ABC 2026, 13(1):79-100
Animal Behavior and Cognition
DOI: https://doi.org/10.26451/abc.13.01.05.2026

Comparative Ilithology: The Study of Birth and Parturitional Behaviors Across Species

Christine E. Webb[1*], Esme Benson[2], Isabelle Leavy[3], and Alecia J. Carter[4]

[1] Department of Environmental Studies, New York University
[2] College of Traditional Midwifery
[3] Department of Anthropology, University of Texas at Austin
[4] Department of Anthropology, University College London

*Corresponding author (Email: christinewebb@nyu.edu)

Citation – Webb, C. E., Benson, E., Leavy, I., & Carter, A. J. (2026). Comparative ilithology: The study of birth and parturitional behaviors across species. *Animal Behavior and Cognition, 13*(1), 79-100. https://doi.org/10.26451/abc.13.01.05.2026

Abstract – Birth is one of the most important life history events for eutherian mammals, yet it also remains one of the least understood. Perhaps surprisingly, there is no systematic field of research focused on birth and parturition through a comparative lens. In this paper, we introduce the field of comparative ilithology (named for *Ilithyia*, the Greek goddess of childbirth and midwifery): the study of birth and parturitional behaviors across species. We outline ten potential new research areas that have historically been overlooked, but which will benefit from comparative study. For each, we provide testable hypotheses and a roadmap for more systematic methodologies and conventions for studying and reporting birth across species. Comparative ilithology has great potential to inform debates around the evolution of human childbirth and inspire novel questions across species surrounding this fundamental life history event.

Keywords – Birth, Parturition, Obstetric Dilemma, Evolution, Comparative Ilithology

---

Birth is a fundamental life history event in eutherian mammalian species. What happens directly before, during, and after birth impacts the survival of the infant and mother, and the reproductive success of both parental lineages. Understanding the process of birth (parturition) is therefore crucial to elucidating the selective pressures that determine individual fitness.

Perhaps surprisingly given its evolutionary importance, the study of parturition has been largely overlooked in nonhuman species. Exceptions typically stem from two sources, with limited cross-referencing: observations of birth in nonhuman primates, which are usually published as case reports in specialized journals (e.g., Demuru et al., 2018; Nguyen et al., 2017; Pan et al., 2014), and the extensive literature on veterinary practice for domesticated animals (e.g., Noakes et al., 2001; Roberts, 2005; Senger, 2015). While behavioral and physiological dimensions of birth are relatively well understood in the latter, intense directional artificial selection in these species complicates inferences about traits shaped by natural selection. We thus focus here on naturally selected populations of mammals, but include relevant examples from the veterinary and domestic animal literature that inform our research areas and hypotheses. For a much more comprehensive account of domesticated animal birth and veterinary practice, we direct readers to the field of theriogenology (Noakes et al., 2001).

Birth is the hormone-initiated process by which pregnant female animals expel a gestated fetus—a term most commonly used in reference to eutherian mammals.[1] Mammalian birth is generally considered to progress in three stages (reviewed in Bazer & Spencer, 2011; Zeller et al., 2018). The first stage is characterized by the onset of strong, progressing uterine contractions that result in cervical change: cervical thinning (effacement) and dilation. This phase (sometimes referred to as labor[2]) also includes the rupture of the amniotic sac and the expulsion of amniotic fluid and/or blood. In many species, these events are accompanied by the onset of visible signs of discomfort and agitation in the parturient. The second stage begins when the cervix is fully dilated. The fetus transitions from the dilated cervix into, and ultimately through, the birth canal. In a number of species, active "pushing" of the fetus facilitates the delivery of the neonate with the umbilical cord attached. This stage is thus sometimes referred to as the delivery phase. The third stage of birth commences after the delivery of the neonate and ends with the expulsion of the placenta.[3] In polytocous mammals (where each fetus has its own amniotic sac and placenta, as in monotocous species), the delivery of placentae may occur in conjunction with stage two (Kustritz, 2005). We refer to the period directly following delivery as the immediate postpartum phase (Zeller et al., 2018), which comprises but also extends beyond stage three. Behaviors typical of mammalian mothers across many species include umbilical cord severance (UCS), and a variety of maternal acts (e.g., licking, nursing, and, for cetaceans and sirenians[4], holding the infant at the water's surface) directed towards the newborn as well as consumption of the placenta (placentophagy).

Human birth is hypothesized to have undergone major selection over the hominin lineage, and evolutionary explanations tend to emphasize the challenges (and inherent risks) of human childbirth compared to other primates (Rosenberg & Trevathan, 2002). Yet the hypothesis that human childbirth is uniquely difficult has recently been challenged on a number of empirical and theoretical grounds (Dunsworth, 2018; Haeusler et al., 2021; Macfarlane, 2018). Developing our understanding of birth-associated behaviors, particularly in extant nonhuman primates, can inform ongoing debates about the evolution of human childbirth. At least part of the reason for controversy surrounding human birth practices may be that comparative studies of birth have infrequently been undertaken as a deliberate research strategy.

Here we introduce a new field of comparative ilithology: the study of birth and parturitional behaviors across species. Named for *Ilithyia*, the Greek goddess of childbirth and midwifery, the name takes after comparative thanatology (from *Thanatos*, the Greek god of death), the study of death and death-related behaviors across species. Comparative thanatology was formally introduced in 2016 (Anderson, 2016), and has generated dozens of scholarly publications (reviewed in Anderson et al., 2018; Gonçalves & Biro, 2018; Gonçalves & Carvalho, 2019). One of the key contributions of comparative thanatology was to zoom out from purely biological (medical, forensic) perspectives on death to incorporate psychological, social, and cultural perspectives on the end of individuals' lives (Anderson, 2016). Likewise, comparative ilithology's scope integrates not only biological but behavioral, social, cultural, cognitive, and affective dimensions of birth.

In this paper, we explore what comparative ilithology has to offer as a research framework and its potential to spur new avenues of interdisciplinary study. Our aim is not to provide an exhaustive review of

---

[1] Eutherian mammals are placental mammals who carry their young to an advanced stage of development in the uterus. This excludes monotremes (e.g., platypuses), who lay eggs, and marsupials (e.g., kangaroos), who give birth to relatively underdeveloped young who continue maturing outside the womb, typically in a pouch. Some non-mammalian species also give live birth (including certain reptiles, amphibians, fish, and invertebrates who carry their developing young inside them). Since this form of birth is relatively rare and evolved independently in these taxa, we focus our discussion of birth on eutherian mammals.

[2] The stages of birth outlined here are also sometimes referred to as the three phases of labor.

[3] An additional fourth stage of labor is often designated within the fields of obstetrics and midwifery. This stage–commonly called the recovery phase–begins with the delivery of the placenta, and in humans generally lasts about two hours post-delivery of the newborn. Before the birth process is considered complete, the uterus continues to contract for several hours, expelling any remaining contents and reestablishing tone.

[4] Cetaceans include whales, dolphins, and porpoises; sirenians include the dugong and manatees. The lifting, pushing, or nudging of the newborn calf near the water's surface just after birth by the mother or other adults has been described in a variety of cetacean and sirenian species (reviewed in Mann, 2009; Zani et al., 2008).

mammalian birth. Instead, we aggregate relevant literature—including empirical reports of births in nonhuman mammals and theory and research on the evolution of human childbirth—to illuminate overlooked and understudied questions about parturition across species. We do not cover closely-related topics that have historically received considerable attention in the mammalian literature—e.g., gestation length, reproductive seasonality, litter size (Brandt & Mitchell, 1971), mother-infant interactions (Hrdy, 2009; Maestripieri & Call, 1996), and maternal effects (Wolf & Wade, 2009), among others. This paper instead focuses on research questions pertaining to the parturition event itself, i.e., occurring during the labor, delivery, and immediate postpartum period. However, we do explore overlapping research areas that have been historically ignored in the literature but raise relevant questions for comparative ilithology, including self-medication and morning sickness. We have structured the presentation of the topics to follow the chronology of birth—from behaviors observed before labor, to labor and delivery and the immediate postpartum period—before expanded discussions of the social and cognitive dimensions of birth. We pose novel, testable hypotheses and offer a roadmap for more systematic methodologies and conventions for studying and reporting birth across species—including providing cohesive terminology and operationalizations for relevant variables (see Table 1). By setting the stage and scope for comparative ilithology, we hope to inspire new research programs that address open, unresolved, and heretofore unasked questions surrounding this fundamental life history event.

Comparative Ilithology: Research Areas

1. Morning Sickness

In humans, most women experience nausea and vomiting during the first trimester of their pregnancies, a condition commonly called ‘morning sickness,’ but referred to as nausea and vomiting in pregnancy (NVP) in the medical literature (Flaxman & Sherman, 2008). NVP is most common between 4 and 20 weeks of human pregnancy and its symptoms include, among others, nausea, vomiting, food and gustatory aversions, and food cravings. The current prevailing evidence suggests that the ultimate explanation for NVP in humans is prophylactic protection of the developing fetus from food-borne mutagens and abortifacients during the critical period of organogenesis. This hypothesis is known as the ‘prophylactic’ or ‘maternal/fetal protection’ hypothesis (Flaxman & Sherman, 2008; Steinmetz et al., 2012). A contrasting hypothesis, known as the ‘by-product’ hypothesis, suggests that NVP is a nonadaptive sequela of the physiological conflict between the fetus and the mother, who ‘fight’ over allocation of resources in an evolutionary arms race (Haig, 1993).

Some have claimed that NVP does not occur in nonhuman mammals (Flaxman & Sherman, 2008); however, we are not aware of research that has specifically investigated whether this is the case. The claim was based on three studies that *support* NVP in mammals, showing a decrease in appetite in early pregnancy in domesticated dogs (*Canis familiaris*), and captive rhesus macaques (*Macaca mulatta*) (reviewed in Sherman & Flaxman, 2002). A comparative approach could usefully inform the debate, by generalizing the predictions of the (a) prophylaxis and (b) by-product hypotheses to populations or species that have (a) greater or lower exposure to mutagens or (b) greater conflict over allocation of resources. For example, support for the prophylactic hypothesis could arise from evidence that NVP is more common during pregnancy in populations or species that regularly ingest bitter and toxic plants, or frequently consume meat. Alternatively, evidence for the by-product hypothesis could come from NVP being more common in K-selected species, or species with more invasive placentae.

.

