nighttime births may be the norm for diurnal primates (Dunn, 2012; Jolly, 1972; Rosenberg & Trevathan, 2002), selection *against* diurnal births may be relaxed in some taxa. On a typical day, most geladas are surrounded by hundreds of conspecifics belonging to many different one-male units (Kawai et al., 1983). This unusually high degree of gregariousness (for social mammals) may provide females that give birth diurnally—and are unable to keep up with the rest of their social unit during parturition—continued protection against potential predators. Why daytime births are so rarely observed in other gregarious, open country diurnal primates like baboons and vervets remains unclear, though their smaller group sizes may be part of the answer.

4.3 | Impact of maternal experience on delivery patterns

At Guassa, gelada mothers with prior experience delivering at least one other infant were more likely to (a) give birth later in the afternoon, (b) give birth away from conspecifics, (c) manually assist infants out of the birth canal, and (d) consume the placenta following delivery of the infant. These results suggest that learning or experience (and their neuroendocrine correlates) may play a role in achieving optimal conditions for birth in geladas, a pattern consistent with reports that prior maternal experience provides female primates opportunities to enhance their parenting skills, making mothers more competent or efficient at providing infant care with subsequent offspring (Fairbanks, 1996; Nguyen, Gesquiere, Alberts, & Altmann, 2012).

4.4 | Fetal emergence patterns and implications for human evolution

The transition to habitual bipedalism in the human lineage (~7 Mya) resulted in a number of architectural changes to the human female pelvis that have had profound implications for human childbirth (Abrams & Rutherford, 2011; Gruss & Schmitt, 2015; Rockwell, Vargas, & Moore, 2003; Trevathan, 2010, 2015). Chief among these is that the pelvis must be commodious enough to accommodate the passage of big brained infants and, at the same time, narrow enough for efficient (bipedal) locomotion (this trade-off between various pelvic functions is known as the "obstetrical dilemma"; Washburn, 1960).

Compared to our closest living relatives (i.e., the quadrupedal great apes), the human biped's pelvis is narrower, with bony projections that protrude into the birth canal on the sides (i.e., the ischial spines), and at the back (i.e., the sacral promontory) (Lovejoy, 2005). These changes were necessary for maintaining balance, and for achieving our striding, bipedal gait (Lovejoy, 2005). However, they have made delivery mechanically difficult for human females because the neonate's head size is roughly the same size as that of the pelvic opening (unlike in great apes where neonatal head size is much smaller than that of the pelvic opening) (Franciscus, 2009). The human birth process became even more obstetrically challenging when brain size (and thus fetal head size) expanded, with the origins of the genus *Homo* (~2 Mya) or perhaps even earlier, in the genus *Australopithecus* (~3.2 Mya) (DeSilva, 2011). To compensate for the "deep curved tube" shape of the human birth canal (Stewart, 1984a, p. 611) and the large size of the neonate's head (and shoulders) relative to that of the pelvic opening (Franciscus, 2009), human neonates must undergo a complex series of rotations as they travel through the birth canal (Trevathan, 2010). These rotations make it possible for the neonate's large head and wide shoulders to pass through the narrow birth canal and past its bony projections safely. At the end of these rotations, the human infant emerges from the birth canal with its face directed towards the mother's spine (in the *occiput anterior position*) (Rosenberg & Trevathan, 2002).

With the infant's head facing away from the mother, human mothers find it difficult to reach down and pull the infant towards them, as this would require pulling the infant against the normal contours of its body which could cause damage to its nerves and muscles (Trevathan, 2010). Although human mothers are capable of giving birth alone, they rarely do so (Trevathan, 1987), which attests to both the difficulty of human childbirth and the potential risks of injury or mortality of delivering alone. Thus, the hominin shift to habitual bipedalism (and large brains) likely also contributed to the near-universal practice of assisted childbirth (or obligate midwifery) in humans today (Rosenberg & Trevathan, 2002; Trevathan, 1988).