Table 1

Glossary

Term	**Definition**
Abnormal fetal disposition	The fetus is not positioned *in utero* in a way that enables it to move into and through the birth canal with (relative) ease or unaided.[5] Abnormal fetal disposition may result in dystocia.
Allomothering	Non-maternal infant care/handling performed by an individual other than the genetic mother (i.e., the parturient); includes carrying, provisioning, grooming, and nursing (specified as *allomaternal nursing*).
Birth	The hormone-initiated process by which a pregnant female mammal expels (a) gestated fetus(es).
Birth Attendant	A non-parturient who attends the delivery, and often majority, of the parturition event, supporting and/or assisting the parturient through birth assistance, grooming, inspections, guarding, and/or lasting or particularly cohesive spatial proximity (i.e., 'midwife,' 'doula').
Birth Assistance	Any direct attempt by a non-parturient to remove the infant from the birth canal, sever the umbilical cord, or remove the placenta.
Delivery	The time period from the first observation of the fetus in the birth canal to the full emergence of the neonate.
Dystocia	Difficulty during labor, usually evident as a lack of progression of labor or delivery.
Fetal Position	Describes the alignment of the fetal vertebral column in relation to the mother's pelvis. Fetuses could be positioned dorsally, with the fetus's spine to the mother's sacrum; ventrally, with the fetus's spine to the mother's pubis; or laterally to the mother's left or right.
Fetal Posture	Describes the position of the extremities (head, neck, and limbs) of the fetus in relation to the fetus's body during delivery. Extremities could be in flexion or extension.
Fetal Presentation	Describes the alignment of the fetus's longitudinal axis in relation to the mother's birth canal. Fetuses could present longitudinally, with either anterior or posterior presentation, depending on whether the head or forelimbs, or rump or hindlimbs, respectively, present in the birth canal first; transversally, with either ventral or dorsal presentation; or, rarely, vertically, with either ventral or dorsal vertical presentation (Noakes et al., 2001).
Gravidity	Total number of pregnancies.
Labor	Includes all relevant/recorded behavior from when impending parturition was first realized (i.e., the first observation of contractions or other indicative behavior) until the appearance of the fetus in the birth canal.
Manual Assistance	Assistance in the delivery via pulling or handling the emerging neonate by the parturient (*self-assistance*) or an attendant (*birth assistance*).
Monotocous	Having one offspring at a time at a birth.
Multiparous	Having given birth two or more times (NB: this term has been used to refer to both an individual who is pregnant with her second offspring(s) and an individual who has given birth twice or more). Since a second pregnancy has not yet resulted in a birth, we refer to second-time pregnant females as primiparous until the birth of the second offspring.[6]
Nulliparous	Having never given birth.
Parity	Category denoting the number of times a female has given birth.
Parous	Having given birth (one or more times).
Parturient	The individual giving birth.
Parturition	The act/process of giving birth; includes labor, delivery, and the immediate postpartum period.
Polytocous	Having more than one offspring at a time at a birth.
Postpartum	Following delivery. Here the immediate postpartum period refers to the hours following delivery.
Placentophagia	The ingestion of any or all of the components of the afterbirth by the parturient (e.g., the placenta, the umbilical cord). Tolerated consumption or sharing of the birthed placenta by a non-parturient may also occur (*non-maternal placentophagia*).
Primiparous	Having given birth once (NB: this term has been used to refer to both an individual who is pregnant with her first offspring(s) and individuals who have given birth once). Since a first pregnancy has not yet resulted in a birth, we refer to first-time pregnant females as nulliparous until the birth of the offspring.
Umbilical Cord Severance (UCS)	Severance of the umbilical cord; partial UCS indicates incomplete or attempted severance of the umbilical cord.

---

[5] In humans, who typically give birth to infants with anterior longitudinal presentation, breech birth (bottom or feet first) would be considered abnormal fetal disposition; in cetaceans, who give birth with posterior presentation, anterior presentation (head-first) would be considered abnormal fetal disposition. Note that in some taxa (pinnipeds), there is no 'most frequent' longitudinal presentation, and only transverse and vertical presentation would be considered an abnormal fetal disposition.

[6] In some zoological literature, the term multiparous instead refers to giving birth to more than one offspring at a time (i.e., polytocous).

2. Nutrition & Self-Medication

During pregnancy and lactation, energy and protein requirements of the female are thought to increase between two- and ten-fold (Blaxter, 1989; Jessops, 1997). To meet these and other nutritional needs, the diets of parturient females in captive settings are commonly supplemented with extra vitamins, minerals, and energy/protein (reviewed in Noakes et al., 2001; Fontaine, 2012; Purohit, 2010). Despite the paucity of research in this area on wild populations, parturients of several other mammalian species appear to adapt their dietary habits to meet these increased nutritional demands. As just one example, field studies have shown that pregnant and lactating lemurs limit foraging costs and eat more young leaves high in protein and low in fiber compared to non-lactating females and adult males (*Lemur catta*: Sauther, 1994; *Varecia variegata rubra* and *Eulemur fulvus albifrons*: Vasey, 2000, 2002).

Related to evidence of changing dietary patterns among parturients is research on self-medicative behavior, such as the selective ingestion of tannins by wild female sifakas (*Propithecus verreauxi verreauxi*) during pregnancy and lactation (Carrai et al., 2003). In several domesticated species—such as grazing sheep (*Ovis aries*) and cows (*Bos taurus*)—tannin consumption is associated with higher weight gain and lactation stimulation (Aerts et al., 1999; Barry & McNabb, 1999). Tannins are also recognized in the veterinary literature for their potential astringent, anti-hemorrhagic, anthelmintic, and anti-abortive properties (Athanasiadou et al., 2001; Biagi & Speroni, 1988). These effects suggest that an increase in tannin intake during the periparturient period could have multiple prophylactic advantages, a possibility that merits further investigation across a broader diversity of animals and settings. Although tentative, evidence for medicinal plant use by pregnant females has received support in other species (Shurkin, 2014). One anecdotal report documents the unusual behavior of a pregnant African elephant (*Loxodonta africana*) consuming the leaves of a particular kind of *Boraginaceae* tree, possibly to induce labor. Intriguingly, local women also use the tree for the same purpose (Biser, 1998). In humans, there is a great deal of interest—and debate—around how nutrition and medication during pregnancy and lactation affect birth and the subsequent development and health of offspring (Marshall et al., 2022; Nichols, 2018). A comparative approach could help bridge our understanding of nutritional and medicinal practices that may mediate birth outcomes in humans and other species alike, literatures that, to our knowledge, are rarely in conversation.

3. Birth Hour

It is widely thought that most mammals, including humans, give birth during the inactive phase of the daily cycle (Honnebier & Nathanielsz, 1994). The proposed advantages of parturition during inactive periods include: reduced predation and infanticide risk, sufficient recovery time for the parturient with less chance of separation from the group, and better conditions for mother-infant bonding (Altmann, 1980; Dunn, 2012; Honnebier & Nathanielsz, 1994; Jolly, 1972; Rosenberg & Trevathan, 2002). Although birth hour may represent a female adaptive strategy, data on hourly distributions of birth in mammals (including in humans) are surprisingly scarce.

Most systematic data on birth hour comes from captive mammalian populations—particularly farm and laboratory animals—where husbandry and management factors are present. These studies generally show that diurnal species tend to give birth at night, while nocturnal species give birth during the day. For instance, research in domestic horses (*Equus caballus*), a diurnal species, consistently reports that 80–90% of foals are born at night (Campitelli et al., 1982; Heidler et al., 2004; Rossdale & Short, 1967). Laboratory studies in which photoperiods are manipulated have further shown that nocturnal and crepuscular mammals such as rats (*Rattus norvegicus*) (Lincoln & Porter, 1976), Syrian hamsters (*Mesocricetus auratus*) (Viswanathan & Davis, 1992), and rabbits (*Oryctolagus cuniculus*) (Hudson et al., 1999) all tend to give birth during their resting phase—typically the subjective day.

Data on birth hour in wild mammalian populations are especially limited, and come mostly from nonhuman primates. In the most comprehensive review on the topic to date, Jolly (1972) noted that, despite variation within a genus or even species, general patterns emerge across both wild and captive primate populations. Nocturnal prosimians (e.g., bushbabies, *Galago senegalensis* and mouse lemurs, *Microcebus* *murinus*) tend to give birth during the daytime. Many or most diurnal New and Old world monkey species (e.g., *Macaca* spp. and *Saimiri* spp.) give birth at night or in the early morning hours. Great apes appear to have more variable birth timing, though a bias towards nocturnal births might appear with more data (all reviewed in Jolly, 1972). The preponderance of nocturnal births among diurnal primates (and mammals more generally) likely partially explains why parturition events are rarely observed during long-term wild studies. However, in recent years, the accumulation of published case studies suggests that a small but considerable contingent of births across diverse diurnal primate species occurs during the day (Benson, 2021). In spite of the obvious observational bias towards daytime births, several authors speculate that selection against diurnal births is relaxed in at least some primate taxa (Chism et al., 1983; Nguyen et al., 2017; Peker et al., 2009).

The hour of birth depends on both the time of onset and the duration of labor, and has been a topic of debate in the human obstetric literature. Earlier studies generally found that human births occur at night, with labor onset between 2100 and 0300 h and delivery between 0100 and 0700 h (Charles, 1953; Jolly, 1972; Kaiser & Halberg, 1962; King, 1956; Malek, 1952; Shettles, 1960; Trevathan, 1987). Most of these results, however, were published before the eighties and exclude multiple births, malpresentations, and medical interventions. More recent research suggests that the predominant nocturnal pattern of birth is disrupted or disappears entirely in highly medicalized human populations (Bernis & Varea, 2012; Heres et al., 2000; Martin et al., 2018; Mathews & Curtin, 2015). Unfortunately, most of the available data on human birth hour come from Western clinical settings (but see: Chaney et al., 2018; Hoque & Hoque, 2010). A comparative lens could help disentangle the extent to which altered temporal distributions of birth are attributable to the commonplace high rates of obstetric interventions in Westernized societies and/or relaxed selection pressure against diurnal births for other reasons (e.g., reduced nighttime threats) that are shared with other mammalian species. Comparative work could also help elucidate possible adaptations of the female body to nocturnal parturition and the proximate mechanisms responsible for the hour of birth, especially circadian rhythms of hormone (e.g., melatonin) release (Honnebier & Nathanielsz, 1994; Olcese et al., 2013; Sharkey et al., 2009). More research is also needed on the extent to which birth hour predicts differential outcomes across species. In humans, evidence for a link between the hour of birth and birth progression (e.g., labor durations: Backe, 1991; Cagnacci et al., 1998) and other obstetric and neonatal outcomes (Macfarlane et al., 2019) remains inconclusive. Studying the extent to which birth in diverse species and populations is adapted to different environmental and temporal niches may foster insights to these (ultimate) fitness consequences.

4. Obstetric Dilemma Hypothesis

Chief among the assumed human-unique birth features is the obstetric dilemma hypothesis, which posits that antagonistic selection for both large brains and bipedalism has resulted in a ‘tight fit’ (of the large infant head in the narrow human birth canal) and high rates of obstructed labors (Rosenberg & Trevathan, 2002). The obstetric dilemma hypothesis has contributed to the pathologizing of birth in humans in many Westernized cultures, with high rates of medical interventions (e.g., caesarean sections, episiotomy) and infant and maternal deaths (Dunsworth, 2018). However, the obstetric dilemma hypothesis has come under recent scientific debate (Dunsworth, 2018; Haeusler et al., 2021; Macfarlane, 2018), and several of its core assumptions remain untested or controversial.

Humans are not the only primates that show a ‘tight fit’ between the obstetrically relevant pelvic measures and the fetal head; ‘too large’ fetal heads are also present in, for example, gibbons (*Hylobates* spp.), squirrel monkeys (*Saimiri* spp.), and baboons and macaques (*Papio* spp. and *Macaca* spp., respectively) (Haeusler et al., 2021). Beyond the primates, a ‘too large’ fetal head is common in the (artificially selected) brachycephalic domesticated dog breeds and a ‘too small’ pelvis in achondroplastic breeds (Noakes et al., 2001). While cetacean fetuses have a large head, the lack of a functional pelvis means there is no obstetric dilemma (Reidenberg & Laitman, 2009) and most cetaceans are also born with posterior presentation (Ransome et al., 2022; Reidenberg & Laitman, 2009; Slijper, 1949), though there is one recorded case of a humpback whale (*Megaptera nodosa*) fetus’s flippers causing dystocia that resulted in the death of the calf and cow (Slijper, 1949). Similarly, pinnipeds'[7] neonates are born extremely large relative to the mother and these species have a functional pelvis; fetuses present equally either anteriorly or posteriorly (Franco-Trecu et al., 2016). This taxon may not suffer from an obstetric dilemma (we found no reports) because the female's pubic symphysis is not fused, and there is less need for a strong pelvic floor because the animal's weight is buoyed by water. Finally, bats (*Chiroptera* spp.), who also give birth to large neonates relative to maternal body size, and with large heads, manage to do so through sexual dimorphism of the pelvis. Females of all species of bat do not have a fused pubic symphysis; additionally, roosting upside-down for large portions of the day means that a strong pelvic floor is not as needed as in terrestrially locomoting species (Grunstra et al., 2019).