While the specific nature of Washburn's "obstetrical dilemma" in humans continues to be debated (Dunsworth, Warrener, Deacon, Ellison, & Pontzer, 2012; Gruss & Schmitt, 2015; Huseynov et al., 2016; Warrener, Lewton, Pontzer, & Lieberman, 2015), there is now growing recognition that, at some level, all mammals that give birth to large-brained infants are under some obstetric pressure to have as commodious a birth canal as possible (Trevathan, 2015). Since humans are not alone in having large-headed infants, a "tight squeeze" can be said to be characteristic of the birth of many monkeys and some apes (e.g., gibbons) (Rosenberg & Trevathan, 1995). In a pioneering study, Stoller (1995) observed, using radiographs, the births of nearly a dozen squirrel monkeys and baboons. She found that all successful deliveries in these species were "tight squeezes" necessitating internal fetal rotation (previously believed to be unique to humans) and culminating in face presentations (in which the infant is born with its neck extended and its face appearing first in the vagina, facing the mother). Face presentations provided the best fit for the fetal head in squirrel monkeys and baboons, allowing the smallest diameter of the fetal head to squeeze through the smallest diameter of the birth canal (Stoller, 1995), and may be far more widespread among nonhuman primates than previously reported (Stoller, 1995; Trevathan, 2015).

Face presentation appears to be the norm among geladas as well. At Guassa, gelada females usually gave birth to infants with their face directed towards the mother's abdomen and face and (in all cases where observers could see, 8 of 8) with the infants' face presenting first. A face-to-face fetal emergence pattern enables the mother to reach down and guide the infant out and up towards her chest "along the normal contours of [the infant's] body" (Trevathan, 2010, p. 94) and has also been documented in other monkeys, and in lemurs and lorises (Trevathan, 1988). Stoller's (1995) review of the literature suggests that the widely reported nonhuman primate fetal emergence pattern—the *occiput posterior position*—may in fact be a misuse of the term, since in obstetrics, this term specifically refers to infants being born facing the mother but with their necks flexed and their occiput presenting (Trevathan, 2015). The mechanics—and aftermath—of deliveries involving occiput versus face presentations can be quite different from one another, so it is important that researchers recognize this distinction whenever possible. Compared to occiput presentations, face presentations usually deliver more successfully in humans (Posner, Black, Jones, & Dy, 2013) (and in squirrel monkeys and baboons; Stoller, 1995) and may be widely underreported in nonhuman primates.

At Guassa, fetal emergence orientation had important fitness consequences for gelada mothers and infants. Of the three gelada females that delivered infants in the human-like *occiput anterior position*, one delivered a healthy infant, while the other two delivered stillborn infants. Unusual presentation of the fetus in relation to the maternal pelvis also contributed to perinatal mortality in Stoller's (1995) study, resulting in two stillbirths (of three malpresented infants). Malpresentation has long been associated with complications (including fetal and maternal mortality) in humans (Posner et al., 2013) and may be a significant, but long overlooked, determinant of mortality for nonhuman primates that give birth to large-headed infants as well.

One especially intriguing question remains. When during primate evolution did infants first begin to be born in the *occiput anterior position* typical of humans? Some have argued that this fetal emergence pattern (long considered unique to humans; Weaver & Hublin, 2009) appeared after *Homo* diverged from *Australopithecus* (Franciscus, 2009; Rosenberg & Trevathan, 2002; Ruff, 1995; Tague & Lovejoy, 1986; Trevathan, 1988; Weaver & Hublin, 2009). Others argue that the shift occurred much earlier (Berge & Goularas, 2010; Berge, Orban-Segebarth, & Schmid, 1984), a view recently corroborated by observations of three captive chimpanzees giving birth to infants in the occiput anterior position (Hirata et al., 2011). Our finding that gelada infants are routinely born facing the mother's face is consistent with the hypothesis that the shift to the occiput anterior fetal emergence pattern typical of humans occurred after hominoids (hominins and great apes) separated from Old World monkeys. Observations of fetal emergence patterns in great apes are, however, limited in number and confined to captive populations, and data from more populations and species are needed for a fuller understanding of the primate birth process.

Our observations of 15 diurnal births in wild geladas—the largest number of births described in any wild nonhuman primate to date—add to a small but steadily growing literature on nonhuman primate obstetrics. As more studies accumulate across a wider variety of taxa, research on nonhuman primate births has the potential to resolve long-standing questions about patterns of fetal growth and development, the mechanics of birth and bipedalism, and the nature of sexual dimorphism itself (Stoller, 1995; Trevathan, 2015). With the growing recognition of the importance of biological sex in animal morphology, behavior and ecology (reviewed in Nelson, 2011), the long overlooked roles of pregnancy, parturition and lactation on the evolution of sexually dimorphic traits (from pelvic morphology to brain structure and function) among mammals are finally receiving some much needed attention (Huseynov et al., 2016; Whitcome, Shapiro, & Lieberman, 2007).

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