For our discussion of the obstetric dilemma, it is the *outcome* of the tight fit that is relevant: dystocia due to cephalopelvic disproportion. In achondroplastic and brachycephalic domesticated dogs, elective caesarean operations are routinely performed because dystocia due to cephalopelvic disproportion is so common (100% of cases; Noakes et al., 2001). Dystocia can occur due to fetopelvic rather than cephalopelvic disproportion: for example, dystocia is more common in cattle (*Bos taurus*) raised for beef production than in those managed for dairy, particularly among breeds with muscular hypertrophy that result in meat cuts with higher market value; presumably this is due to the strong artificial selection that results in large fetal size in beef breeds (Noakes et al., 2001). Dystocia is similarly common in guinea pigs (*Cavia porcellus*) and thought to result from fetuses that are large relative to the maternal pelvis—a problem exacerbated by inadequate separation of the pubic symphysis in sows (reviewed in Vieu et al., 2024). Dystocia has also emerged as a concern in captive African and Asian elephant (*Elephas maximus*) populations, where fetal dimensions and the specific anatomy of the reproductive tract contribute to delivery challenges (Hermes et al., 2008). Elephants predominantly exhibit posterior presentation, a trait possibly inherited from their marine ancestry that may help reduce dystocia by minimizing risks associated with malposition of the head (Hermes et al., 2008; Schmidt, 1999).

Aside from domesticated species of commercial interest, surprisingly little research has tested systematically whether humans have uniquely high rates of birth difficulties compared to other mammals. In those studies that have described large samples of births in captive primate colonies, for example, where these data are easier to collect, rates of birth difficulties are non-negligible (Haeusler et al., 2021). For example, in a colony of baboons (*Papio* spp.), 1.09% of births were dystocic (Schlabritz-Loutsevitch et al., 2018); in humans, this rate is 1.5-15%, depending on the population and definition (Haeusler et al., 2021). Better comparative data on species not under artificial selection could test the assumption that human birth is difficult because of selection on bipedalism, and could indicate other pressures common to several species.

5. Obligate Midwifery and Fetal Position

Due to the obstetric dilemma (encephalization and pelvic adaptations for bipedalism), human neonates tend to emerge from the birth canal in a ventral position, facing the parturient's back. It is commonly thought that the parturient herself cannot pull out a ventrally positioned neonate without risking injury to the neonate (Trevathan, 1987). Therefore, human birth generally requires someone who can provide assistance and support to the parturient, known as the obligate midwifery hypothesis (Rosenberg & Trevathan, 2002). Obligate midwifery is considered another unique feature of human births, yet recent research describes instances of nonhuman primates manually assisting the delivery of others' neonates (captive bonobos, *Pan paniscus*: Demuru et al., 2018; wild snub-nosed monkeys, *Rhinopithecus* spp.: Ding et al., 2013; Li et al., 2020; Yang et al., 2016; wild white-headed langur, *Trachypithecus leucocephalus*, Pan et al., 2014). There are also reports of birth assistance in laboratory Djungarian hamsters (*Phodopus campbelli*), where paternal behaviors include manually assisting in the delivery by tugging on the pup with forepaws or incisors (Jones & Wynne-Edwards, 2000).

---

[7] Pinnipeds include seals, sea lions, and walrus.

Social assistance does not appear to be a biological requirement in these species, begging questions about why and how the behavior evolved. A comparative approach could help elucidate the selection pressures that give rise to social support during births in other species, and spur a more nuanced understanding of the social evolution of birth attendance in humans. Moreover, humans are not the only primate with anterior longitudinal presentation and dorsal position during emergence. Though most other primate neonates emerge in the ventral position (which allows the mother to assist manually in the birth of her infant), there are reports of successful births with posterior presentation and dorsal position (Hirata et al., 2011; Moreno et al., 1991; Nakamichi et al., 1992) and even evidence of successful manual self-assistance with anterior presentation and ventral position (Nguyen et al., 2017).

6. Maternal Position

In humans, there is an ongoing debate around the overmedicalization of birth (and dorsal recumbent positions that are preferred by medical practitioners, particularly the lithotomy position) and the birth positions that result in better birth outcomes, such as lower injuries, blood loss, or shorter second stages of labor (e.g., Berta et al., 2019; Dundes, 1988). In studies of home births in contemporary, Western cultures, the majority of women (65%) spontaneously adopt positions that allow the sacrum to flex (Edqvist et al., 2016), providing more space for the neonate to pass through. However, variation in birth position is the 'rule' across mammals. Most descriptions of maternal birth position include changes in posture in response to assumed pain (e.g., Jarman, 1976; Lent, 1974; Manski, 1991; Martínez-Burnes et al., 2021; Noakes et al., 2001; Sauther, 1991). Some other broad generalizations can be made. For example, many domestic mammal species, including cats (*Felis catus*), dogs, horses, sheep, and pigs (*Sus domesticus*), give birth in lateral recumbency; cows will often adopt sternal recumbency late in the second stage of labor (Noakes et al., 2001). Beyond these species, maternal position during labor is not well-documented.

Maternal positions in primates are highly variable (see Benson, 2021), as in humans, with observations of recumbent birth in apes (captive orangutan, *Pongo pygmaeus*: Abelló & Fernández, 2003; captive lowland gorilla, *Gorilla gorilla gorilla*: Beck, 1984) and squatting in apes (captive bonobo: Coppola et al., 2011; wild mountain gorilla, *G. gorilla beringei*: Stewart, 1977), strepsirrhines (free-ranging ring-tailed lemurs: Sauther, 1991) and other monkeys, such as baboons (wild hamadrayas baboons, *P. hamadryas*: Abegglen & Abegglen, 1976; wild chacma baboons, *P. ursinus*: Vittoria Roatti, pers. comm.) and macaques (captive Java-macaques, *Macaca fascicularis*: Kemps & Timmermans, 1982; wild Japanese macaques, *Macaca fuscata*: Turner et al., 2010).

In other mammals, there are fewer comparative data. However, a combination of standing and lateral recumbent positions appear common, as is the case in many ungulates (Lent, 1974). For instance, wild hippopotamuses (*Hippopotamus amphibius*), hogs (*Suidae* spp.) and zebras (*Equus burchelli boehmi*) reportedly lie on their side during birth (Frädrich, 1974; Klingel, 1969; Lent, 1974; Leuthold, 1977), while giraffes (*Giraffa camelopardalis*) remain the classic example of birthing while standing (Backues, 2015). Lateral recumbency also appears to be the norm among *Camelidae* (Pilters, 1956), but other research has described a dromedary giving birth while standing (Naaktgeboren & Vandendriessche, 1962). Among cetaceans, maternal positions are difficult to discern due to limited underwater visibility. However, some observations—such as wild sperm (*Physeter* spp.) and right whales (*Eubalaena glacialis*) rolling onto one side, breaching, and thrashing their tails—have been documented immediately prior to birth (Correia-Fagundes & Romano, 2013; Weilgart & Whitehead, 1986; Zani et al., 2008).

Unfortunately, most of the available reports in nonhuman mammals are anecdotal and isolated, offering little systematic insight into how variation in maternal position may influence labor duration, dystocia, and other birth outcomes (and simultaneously, limited insight into the evolutionary factors that may shape maternal position in humans). We thus encourage future comparative research on maternal position, particularly as a predictor of variation in birth outcomes.

7. Parity

In the human and theriogenology literatures, primiparity is widely considered to be an intrapartum obstetric risk factor (Ananth et al., 2007; Hashim et al., 2012; Malkiel et al., 2008; Noakes et al., 2001). Relatedly, parity is a predictive factor of variation in labor duration and progression (Heres et al., 2000; Nesheim, 1988; Noakes et al., 2001; Rosenbloom et al., 2020; Vahratian et al., 2006; Wild & Yon, 2024) and parturients' psychological experiences of birth (Dahlen et al., 2010; Waldenström, 1999). Comparative studies could help elucidate how birth processes and outcomes vary with respect to parturient characteristics (including parity, age, rank, socioeconomic and other demographic variables) and potentially help disentangle biological and cultural explanations for these and other obstetric risk factors.

Beyond obstetric and veterinary medical studies, parity appears to be a predictor of variation in mammalian parturitional behaviors (Moreno et al., 1991; Nguyen et al., 2017; Peker et al., 2009; Timmermans & Vossen, 1996) and fetus viability (Frank & Glickman, 1994). In the first case, in a study of 15 diurnal parturition events in a population of wild gelada baboons (*Theropithecus gelada*), Nguyen and colleagues (2017) found that parous parturients were more likely than nulliparous parturients to: (a) give birth later in the afternoon, (b) give birth away from conspecifics, (c) exhibit placentophagy, and (d) manually aid the infant from the birth canal (i.e., self-assistance). In the second case, dystocia and resulting stillbirth is common in captive primiparous spotted hyena (*Crocuta crocuta*) due to the masculinization of their genitalia (females give birth through a 'penile' clitoris). Parturition in parous hyenas is relatively easier because the clitoris has been stretched and torn during the first birth (Frank & Glickman, 1994).

The possibility that parous mothers behave more skillfully and efficiently than do primiparous mothers highlights that experience and learning may play an important role in achieving optimal birth conditions. Indeed, in their study of wild mantled howler monkeys (*Alouatta palliata*), Moreno and colleagues (1991) suggest that experienced mothers may be relatively more successful in dealing with potential life-threatening occurrences such as breech presentation by engaging in manual self-assistance. It has also been suggested that in some highly social species, namely elephants and pigs, primiparous parturients with greater prior exposure to multiparous conspecifics and birth events will have reduced stress at parturition and diminished neophobia towards neonates immediately postpartum (Wild & Yon, 2024). However, much more research is needed to test whether parity and other forms of experience with birth (along with their behavioral and biological correlates) reliably predict differential birth outcomes within and across species.

8. Placentophagy

Placentophagy is characteristic of the majority of placental mammals, including strictly herbivorous taxa such as rabbits and ungulates (reviewed in Mota-Rojas et al., 2020). However, to date there is controversy over the causes and consequences of this behavior. Several hypotheses have been proposed to explain the adaptive value of placentophagy in mammalian species in which the behavior regularly occurs (reviewed in Kristal, 1980; Mota-Rojas et al., 2020); we summarize four here. According to one hypothesis, herbivorous parturients undergo a shift in preference toward carnivory at the time of birth to satisfy *specific* nutritional deficits (Lehrman, 1961), which received some early support in captive rhesus macaques (Tinklepaugh & Hartman, 1930) and domesticated bovines (Hafez et al., 1969). A second hypothesis is that placentophagy is a response to *general* hunger and serves to help the parturient maintain overall homeostatic nutritional requirements. Although research in laboratory monkeys and rats provides some evidence against both specific- and general-hunger interpretations (Kristal, 1980), one could conceivably test these hypotheses more systematically by comparing rates of placentophagy across herbivorous, carnivorous, and omnivorous species in relation to standard nutrient profiles.

A third hypothesis to explain placentophagy often cited in the literature is that mothers eat the afterbirth to maintain the hygiene of the nest site and/or to avoid attracting predators (Fraser, 1968; Tinklepaugh & Hartman, 1930). Kristal (1980) ruled out this hypothesis based on a general overview of extant studies (e.g., mothers of relatively unchallenged predatory species often eat the afterbirth). However, humpback whale parturients in some geographic areas are known to move away from the placenta, a behavior thought to decrease the risk of predation from sharks, who were attracted to blood in the water and did scavenge and consume the placenta (Ransome et al., 2022). A formal test of this third hypothesis would require systematic comparisons of the prevalence of placentophagy across species and populations with varying predation risk. Finally, a fourth hypothesis suggests that placentophagy occurs to manipulate maternal hormones postpartum. For example, studies of placentophagy in laboratory rodents (reviewed in Kristal et al., 2012) have shown that placentophagy enhances pain tolerance in postpartum rats via elevation of naturally occurring opioid-mediated analgesia (DiPirro & Kristal, 2004; Kristal, 1991). Similar mechanisms could operate in other mammalian species, though this remains to be tested. Studies have also shown that consuming the placenta increases the onset and intensity of maternal behavior in rats (defined as contact and licking of pups) (Kristal, 1991). However, authors carefully caution against extending this limited evidence to support the practice in humans.

Despite its near ubiquity among eutherian mammals, placentophagy appears absent in most contemporary human cultures (Kristal, 1980; Young & Benyshek, 2010; but see Ober, 1979 for historical evidence of placentophagy and its persistence in certain cultural contexts). However, the practice is now growing in popularity, particularly among postpartum women in Western societies, often through placenta encapsulation (Coyle et al., 2015; Farr et al., 2018; Hayes, 2016). Advocates of placentophagy in humans generally assume, in line with the general theories outlined above, that the behavior replenishes nutrients and hormones lost during birth, which can in turn stabilize mood (e.g., prevent postpartum depression), reduce pain, enhance recovery, and increase energy and milk production (Apari & Rózsa, 2006; Beacock, 2012; Selander et al., 2013). Yet despite the many claimed advantages of this practice (and potential risks—e.g., see: Buser et al., 2017), virtually no studies have systematically examined the effects of placentophagy in humans.

9. Parturitional Sociality

Beyond the birth assistance behaviors noted earlier (see Section 5, "Obligate Midwifery and Fetal Position"), various other forms of social interaction can take place throughout parturition. Although parturitional sociality has been reported in diverse taxa (reviewed in Wild & Yon, 2024), research on these interactions remains fragmented and limited, partly because it is commonly assumed that many mammals tend to give birth in isolation (Lent, 1974; Trevathan, 1987).

Isolation allows birth to occur less conspicuously, which presumably avoids drawing the attention of predators, but may also protect females and their infants from the adverse responses of conspecifics, including infanticide and aggression. In line with this, some otherwise highly social mammals do commonly isolate themselves to give birth—such as wild African lions (*Panthera leo*; Packer et al., 2001) and several social ungulate species (reviewed in Lent, 1974)[8]. Notably, wild female humpback whales are harassed by lekking males and appear to attempt to 'escape' from males' presence during birth (Ransome et al., 2022). Males may harass females during labor because this species has postpartum estrus, and males may mate with females soon after birth. Similarly, captive female prairie voles (*Microtus ochrogaster*), despite both being monogamous and having biparental care of offspring, isolate during parturition, and can exhibit aggression towards their mates (McGuire et al., 2003). Female isolation and aggression in this species (which also exhibits postpartum estrus) could arise to allow females to avoid copulation immediately postpartum.

While isolation during birth may be common, the proximity of conspecifics is not as uncommon as conventionally assumed, at least in primates: 59.8% (N = 122 of 204 reports) of primate parturition events occurred in proximity (< 3 m) to conspecifics (Leavy, unpublished data). Of these 122 events, in 85% of cases, the individuals in close proximity were females. In a similar analysis, Benson (2021) found that the

---

[8] Seasonal breeders such as wild wildebeest (*Connochaetes tauvinus*; Estes & Estes, 1979) and caribou (*Rangifer tarandus*; Lent, 1966) appear to be the exception.

majority (69.3%) of reported primate birth events occurred in a social context and often involved the proximity of other parous, adult females. However, such preliminary findings must be interpreted with caution especially given sampling and reporting biases (i.e., birth events when parturients do not self-isolate are far more likely to be observed and documented by researchers).

Beyond primates, parturients of diverse mammalian species—including elephants, cetaceans, bovids, pinnipeds, and bats—appear to maintain, or even actively seek, proximity to conspecifics despite being in active labor or exhibiting signs of distress (Wild & Yon, 2024). Moreover, in some cases, conspecifics appear to take an active interest in the birth event itself. In wild African elephants, for instance, herd mates may congregate around the parturient throughout birth, exhibiting signs of arousal (e.g., increased rumbling and ear flapping) and adopting defensive postures (Leuthold & Leuthold, 1975; McKnight, 1992)

Social behaviors around birth are not limited to proximity or protection. Allomaternal care (allomothering) throughout parturition has been documented in several social mammalian taxa. For example, in wild cetaceans, multiple conspecifics (often of unidentified sex or relatedness to the parturient) have taken turns raising the neonate to the surface to breathe until the infant is able to swim independently (Béland et al., 1990; Notarbartolo-Di-Sciara et al., 1997; Stacey & Baird, 1997). In wild African elephants, observers have documented adult females assisting with the removal of fetal membranes immediately after delivery, and temporarily caring for the neonate while the mother went to drink water (Leuthold & Leuthold, 1975). Similar prosocial behaviors are seen in primates. In the birth of a white-headed langur (*Trachypithecus leucocephalus*), for instance, a multiparous female relative (either the mother or the aunt of the nulliparous parturient) participated actively in the birth event. The attendant first manually assisted in the removal of the neonate; she then carried the neonate, along with her own infant, for over 10 minutes while the parturient consumed the placenta (Pan et al., 2014). In the immediate postpartum period, allomaternal nursing (e.g., Pan et al., 2014), umbilical cord severance (Li et al., 2020), and placenta sharing (non-maternal placentophagy: e.g., Coppola et al., 2011; Douglas, 2014; Fujisawa et al., 2016) have also been observed in several primate species.

In their review of parturitional sociality in mammals, Wild & Yon (2024) suggest that multiparous females—presumably with greater experience with birth—are the primary providers of supportive social behaviors during labor, delivery, and the immediate postpartum period. While they reference some supporting evidence from primate studies, systematic comparative data are needed to evaluate the extent and generality of this pattern.

Primate data suggest that the nature of social interactions with the parturient may also reflect the social and mating systems of a given species. For example, the preponderance of female sociality in available birth reports in both captive (Coppola et al., 2011; Demuru et al., 2018) and wild (Douglas, 2014) bonobos is perhaps unsurprising given the importance of female-female bonds in this species. Likewise, male birth assistance and attendance have been reported in various species exhibiting paternal care—e.g., wild black-and-white snub-nosed monkeys (Li et al., 2020) and titi monkeys (*Callicebus oenanthe*: DeLuycker, 2014); captive cotton-top tamarins (*Saguinus oedipus*: Price, 1990) and Djungarian hamsters (*Phodopus campbelli*: Jones & Wynne-Edwards, 2000). Deluycker (2014) goes so far as to argue that males play an integral role during births in part to establish a bond with the neonate and provide reinforcement to the female during a vulnerable time.

This raises broader questions about the adaptive significance of parturitional sociality. A comparative research program could explore the species and circumstances in which the presence of conspecifics during labor reinforces valuable social relationships and has other fitness consequences (including infant and maternal survival). In humans, continuous support from a birthing partner has been shown to reduce anxiety, labor duration, and the need for medical intervention (Scott et al., 1999)—and is now recognized as one of the four key interventions for preventing dystocia (Kissler & Hurt, 2023). Social support mechanisms may likewise influence parturition outcomes in other socially complex mammals. In both captive Asian and African elephants, for example, separation of the parturient from conspecifics during birth has been associated with an increased risk of dystocia (reviewed in Hartley, 2016). Although the functions of parturitional sociality remain understudied, it holds significant implications for animal welfare, particularly in managed settings where facilitating appropriate social environments could promote maternal and neonatal health.

10. Implications for Animal Cognition

Birth represents a novel and potentially generative context in which to address questions about animal minds. For instance, ongoing debates about the presence and extent of animal prosociality (Jensen, 2016) would be usefully informed by considering parturitional behaviors like birth assistance, birth attendance, placenta-sharing, allomothering, and allomaternal nursing (see Section 4, “Obstetric Dilemma Hypothesis,” Section 9, “Parturitional Sociality,” and Table 1). In particular, one could study whether birth assistance is tailored to parturients’ specific situations and needs (i.e., instrumental/targeted helping) as a window onto underlying psychological mechanisms like perspective-taking and theory of mind (de Waal, 2008). Moreover, studying the social relationship between birthing individuals and those who come to their aid could elucidate whether such acts are motivated primarily by inclusive fitness (and likewise, help address outstanding questions about the nature of non-kin cooperation in animal societies: Clutton-Brock, 2009).

Women across many human cultures report that birth is among the most physically and emotionally intense moments of their lives. Yet we know next to nothing about the emotional valence of birth for other species. Moreover, contrary to extensive research in humans, there are limited pain studies associated with the birth process in captive and domesticated animals (reviewed in Martínez-Burnes et al., 2021), and we are aware of no such studies in the wild. The recognition (and potential treatment) of pain during parturition represents a potential welfare concern and an overlooked area in which to investigate questions about animal sentience more broadly.

The study of birth also provides a novel context for testing hypotheses about cognitive processes like learning and memory. Future research could elucidate the role of learning and maternal experience in navigating and understanding birth by comparing the births of first-time and experienced mothers and/or the social responses of nulliparous versus parous females to the birth. In the first case, evidence that parturients become more competent with successive births could provide novel evidence for individual learning strategies (Nguyen et al., 2017) and potentially conscious recollection of unique personal experiences (i.e., episodic memory). In the second case, various case reports document parous (experienced) females assisting others’ births (Demuru et al., 2018; Ding et al., 2013; Douglas, 2014; Li et al., 2020; Wild & Yon, 2024; Yang et al., 2016). Having gone through a similar experience oneself could conceivably motivate one to help (affective empathy) or even improve the quality/suitability of support (cognitive empathy). Research might consider what other kinds of social learning outlets (e.g., opportunities to witness others’ births) might allow parturients and other group members to develop a better understanding of parturition events.

A birth case report in fruit bats (*Pteropus rodricensis*) describes an attending female who “tutored” the parturient into a feet-down birth posture and physically assisted her by maneuvering the pup into a suckling position (Kunz et al., 1994). Except for one occurrence, the mother assumed the feet-down birth position only after the helper assumed a similar position. Each of the four times this happened, the helper moved to a position in full view of the mother and assumed a feet-down posture. Whether the helper was demonstrating for the parturient and/or the parturient copied the posture of the helper remains unknown. However, this intriguing study highlights birth’s potential to inform contemporary debates about animal cognitive capacities like teaching and imitation (Hoppitt et al., 2008). Relatedly, a broad comparative approach is necessary to test whether parturitional behaviors are socially learned and group-specific, potentially adding to the diversity of behavioral domains in which animal cultures have been documented (Whiten, 2021).

In addition to the empirically tractable questions outlined above, there are a number of broader theoretical questions for comparative ilithologists to consider. Birth coincides with the sudden arrival of a new, stranger conspecific. What cognitive capacities are required of the mother and other group members to make sense of this event? Drawing on recent inquiries into whether other species possess a concept of death (Anderson, 2016; Anderson et al., 2018; Monsó & Osuna-Mascaró, 2021), could other animals be said to have a concept of birth, and how do they acquire this concept? How do the mother and other group members come to recognize that newborns are living, agentic beings (who may look, move, smell, and sound very different from other conspecifics)? Especially given the bodily changes she undergoes, what awareness does the mother have before, during, and after birth of its significance? What can parturition tell us about animals' awareness of life (and death) in a general sense? Answers to these questions have broad philosophical applications and highlight the potential for fruitful dialogues between comparative thanatologists and ilithologists.

Suggested Research Program

In the preceding sections we have outlined ten potential new areas of research that have been historically overlooked. Here we briefly propose how researchers could tackle questions around parturition and related behaviors, including the types of data that could be collected and technology that could be used to facilitate observations. First, we acknowledge the difficulty of observing birth events, particularly in the wild. The date of the birth after conception, while not unpredictable, usually has large variation around the mean (1 SD = 13 days in humans) and a relatively flat distribution (Bergsjø et al., 1990; Jukic et al., 2013). In addition, the event itself is relatively short, with the result that breaks in observation could result in data loss.

Despite the challenges, we believe that a dedicated research program is possible with strategic choice of research subject and adoption of novel technologies, provided both are guided by strict ethical standards (e.g., minimal disturbance and full attention to animal welfare). In the first case, studying seasonally breeding mammals allows more targeted data collection and prudent allocation of resources. In addition, where permissible, captive study coupled with remote cameras allows continuous recording so that events are not missed. Finally, species with physical indicators of ovulation (such as sexual swellings) or pregnancy (such as changes in paracollosal skin coloration) could be chosen to facilitate predictions of birth dates and periods for heightened observation.

In the second case, one potentially useful technology for observing birth behavior is that of thermal imaging and night vision (Allison & Destefano, 2006). Technologies have advanced sufficiently in the past decade such that detailed nocturnal behavioral observations can be made of animals in the wild (e.g. Burger et al., 2020). The use of such technology would work particularly well for diurnal mammals who use observable refuges to sleep, such as on (small) cliff faces or in trees. Nocturnally recorded observations could address, among others, questions about the hour of birth and labor duration, and, if conditions allow, manual assistance and fetal emergence positions. Thermal images could possibly be used to indicate nausea in early-term pregnant females (Clark et al., 2007; Zhang et al., 1997).

While dedicated research programs on ilithology will shed light on many of our proposed areas of research, we are also aware that collaborative data sharing of incidentally-observed births and birth-related behaviors can inform research questions with a comparative focus—as has recently been done in other fields (e.g., Watanabe et al., 2007). For example, records of placentophagy and placenta abandonment across diverse species and populations can address the question about the causes of this behavior. Records of dystocic births could also be used in a comparative framework to address whether humans have a uniquely 'tight fit' of the neonate skull. We thus encourage researchers to proactively collect and collaboratively share data in both captive and field contexts.

Finally, 'old-fashioned' close behavioral observation and physical anthropology can inform the remaining proposed questions. For example, careful observation of foraging behavior and consideration of appropriate controls can provide evidence for NVP and medicinal plant use in nonhuman mammals, while more detailed data on primate pelves and neonate skull size could shed light on the uniqueness (or ubiquity) of the obstetric dilemma. An emphasis on multiple methods and long-term, individually-based behavioral observations will facilitate integrated understandings of the diverse environmental, social, cognitive, and individual factors (e.g., parity) that modulate parturition.

Conclusion

Comparative ilithology has great potential to address proximate and ultimate questions about birth across species, including our own. As we have argued, to date this potential has largely been overlooked—in part because birth is often viewed as a specialized or "niche" topic rather than the fundamental life history event that it is. Indeed, many of the assumptions about the uniqueness of human childbirth rest on studies that are dated, inconclusive, or have yet to be systematically tested with cross-species data, including those pertaining to dystocic labor, placentophagy, and morning sickness. At the same time, birth scholars and practitioners frequently appeal to evolutionary explanations (e.g., nocturnal patterns of birth amongst diurnal mammals and other "natural" adaptations) with limited knowledge of the frequency, phylogenetic history, or adaptive significance of a given trait across species. Systematic and updated comparative data are necessary to inform these evolutionary positions and understand the positive and relaxed selection pressures that have shaped parturition across species. While primate studies are critical for understanding the evolution of human childbirth, comparative data would ideally include observations from a much greater diversity of wild animal populations. Studies could even extend beyond eutherian mammals to encompass non-mammalian species in which viviparity evolved independently, thus offering insights on convergent evolution. Integrating more data on domesticated species in which natural selection pressures have been attenuated (e.g., predation) or altered (e.g., nutrition) could offer further insights into the evolutionary pressures shaping birth. And beyond viviparous species, some questions explored here—such as those concerning animal cognition—may also apply to oviparous species, who must likewise behaviorally and psychologically adapt to the birth of offspring.

While pointing to gaps in current knowledge, the ten research areas outlined here are but a subset of the potential scope of comparative ilithology. Researchers from a wide range of disciplines are comparative thanatologists—including but not limited to medicine, biology, psychology, anthropology, paleontology, sociology, and philosophy. Likewise, comparative ilithology is an inherently interdisciplinary topic, impacting research in the same breadth of disciplines as thanatology. As such, there are a number of parturitional behaviors and related issues not covered in this review for which a comparative approach would be generative—such as umbilical cord severance (see ongoing debates in the human obstetric literature about the trade-offs of early versus delayed severance, which cross-species data could usefully inform: Andersson et al., 2011). We have also omitted a number of clinically relevant topics (e.g., postpartum depression, preeclampsia, placental abruption, gestational hypertension) for which some cross-species data exist, as mentioned in recent calls for comparative approaches to female health more broadly (Natterson-Horowitz et al., 2022). Finally, birth raises various epistemic, ontological, ethical, and metaphysical questions, yet these remain largely unaddressed in philosophy (but see Banks, 2023 and also recent philosophical engagement with pregnancy: Kingma, 2020; Sidzinska, 2017). A richer understanding of birth's implications for animal (including human) minds calls for greater collaboration between scientists and philosophers, which a broad comparative field of birth will facilitate.

Comparative ilithology also has significant implications for animal welfare and conservation efforts. For instance, knowledge of ideal birth conditions—such as the need for privacy (or social interaction), specific habitats, or environmental cues (e.g., light exposure)—can increase the likelihood of successful animal births across a range of captive (e.g., zoos and sanctuaries) and wild settings. This information is thus crucial for developing effective and ethically responsible breeding programs for endangered species and supporting successful species recovery plans. In domesticated (e.g., companion and farmed) animals, better understanding of the social and psychological aspects of birth can reduce stress, prevent complications, and improve postpartum care. Overall, insights into birthing behaviors are vital for the health and survival of both mothers and offspring, underscoring their importance for both individual animal well-being and the viability of animal populations.

Last but not least, despite technological advancements, growing medical knowledge, and increasing obstetric interventions, human pregnancy and birth-related mortalities and morbidities are on the rise in many parts of the world (Souza et al., 2024; World Health Organization, 2023), including, until very recently, the United States (Hoyert, 2023). Adverse birth outcomes in humans in Western settings typically reflect pervasive systems of sexual, racial, and socioeconomic discrimination (Hoyert, 2023; Jones et al., 2022). These disparities underscore the need for rigorous science, an evolutionarily grounded understanding of birth, and interdisciplinary dialogue, all of which comparative ilithology is poised to contribute.

Acknowledgements

Author Contributions: Conceptualization: CEW, EB, AJC; Investigation: CEW, EB, IL, AJC; Writing-original draft: CEW, EB, AJC; Writing-review & editing: CEW, EB, IL, AJC

Funding: N/A

Conflict of Interest: The authors declare no conflict of interest.

References

Abegglen, H., & Abegglen, J. J. (1976). Field observation of a birth in hamadryas baboons. *Folia Primatologica; International Journal of Primatology*, *26*(1), 54–56. https://doi.org/10.1159/000155729

Abelló, M. T., & Fernández, J. (2003). Parturition and lactation in a Bornean orangutan. *International Zoo Yearbook*, *38*(1), 186–191. https://doi.org/10.1111/j.1748-1090.2003.tb02079.x

Aerts, R. J., Barry, T. N., & McNabb, W. C. (1999). Polyphenols and agriculture: Beneficial effects of proanthocyanidins in forages. *Agriculture, Ecosystems & Environment*, *75*, 1–12. https://doi.org/10.1016/S0167-8809(99)00062-6

Allison, N. L., & Destefano, S. (2006). Equipment and techniques for nocturnal wildlife studies. *Wildlife Society Bulletin*, *34*(4), 1036–1044. https://doi.org/10.2193/0091-7648(2006)34[1036:eatfnw]2.0.co;2

Altmann, J. (1980). *Baboon Mothers and Infants*. Harvard University Press.

Ananth, C. V., Peltier, M. R., Getahun, D., Kirby, R. S., & Vintzileos, A. M. (2007). Primiparity: An "intermediate" risk group for spontaneous and medically indicated preterm birth. *Journal of Maternal-Fetal and Neonatal Medicine*, *20*(8), 605–611. https://doi.org/10.1080/14767050701451386

Anderson, J. R. (2016). Comparative thanatology. *Current Biology*, *26*(13), R553–R556. https://doi.org/10.1016/j.cub.2015.11.010

Anderson, J. R., Biro, D. & Pettitt, P. (2018). Evolutionary thanatology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*, 20170262. https://doi.org/10.1098/rstb.2017.0262

Andersson, O., Hellström-Westas, L., Andersson, D., & Domellöf, M. (2011). Effect of delayed versus early umbilical cord clamping on neonatal outcomes and iron status at 4 months: A randomised controlled trial. *British Medical Journal*, *343*, d7157. https://doi.org/10.1136/bmj.d7157

Apari, P., & Rózsa, L. (2006). Deal in the womb: Fetal opiates, parent-offspring conflict, and the future of midwifery. *Medical Hypotheses*, *67*(5), 1189–1194. https://doi.org/10.1016/j.mehy.2006.03.053

Athanasiadou, S., Kyriazakis, I., Jackson, D., & Coop, R. L. (2001). Direct anthelmintic effects of condensed tannins towards different gastrointestinal nematodes of sheep: in vitro and in vivo studies. *Veterinary Parasitology*, *99*(3), 205–219. https://doi.org/10.1016/S0304-4017(01)00467-8

Backe, B. (1991). A circadian variation in the observed duration of labor. *Acta Obstetricia et Gynecologica Scandinavica*, *70*(6), 465–468. https://doi.org/10.3109/00016349109007161

Backues, K. A. (2015). Giraffe medicine made easy. *North American Veterinary Conference*, 1435–1438.

Banks, J. (2023). *Natality: Toward a Philosophy of Birth*. Norton.

Barry, T. N., & McNabb, W. C. (1999). The implications of condensed tannins on the nutritive value of temperate forages fed to ruminants. *British Journal of Nutrition*, *81*(4), 263–272. https://doi.org/10.1017/s0007114599000501

Bazer, F. W., & Spencer, T. E. (2011). Hormones and pregnancy in eutherian mammals. In D. O. Norris & K. H. Lopez (Eds.), *Hormones and reproduction of vertebrates* (pp. 73–94). Academic Press.

Beacock, M. (2012). Does eating placenta offer postpartum health benefits? *British Journal of Midwifery*, *20*(7), 464–469. https://doi.org/10.12968/bjom.2012.20.7.464

Beck, B. B. (1984). The birth of a lowland gorilla in captivity. *Primates*, *25*, 378–383. https://doi.org/10.1007/BF02382276

Béland, P., Faucher, A., & Corbeil, P. (1990). Observations on the birth of a beluga whale (*Delphinapterus leucas*) in the St Lawrence Estuary, Quebec, Canada. *Canadian Journal of Zoology*, *68*(6), 1327–1329. https://doi.org/10.1139/z90-198

Benson, E. (2021). *Primate Ilithology: The Comparative Study of Birth and Parturitional Behaviors*. Harvard University Bachelor of Arts Honors Thesis.

Bergsjø, P., Denman, D. W., Hoffman, H. J., & Meirik, O. (1990). Duration of human singleton pregnancy: A population-based study. *Acta Obstetricia et Gynecologica Scandinavica*, *69*(3), 197–207. https://doi.org/10.3109/00016349009028681

Bernis, C., & Varea, C. (2012). Hour of birth and birth assistance: From a primate to a medicalized pattern? *American Journal of Human Biology*, *24*(1), 14–21. https://doi.org/10.1002/ajhb.21228

Berta, M., Lindgren, H., Christensson, K., Mekonnen, S., & Adefris, M. (2019). Effect of maternal birth positions on duration of second stage of labor: Systematic review and meta-analysis. *BMC Pregnancy and Childbirth*, *19*(1), 1–8. https://doi.org/10.1186/s12884-019-2620-0

Biagi, G. L., & Speroni, E. (1988). *Farmacognosia*. Pàtron.

Biser, J. A. (1998). Really wild remedies—medicinal plant use by animals. *ZooGoer*, *27*(1), 1–6.

Blaxter, K. L. (1989). *Energy Metabolism in Animals and Man.* Cambridge University Press.

Brandt, E. M., & Mitchell, G. (1971). Parturition in primates: Behavior related to birth. In L. A. Rosenblum (Ed.), *Primate Behaviour: Developments in Field and Laboratory Research, Vol. 2* (pp. 178–223). Academic Press.

Burger, A. L., Fennessy, J., Fennessy, S., & Dierkes, P. W. (2020). Nightly selection of resting sites and group behavior reveal antipredator strategies in giraffe. *Ecology and Evolution*, *10*(6), 2917–2927. https://doi.org/10.1002/ece3.6106

Buser, G. L., Mató, S., Zhang, A. Y., Metcalf, B. J., Beall, B., & Thomas, A. R. (2017). Notes from the field: Late-onset infant group B streptococcus infection associated with maternal consumption of capsules containing dehydrated placenta-Oregon, 2016. *US Department of Health and Human Services/Centers for Disease Control and Prevention: Morbidity and Mortality Weekly Report,* *66*(25), 677–678. https://doi.org/10.1097/AOG.0000000000002274

Cagnacci, A., Soldani, R., Melis, G. B., & Volpe, A. (1998). Diurnal rhythms of labor and delivery in women: Modulation by parity and seasons. *American Journal of Obstetrics and Gynecology*, *178*(1), 140–145. https://doi.org/10.1016/S0002-9378(98)70641-6

Campitelli, S., Carenzi, C., & Verga, M. (1982). Factors which influence parturition in the mare and development of the foal. *Applied Animal Ethology*, *9*, 7–14. https://doi.org/10.1016/0304-3762(82)90161-4

Carrai, V., Borgognini-Tarli, S. M., Huffman, M. A., & Bardi, M. (2003). Increase in tannin consumption by sifaka (*Propithecus verreauxi verreauxi*) females during the birth season: A case for self-medication in prosimians? *Primates*, *44*(1), 61–66. https://doi.org/10.1007/s10329-002-0008-6

Chaney, C., Goetz, L. G., & Valeggia, C. (2018). A time to be born: Variation in the hour of birth in a rural population of Northern Argentina. *American Journal of Physical Anthropology*, *166*(4), 975–978. https://doi.org/10.1002/ajpa.23483

Charles, E. (1953). The hour of birth. A study of the distribution of times of onset of labour and of deliveries through 24 h period. *British Journal of Preventative and Social Medicine*, *7*, 43–59. https://doi.org/10.1136/jech.7.2.43

Chism, J., Olson, D. K., & Rowell1, T. E. (1983). Diurnal births and perinatal behavior among wild patas monkeys: Evidence of an adaptive pattern. *International Journal of Primatology*, *4*(2), 167–184. https://doi.org/10.1007/BF02743756

Clark, A. T., Mangat, J. S., Tay, S. S., King, Y., Monk, C. J., White, P. A., & Ewan, P. W. (2007). Facial thermography is a sensitive and specific method for assessing food challenge outcome. *Allergy: European Journal of Allergy and Clinical Immunology*, *62*(7), 744–749. https://doi.org/10.1111/j.1398-9995.2007.01363.x

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*(7269), 51–57. https://doi.org/10.1038/nature08366

Coppola, F., Demuru, E., & Palagi, E. (2011). Birth in bonobos (*Pan paniscus*): A case report. *Atti Della Societa Toscana Di Scienze Naturali, Memorie Serie B*, *118*, 111–116. https://doi.org/10.2424/ASTSN.M.2011.30

Correia-Fagundes, C., & Romano, H. (2013). Observation of a birth of a Sperm whale *Physeter macrocephalus* at Madeira (NE Atlantic). *Bocagiana*, *236*, 1–3. http://publications.cm-funchal.pt/handle/100/1655

Coyle, C. W., Hulse, K. E., Wisner, K. L., Driscoll, K. E., & Clark, C. T. (2015). Placentophagy: Therapeutic miracle or myth? *Archives of Women's Mental Health*, *18*(5), 673–680. https://doi.org/10.1007/s00737-015-0538-8

Dahlen, H. G., Barclay, L. M., & Homer, C. S. E. (2010). The novice birthing: theorising first-time mothers' experiences of birth at home and in hospital in Australia. *Midwifery*, *26*(1), 53–63. https://doi.org/10.1016/j.midw.2008.01.012

de Waal, F. B. M. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology*, *59*, 279–300. https://doi.org/10.1146/annurev.psych.59.103006.093625

DeLuycker, A. M. (2014). Observations of a daytime birthing event in wild titi monkeys (*Callicebus oenanthe*): Implications of the male parental role. *Primates*, *55*(1), 59–67. https://doi.org/10.1007/s10329-013-0368-0

Demuru, E., Ferrari, P. F., & Palagi, E. (2018). Is birth attendance a uniquely human feature? New evidence suggests that bonobo females protect and support the parturient. *Evolution and Human Behavior*, *39*(5), 502–510. https://doi.org/0.1016/j.evolhumbehav.2018.05.003

Ding, W., Yang, L. & Xiao, W. (2013). Daytime birth and parturition assistant behavior in wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) Yunnan, China. *Behavioural Processes*, *94*(May 2012), 5–8. https://doi.org/10.1016/j.beproc.2013.01.006

DiPirro, J. M., & Kristal, M. B. (2004). Placenta ingestion by rats enhances κ- and δ-opioid antinociception, but suppresses μ-opioid antinociception. *Brain Research*, *1014*, 22–33. https://doi.org/10.1016/j.brainres.2004.04.006

Douglas, P. H. (2014). Female sociality during the daytime birth of a wild bonobo at Luikotale, Democratic Republic of the Congo. *Primates*, *55*(4), 533–542. https://doi.org/10.1007/s10329-014-0436-0

Dundes, L. (1988). The evolution of maternal birthing position. *Obstetrical and Gynecological Survey*, *43*(1), 47–48. https://doi.org/10.1097/00006254-198801000-00013

Dunn, R. (2012). Night shift. *Natural History*, *120*(3), 10–13.

Dunsworth, H. M. (2018). There is no "obstetrical dilemma": Towards a braver medicine with fewer childbirth interventions. *Perspectives in Biology and Medicine*, *61*(2), 249–263. https://doi.org/10.1353/pbm.2018.0040

Edqvist, M., Blix, E., Hegaard, H. K., Ólafsdottir, O. Á., Hildingsson, I., Ingversen, K., Mollberg, M., & Lindgren, H. (2016). Perineal injuries and birth positions among 2992 women with a low risk pregnancy who opted for a homebirth. *BMC Pregnancy and Childbirth*, *16*(1). https://doi.org/10.1186/s12884-016-0990-0

Estes, R. D., & Estes, R. K. (1979). The birth and survival of wildebeest calves. *Zeitschrift Für Tierpsychologie*, *50*, 45–95. https://doi.org/10.1111/j.1439-0310.1979.tb01015.x

Farr, A., Chervenak, F. A., McCullough, L. B., Baergen, R. N., & Grünebaum, A. (2018). Human placentophagy: a review. *American Journal of Obstetrics and Gynecology*, *218*(4), 401–410. https://doi.org/10.1016/j.ajog.2017.08.016

Flaxman, S. M., & Sherman, P. W. (2008). Morning sickness: Adaptive cause or nonadaptive consequence of embryo viability? *American Naturalist*, *172*(1), 54–62. https://doi.org/10.1086/588081

Fontaine, E. (2012). Food intake and nutrition during pregnancy, lactation and weaning in the dam and offspring. *Reproduction in Domestic Animals*, *47*(6), 326–330. https://doi.org/10.1111/rda.12102

Frädrich, H. (1974). A comparison of behavior in the Suidae. In V. Geist & F. Walther (Eds.), *The Behaviour of Ungulates and its Relation to Management* (pp. 133–143). IUCN Publications.

Franco-Trecu, V., García-Olazábal, M. D., Tassino, B., & Acevedo, J. (2016). Parturition process in an amphibian mammal species: New evidences in South American fur seal (*Arctocephalus australis*). *Animal Biology*, *66*, 21–29. https://doi.org/10.1163/15707563-00002484

Frank, L. G., & Glickman, S. E. (1994). Giving birth through a penile clitoris: parturition and dystocia in the spotted hyaena (*Crocuta crocuta*). *Journal of Zoology*, *234*(4), 659–665. https://doi.org/10.1111/j.1469-7998.1994.tb04871.x

Fraser, A. F. (1968). *Reproductive Behavior in Ungulates*. Academic Press.

Fujisawa, M., Hockings, K. J., Soumah, A. G., & Matsuzawa, T. (2016). Placentophagy in wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *Primates*, *57*(2), 175–180. https://doi.org/10.1007/s10329-016-0510-x

Gonçalves, A., & Biro, D. (2018). Comparative thanatology, an integrative approach: Exploring sensory/cognitive aspects of death recognition in vertebrates and invertebrates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*, 20170263. https://doi.org/10.1098/rstb.2017.0263

Gonçalves, A., & Carvalho, S. (2019). Death among primates: A critical review of non-human primate interactions towards their dead and dying. *Biological Reviews*, *94*(4), 1502–1529. https://doi.org/10.1111/brv.12512

Grunstra, N. D. S., Zachos, F. E., Herdina, A. N., Fischer, B., Pavličev, M., & Mitteroecker, P. (2019). Humans as inverted bats: A comparative approach to the obstetric conundrum. *American Journal of Human Biology*, *31*(2), 1–18. https://doi.org/10.1002/ajhb.23227

Haeusler, M., Grunstra, N. D. S., Martin, R. D., Krenn, V. A., Fornai, C., & Webb, N. M. (2021). The obstetrical dilemma hypothesis: There's life in the old dog yet. *Biological Reviews*, *96*(5), 2031–2057. https://doi.org/10.1111/brv.12744

Hafez, E. S. E., Shein, M. W., & Ewbank, R. (1969). The behaviour of cattle. In E. S. E. Hafez (Ed.), *The Behaviour of Domestic Animals*. Williams and Wilkins.

Haig, D. (1993). Genetic conflict in human pregnancy. *Quarterly Review of Biology*, *68*(4), 495–532. http://doi.org/10.1086/418300

Hartley, M. (2016). Assessing risk factors for reproductive failure and associated welfare impacts in elephants in European zoos. *Journal of Zoo and Aquarium Research*, *4*(3), 1–12. https://doi.org/10.19227/jzar.v4i3.162

Hashim, N., Naqvi, S., Khanam, M., & Jafry, H. F. (2012). Primiparity as an intrapartum obstetric risk factor. *JPMA. The Journal of the Pakistan Medical Association*, *62*(7), 694–698.

Hayes, E. H. (2016). Consumption of the placenta in the postpartum period. *Journal of Obstetric, Gynecologic, & Neonatal Nursing*, *45*(1), 78–89. https://doi.org/10.1016/j.jogn.2015.10.008

Heidler, B., Aurich, J. E., Pohl, W., & Aurich, C. h. (2004). Body weight of mares and foals, estrous cycles and plasma glucose concentration in lactating and non-lactating Lipizzaner mares. *Theriogenology*, *61*(5), 883–893. https://doi.org/10.1016/s0093-691x(03)00279-6

Heres, M. H. B., Pel, M., Borkent-Polet, M., Treffers, P. E., & Mirmiran, M. (2000). The hour of birth: Comparisons of circadian pattern between women cared for by midwives and obstetricians. *Midwifery*, *16*(3), 173–176. https://doi.org/10.1054/midw.1999.0210

Hermes, R., Saragusty, J., Schaftenaar, W., Göritz, F., Schmitt, D. L., & Hildebrandt, T. B. (2008). Obstetrics in elephants. *Theriogenology*, *70*(2), 131–144. https://doi.org/10.1016/j.theriogenology.2008.04.003

Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., & Takeshita, H. (2011). Mechanism of birth in chimpanzees: Humans are not unique among primates. *Biology Letters*, *7*(5), 686–688. https://doi.org/10.1098/rsbl.2011.0214

Honnebier, M. B. O. M., & Nathanielsz, P. W. (1994). Primate parturition and the role of the maternal circadian system. *European Journal of Obstetrics and Gynecology and Reproductive Biology*, *55*(3), 193–203. https://doi.org/10.1016/0028-2243(94)90038-8

Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., & Laland, K. N. (2008). Lessons from animal teaching. *Trends in Cognitive Sciences*, *23*(9), 486–493. https://doi.org/10.1016/j.tree.2008.05.008

Hoque, M., & Hoque, S. (2010). Timing of spontaneous birth and the risk of adverse perinatal outcome. *Southern African Journal of Epidemiology and Infection*, *25*(4), 35–38. https://doi.org/10.1080/10158782.2010.11441407

Hoyert, D. L. (2023). Maternal Mortality Rates in the United States, 2021. In *National Center for Health Statistics*. https://doi.org/10.15620/cdc:113967

Hrdy, S. B. (2009). *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Harvard University Press. https://doi.org/10.2307/j.ctv5rf3wk.13

Hudson, R., Cruz, Y., Lucio, R. A., Ninomiya, J., & Martínez-Gómez, M. (1999). Temporal and behavioral patterning of parturition in rabbits and rats. *Physiology and Behavior*, *66*(4), 599–604. https://doi.org/10.1016/S0031-9384(98)00331-X

Jarman, M. V. (1976). Impala social behaviour: Birth behaviour. *African Journal of Ecology*, *14*, 153–167. https://doi.org/10.1111/j.1365-2028.1976.tb00159.x

Jensen, K. (2016). Prosociality. *Current Biology*, *26*(16), R748–R752. https://doi.org/10.1016/j.cub.2016.07.025

Jessops, N. S. (1997). Protein metabolism during lactation. *Proceedings of the Nutrition Society*, *56*, 169–175. https://doi.org/10.1079/PNS19970019

Jolly, A. (1972). Hour of birth in primates and man. *Folia Primatologica, 18*(1), 108–121. https://doi.org/10.1159/000155472

Jones, G. L., Mitchell, C. A., Hirst, J. E., & Anumba, D. O. C. (2022). Understanding the relationship between social determinants of health and maternal mortality: Scientific Impact Paper No. 67. *BJOG: An International Journal of Obstetrics and Gynaecology*, *129*(7), 1211–1228. https://doi.org/10.1111/1471-0528.17044

Jones, J. S., & Wynne-Edwards, K. E. (2000). Paternal hamsters mechanically assist the delivery, consume amniotic fluid and placenta, remove fetal membranes, and provide parental care during the birth process. *Hormones and Behavior*, *37*(2), 116–125. https://doi.org/10.1006/hbeh.1999.1563

Jukic, A. M., Baird, D. D., Weinberg, C. R., McConnaughey, D. R., & Wilcox, A. J. (2013). Length of human pregnancy and contributors to its natural variation. *Human Reproduction*, *28*(10), 2848–2855. https://doi.org/10.1093/humrep/det297

Kaiser, I., & Halberg, F. (1962). Circadian periodic aspects of birth. *Annals of the New York Academy of Sciences*, *98*(4), 1056–1068. https://doi.org/10.1111/j.1749-6632.1962.tb30618.x

Kemps, A., & Timmermans, P. (1982). Parturition behaviour in pluriparous Java-macaques (*Macaca fascicularis*). *Primates*, *23*(1), 75–88. https://doi.org/10.1007/BF02381439

King, P. (1956). Increased frequency of births in the morning hours. *Science*, *123*(3205), 985–986. https://doi.org/10.1126/science.123.3205.985

Kingma, E. (2020). Biological individuality, pregnancy, and (mammalian) reproduction. *Philosophy of Science*, *87*(5), 1037–1048. https://doi.org/10.1086/710612

Kissler, K., & Hurt, K. J. (2023). The pathophysiology of labor dystocia: Theme with variations. *Reproductive Sciences*, *30*(3), 729–742. https://doi.org/10.1007/s43032-022-01018-6

Klingel, H. (1969). Reproduction in the plains zebra, Equus burchelli boehmi: Behavior and ecological factors. *Journal of Reproduction and Fertility*, *6*, 339–345.

Kristal, M. B. (1980). Placentophagia: A biobehavioral enigma (or De gustibus non disputandum est). *Neuroscience and Biobehavioral Reviews*, *4*(2), 141–150. https://doi.org/10.1016/0149-7634(80)90012-3

Kristal, M. B. (1991). Enhancement of opioid-mediated analgesia: A solution to the enigma of placentophagia. *Neuroscience and Biobehavioral Reviews*, *15*, 425–435.

Kristal, M. B., DiPirro, J. M., & Thompson, A. C. (2012). Placentophagia in humans and nonhuman mammals: Causes and consequences. *Ecology of Food and Nutrition*, *51*(3), 177–197. https://doi.org/10.1080/03670244.2012.661325

Kunz, T. H., Allgaier, A. L., Seyjagat, J. & Caligiuri, R. (1994). Allomaternal care: helper-assisted birth in the Rodrigues fruit bat, *Pteropus rodricensis* (Chiroptera: Pteropodidae). *Journal of Zoology*, *232*(4), 691–700. https://doi.org/10.1111/j.1469-7998.1994.tb04622.x

Kustritz, M. V. R. (2005). Reproductive behavior of small animals. *Theriogenology*, *64*(3), 734–746.

Lehrman, D. S. (1961). Hormonal regulation of parental behavior in birds and infrahuman mammals. In W. C. Young (Ed.), *Sex and Internal Secretions.* (Volume 2). Williams and Wilkins.

Lent, P. C. (1966). Calving and related social behavior in the barren-ground caribou. *Zeitschrift Für Tierpsychologie*, *23*, 702–756. https://doi.org/10.2307/3797511

Lent, P. C. (1974). Mother-infant relationships in ungulates. In V. Geist & F. Walther (Eds.), *The Behaviour of Ungulates and its Relation to Management* (pp. 14–55). IUCN Publications.

Leuthold, W. (1977). *African Ungulates: A Comparative Review of their Ethology and Behavioral Ecology.* Springer.

Leuthold, W., & Leuthold, B. M. (1975). Parturition and Related Behaviour in the African Elephant. *Zeitschrift Für Tierpsychologie*, *39*(1–5), 75–84. https://doi.org/10.1111/j.1439-0310.1975.tb00901.x

Li, Y. P., Zhong, T., Huang, Z. P., Pan, R. L., Garber, P. A., Yu, F. Q., & Xiao, W. (2020). Male and female birth attendance and assistance in a species of non-human primate (*Rhinopithecus bieti*). *Behavioural Processes*, *181*(August), 104248. https://doi.org/10.1016/j.beproc.2020.104248

Lincoln, D. W., & Porter, D. G. (1976). Timing of the photoperiod and the hour of birth in Rats. *Nature*, *260*(5554), 780–781. https://doi.org/10.1038/260780a0

Macfarlane, A., Dattani, N., Gibson, R., Harper, G., Martin, P., Scanlon, M., Newburn, M., & Cortina-Borja, M. (2019). Births and their outcomes by time, day and year: a retrospective birth cohort data linkage study. *Health Services and Delivery Research*, *7*(18), 1–268. https://doi.org/10.3310/hsdr07180

Macfarlane, D. (2018). Controversy regarding the obstetric dilemma. *Aisthesis*, *9*, 27–30.

Maestripieri, D., & Call, J. (1996). Mother-infant communication in primates. *Advances in the Study of Behavior*, *25*, 613–642. https://doi.org/https://doi.org/10.1016/S0065-3454(08)60344-7

Malek, J. (1952). The manifestation of biological rhythms in delivery. *Gynaecologia*, *133*, 365–372.

Malkiel, A., Mor, P., Cnn, R. N., Aloni, H. & Gdansky, E. (2008). Primiparity: A traditional intrapartum obstetric risk reconfirmed. *Israel Medical Association Journal*, *10*(July), 508–511.

Mann, J. (2009). Parental behavior. In *Encyclopedia of Marine Mammals* (pp. 830–836).

Manski, D. A. (1991). Reproductive behavior of addax antelope. *Applied Animal Behaviour Science*, *29*(1–4), 39–66. https://doi.org/10.1016/0168-1591(91)90237-R

Marshall, N. E., Abrams, B., Barbour, L. A., Catalano, P., Christian, P., Friedman, J. E., Hay Jr., W. W., Hernandez, T. L., Krebs, N. F., Oken, E., Purnell, J. Q., Roberts, J. M., Soltani, H., Wallace, J., & Thornburg, K. L. (2022). The importance of nutrition in pregnancy and lactation: lifelong consequences. *American Journal of Obstetrics and Gynecology*, *226*(5), 607–632. https://doi.org/10.1016/j.ajog.2021.12.035

Martin, P., Cortina-Borja, M., Newburn, M., Harper, G., Gibson, R., Dodwell, M., Dattani, N., & Macfarlane, A. (2018). Timing of singleton births by onset of labour and mode of birth in NHS maternity units in England, 2005–2014: A study of linked birth registration, birth notification, and hospital episode data. *PLoS ONE*, *13*(6), 2005–2014. https://doi.org/10.1371/journal.pone.0198183

Martínez-Burnes, J., Muns, R., Barrios-García, H., Villanueva-García, D., Domínguez-Oliva, A., & Mota-Rojas, D. (2021). Parturition in mammals: Animal models, pain and distress. *Animals*, *11*(10), 1–26. https://doi.org/10.3390/ani11102960

Mathews, T. J., & Curtin, S. (2015). When are babies born: morning, noon, or night? Birth certificate data for 2013. *NCHS Data Brief*, *200*, 1–7.

McGuire, B., Henyey, E., McCue, E., & Bemis, W. E. (2003). Parental behavior at parturition in prairie voles (*Microtus ochrogaster*). *Journal of Mammalogy*, *84*(2), 513–523. https://doi.org/10.1644/1545-1542(2003)084<0513:PBAPIP>2.0.CO;2

McKnight, B. L. (1992). Birth of an African elephant in Tsavo East National Park, Kenya. *African Journal of Ecology*, *30*, 87–89. https://doi.org/10.1111/j.1365-2028.1997.095-89095.x

Monsó, S., & Osuna-Mascaró, A. J. (2021). Death is common, so is understanding it: The concept of death in other species. *Synthese, 199,* 2251–2275.

Moreno, L. I., Salas, I. C., & Glander, K. E. (1991). Breech delivery and birth-related behaviors in wild mantled howling monkeys. *American Journal of Primatology*, *23*(3), 197–199. https://doi.org/10.1002/ajp.1350230306

Mota-Rojas, D., Orihuela, A., Strappini, A., Villanueva-García, D., Napolitano, F., Mora-Medina, P., Barrios-García, H. B., Herrera, Y., Lavalle, E., & Martínez-Burnes, J. (2020). Consumption of maternal placenta in humans and nonhuman mammals: Beneficial and adverse effects. *Animals*, *10*(12), 1–16. https://doi.org/10.3390/ani10122398

Nakamichi, M., IImakawa, S., Kojima, Y., & Natsume, A. (1992). Parturition in a free-ranging Japanese monkey (*Macaca fuscata*). *Primates, 33*(3), 413–418.

Natterson-Horowitz, B., Boddy, A. M., & Zimmerman, D. (2022). Female health across the tree of life: Insights at the interaction of women's health, one health and planetary health. *PNAS Nexus*, *1*(2), 1–7. https://doi.org/10.1093/pnasnexus/pgac044

Nesheim, B. (1988). Duration of labor. *Acta Obstetricia et Gynecologica Scandinavica*, *67*, 121–124.

Nguyen, N., Lee, L. M., Fashing, P. J., Nurmi, N. O., Stewart, K. M., Turner, T. J., Barry, T. S., Callingham, K. R., Goodale, C. B., Kellogg, B. S., Burke, R. J., Bechtold, E. K., Claase, M. J., Eriksen, G. A., Jones, S. C. Z., Kerby, J. T., Kraus, J. B., Miller, C. M., Trew, T. H., Zhao, Y., Beierschmitt, E.C., Ramsay, M.S., Reynolds, J.D., & Venkataraman, V. V. (2017). 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. *American Journal of Physical Anthropology*, *163*(1), 14–29. https://doi.org/10.1002/ajpa.23141

Nichols, L. (2018). *Real Food for Pregnancy: The Science and Wisdom of Optimal Prenatal Nutrition*. Lily Nichols.

Noakes, D. E., Parkinson, T. J., & England, G. C. (Eds.). (2001). *Arthur's Veterinary Reproduction and Obstetrics*. Harcourt Publishers Ltd.

Notarbartolo-Di-Sciara, G., Barbaccia, G., & Azzellino, A. (1997). Birth at sea of a false killer whale, *Pseudorca crassidens*. *Marine Mammal Science*, *13*(3), 508–511. https://doi.org/10.1111/j.1748-7692.1997.tb00660.x

Ober, W. B. (1979). Notes on placentophagy. *Bulletin of the New York Academy of Medicine: Journal of Urban Health*, *55*(6), 591–599.

Olcese, J., Lozier, S., & Paradise, C. (2013). Melatonin and the circadian timing of human parturition. *Reproductive Sciences*, *20*(2), 168–174. https://doi.org/10.1177/1933719112442244

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science*, *293*(5530), 690–693. https://doi.org/10.1126/science.1062320

Pan, W., Gu, T., Pan, Y., Feng, C., Long, Y., Zhao, Y., Meng, H., Liang, Z., & Yao, M. (2014). Birth intervention and non-maternal infant-handling during parturition in a nonhuman primate. *Primates*, *55*(4), 483–488. https://doi.org/10.1007/s10329-014-0427-1

Peker, S., Kowalewski, M. M., Pavé, R. E., & Zunino, G. E. (2009). Births in wild black and gold howler monkeys (*Alouatta caraya*) in northern Argentina. *American Journal of Primatology*, *71*(3), 261–265. https://doi.org/10.1002/ajp.20643

Price, E. C. (1990). Parturition and perinatal behaviour in captive cotton-top tamarins (*Saguinus oedipus*). *Primates*, *31*(4), 523–535. https://doi.org/10.1007/BF02382535

Purohit, G. (2010). Parturition in domestic animals: A review. *WebmedCentral: Reproduction*, *1*(10), WMC00748.

Ransome, N., Bejder, L., Jenner, M., Penfold, G., Brosig, V. J., Kitson, C., Skjothaug, R., Neilson, E., Loneragan, N. R., & Smith, J. N. (2022). Observations of parturition in humpback whales (*Megaptera novaeangliae*) and occurrence of escorting and competitive behavior around birthing females. *Marine Mammal Science*, *38*(2), 408–432. https://doi.org/10.1111/mms.12864

Reidenberg, J. S., & Laitman, J. T. (2009). Cetacean prenatal development. In W. F. Perrin, B. Würsig & J. G. M. Thewissen (Eds.), *Encyclopedia of Marine Mammals* 2nd edition, pp. 220–230. Academic Press.

Roberts, S. J. (2005). *Veterinary Obstetrics and Genital Diseases*. CBS Publishers & Distributors.

Rosenberg, K., & Trevathan, W. R. (2002). Birth, obstetrics and human evolution. *BJOG: An International Journal of Obstetrics and Gynaecology*, *109*(11), 1199–1206. https://doi.org/10.1046/j.1471-0528.2002.00010.x

Rosenbloom, J. I., Rottenstreich, A., Yagel, S., Sompolinksy, Y., & Levin, G. (2020). The length of the second stage of labor in nulliparous, multiparous, grand-multiparous, and grand-grand multiparous women in a large modern cohort. *European Journal of Obstetrics and Gynecology and Reproductive Biology*, *253*, 273–277. https://doi.org/10.1016/j.ejogrb.2020.08.029

Rossdale, P. D., & Short, R. V. (1967). The time of foaling of thoroughbred mares. *Journal of Reproduction and Fertility*, *13*(2), 341–343. https://doi.org/10.1530/jrf.0.0130341

Sauther, M. L. (1991). Reproductive behavior of free-ranging Lemur catta at Beza Mahafly Special Reserve, Madagascar. *American Journal of Physical Anthropology*, *84*, 463–477. https://doi.org/10.1002/ajpa.1330840409

Sauther, M. L. (1994). Wild plant use by pregnant and lactating ringtailed lemurs with implications for early hominid foraging. In *Eating on the Wild Side* (pp. 240–256). The University of Arizona Press.

Schlabritz-Loutsevitch, N., Maher, J., Sullivan, R., Mari, G., Schenone, M., Cohen, H. L., Word, R. A., Hubbard, G. B., & Dick, E. J. (2018). Parturition in baboons (*Papio* spp.). *Scientific Reports*, *8*(1), 8–13. https://doi.org/10.1038/s41598-018-19221-4

Schmidt, M. J. (1999). Calving elephants. In M. E. Fowler & R. E. Miller (Eds.), *Fowler's Zoo and Wild Animal Medicine* (pp. 521–522). W. B. Saunders.

Scott, K. D., Klaus, P. H., & Klaus, M. H. (1999). The obstetrical and postpartum benefits of continuous support during childbirth. *Journal of Women's Health and Gender-Based Medicine*, *8*(10), 1257–1264. https://doi.org/10.1089/jwh.1.1999.8.1257

Selander, J., Cantor, A., Young, S. M., & Benyshek, D. C. (2013). Human maternal placentophagy: A survey of self-reported motivations and experiences associated with placenta consumption. *Ecology of Food and Nutrition*, *52*(2), 93–115. https://doi.org/10.1080/03670244.2012.719356

Senger, P. L. (2015). *Pathways to Pregnancy and Parturition* (3rd ed.). Current Conceptions Inc.

Sharkey, J. T., Puttaramu, R., Word, R. A., & Olcese, J. (2009). Melatonin synergizes with oxytocin to enhance contractility of human myometrial smooth muscle cells. *The Journal of Clinical Endocrinology & Metabolism*, *94*, 421–427. https://doi.org/10.1210/jc.2008-1723

Sherman, P. W., & Flaxman, S. M. (2002). Nausea and vomiting of pregnancy in an evolutionary perspective. *American Journal of Obstetrics and Gynecology*, *186*(5), S190–S197. https://doi.org/10.1067/mob.2002.122593

Shettles, L. S. (1960). Hourly variation in onset of labor and rupture of membranes. *American Journal of Obstetrics and Gynecology*, *79*, 177–179. https://doi.org/10.1016/0002-9378(60)90382-3

Shurkin, J. (2014). Animals that self-medicate. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(49), 17339–17341. https://doi.org/10.1073/pnas.1419966111

Sidzinska, M. (2017). Not one, not two: Toward an ontology of pregnancy. *Feminist Philosophy Quarterly*, *3*(4), 1–22. https://doi.org/10.5206/fpq/2017.4.2

Slijper, E. J. (1949). On some phenomena concerning pregnancy and parturition of the Cetacea. *Bijdragen Tot de Dierkunde*, *28*(1), 416–448. https://doi.org/10.1163/26660644-02801049

Souza, J. P., Day, L. T., Rezende-Gomes, A. C., Zhang, J., Mori, R., Baguiya, A., Jayaratne, K., Osoti, A., Vogel, J. P., Campbell, O., Mugerwa, K. Y., Lumbiganon, P., Tunçalp, Ö., Cresswell, J., Say, L., Moran, A. C., & Oladapo, O. T. (2024). A global analysis of the determinants of maternal health and transitions in maternal mortality. *The Lancet Global Health*, *12*(2), e306–e316. https://doi.org/10.1016/S2214-109X(23)00468-0

Stacey, P. J., & Baird, R. W. (1997). Birth of a "resident" killer whale off Victoria, British Columbia, Canada. *Marine Mammal Science*, *13*(3), 504–508. https://doi.org/10.1111/j.1748-7692.1997.tb00659.x

Steinmetz, A. R., Abrams, E. T., & Young, S. L. (2012). Patterns of nausea, vomiting, aversions, and cravings during pregnancy on Pemba Island, Zanzibar, Tanzania. *Ecology of Food and Nutrition*, *51*(5), 418–430. https://doi.org/10.1080/03670244.2012.696011

Stewart, K. J. (1977). The birth of a wild mountain gorilla (*Gorilla gorilla beringei*). *Primates*, *18*(4), 965–976.

Timmermans, P. J. A., & Vossen, J. M. H. (1996). The influence of repeated motherhood on periparturitional behavior in Cynomolgus macaques (*Macaca fascicularis*). *International Journal of Primatology*, *17*(2), 277–296. https://doi.org/https://doi.org/10.1007/BF02735453

Tinklepaugh, O. L., & Hartman, C. G. (1930). Behavioral aspects of parturition in the monkey (*Macacus rhesus*). *Journal of Comparative Psychology*, *11*(1), 63–98. https://doi.org/10.1037/h0070309

Trevathan, W. R. (1987). *Human Birth: An Evolutionary Perspective*. Aldine de Gruyter.

Turner, S. E., Fedigan, L. M., Nakamichi, M., Matthews, H. D., McKenna, K., Nobuhara, H., Nobuhara, T. & Shimizu, K. (2010). Birth in free-ranging *Macaca fuscata*. *International Journal of Primatology*, *31*(1), 15–37. https://doi.org/10.1007/s10764-009-9376-8

Vahratian, A., Hoffman, M. K., Troendle, J. F., & Zhang, J. (2006). The impact of parity on course of labor in a contemporary population. *Birth*, *33*(1), 12–17. https://doi.org/10.1111/j.0730-7659.2006.00069.x

Vasey, N. (2000). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*. I. Interspecific patterns. *American Journal of Physical Anthropology*, *112*,411–431. https://doi.org/10.1002/1096-8644(200007)112:3<411::AID-AJPA10>3.0.CO;2-R

Vasey, N. (2002). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*. II. Intraspecific patterns. *American Journal of Physical Anthropology*, *118*, 169–183. https://doi.org/10.1002/ajpa.10054Digit

Vieu, S., Hugon, H., Boucher, S., Bercker, C., Bruyas, J. F., & Fusellier, M. (2024). Assessing pubic symphysis evolution in guinea pigs (*Cavia procellus*): Insights from computer tomography on primiparous and non-breeding females. *Veterinary Medicine and Science*, *10*(6), e70076. https://doi.org/10.1002/vms3.70076

Viswanathan, N., & Davis, F. C. (1992). Timing of birth in Syrian hamsters. *Biology of Reproduction*, *47*(1), 6–10. https://doi.org/10.1095/biolreprod47.1.6

Waldenström, U. (1999). Experience of labor and birth in 1111 women. *Journal of Psychosomatic Research*, *47*(5), 471–482. https://doi.org/10.1016/S0022-3999(99)00043-4

Watanabe, J., Wakaguri, H., Sasaki, M., Suzuki, Y., & Sugano, S. (2007). Comparasite: A database for comparative study of transcriptomes of parasites defined by full-length cDNAs. *Nucleic Acids Research*, *35*, D431–D438. https://doi.org/10.1093/nar/gkl1039

Weilgart, L. S., & Whitehead, H. (1986). Observations of a sperm whale (*Physeter catodon*) birth. *Journal of Mammalogy*, *67*(2), 399–401. https://doi.org/10.2307/1380896

Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, *372*(6537). https://doi.org/10.1126/SCIENCE.ABE6514

WHO. (2023). *Trends in maternal mortality 2000 to 2020: Estimates by WHO, UNICEF, UNFPA, World Bank Group and UNDESA/Population Division*. https://www.who.int/reproductivehealth/publications/maternal-mortality-2000-2017/en/

Wild, C. A., & Yon, L. (2024). Commentary on the adaptive significance of sociality around parturition events, and conspecific support of parturient females in some social mammals. *Animals*, *14*(24), 1–22. https://doi.org/10.3390/ani14243601

Wolf, J. B., & Wade, M. J. (2009). What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1520), 1107–1115. https://doi.org/10.1098/rstb.2008.0238

Yang, B., Zhang, P., Huang, K., Garber, P. A., & Li, B. G. (2016). Daytime birth and postbirth behavior of wild *Rhinopithecus roxellana* in the Qinling Mountains of China. *Primates*, *57*(2), 155–160. https://doi.org/10.1007/s10329-015-0506-y

Young, S. M., & Benyshek, D. C. (2010). In search of human placentophagy: A cross-cultural survey of human placenta consumption, disposal practices, and cultural beliefs. *Ecology of Food and Nutrition*, *49*(6), 467–484. https://doi.org/10.1080/03670244.2010.524106

Zani, M. A., Taylor, J. K. D., & Kraus, S. D. (2008). Observation of a right whale (*Eubalaena glacialis*) birth in the coastal waters of the Southeast United States. *Aquatic Mammals*, *34*(1), 21–24. https://doi.org/10.1578/AM.34.1.2008.21

Zeller, U., Ferner, K., Göttert, T., & Starik, N. (2018). Eutherians: placental mammals. In M. K. Skinner (Ed.), *Encyclopedia of Reproduction* (pp. 617-624.). Academic Press.

Zhang, X., Tong, B., Gu, H., Wang, L., Wu, J., & Yu, X. (1997). Comparison of evaluation methods on changes of facial microcirculation during induction of motion sickness. *Space Medicine & Medical Engineering*, *10*(3), 182–176