

Chapter 6

Hormones and pregnancy in eutherian mammals

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ABBREVIATIONS

5α-DHPs	5-alpha reduced progestins
CG	chorionic gonadotropin
CL	corpus luteum
IGF	insulin-like growth factor
LH	luteinizing hormone

1 INTRODUCTION

To both provide a general view of gestational endocrinology in mammals and highlight the considerable diversity among mammalian lineages, we have structured this chapter into two broad sections. The first section, The Generalized Mammalian Pregnancy, covers the majority of gestational endocrinology, including mechanisms of pregnancy recognition and placental diversity. In the second section, Comparative Endocrinology and Physiology of Gestation, we review gestational endocrinology in each order of eutherian mammals (see Fig. 1), focusing primarily on aspects of gestational physiology that are notable or diverse within each. Together, these sections aim to provide readers with an introduction to the terminology of gestational physiology and highlight traits that vary among eutherian mammals. This chapter is not exhaustive and generalizes, especially with respect to the biology of individual species. Our discussion is notably limited by model organisms that are the focus of most biomedical and agricultural research and thus for which the most mechanistic reproductive biology is known. By reviewing the literature that currently exists across all eutherians, we outline areas where additional investigation is needed to expand our understanding of the hormones and cellular mechanisms that control eutherian gestation.

2 THE GENERALIZED MAMMALIAN PREGNANCY

2.1 The major endocrine organs of gestation: The ovary, the uterus, and the placenta

A successful pregnancy depends on intimate and dynamic interactions between two genetically-distinct individuals: the gestating parent and the fetus. Both individuals contribute to hormone production across gestation and both are important parts of gestational endocrinology. The predominant endocrine organs from the gestational parent include the ovaries and the uterus, though their function depends on endocrine input from other parts of the maternal endocrine system (namely, the hypothalamo-pituitary-gonadal axis) (Grant et al., 2018). Within the ovaries, gestational hormones are primarily derived from ovarian corpora lutea (CLs) (see Chapter 5 in this volume). In the uterus, gestational hormones are produced by the endometrium, the lining of the uterus that is directly involved in implantation. Although the fetus also makes important endocrine contributions, the majority of fetal contributions to the endocrine milieu (specifically, glucocorticoids derived from fetal adrenal glands) occurs during late gestation and is involved in parturition, and thus, we do not discuss this further here (see Chapter 7 in this volume for further details).

Both the gestational parent and the fetus contribute to what is arguably the most dynamic gestational endocrine organ: the placenta. Although we will focus on the endocrine role of the placenta in this chapter, the placenta is multipurpose. To support fetal growth, the placenta is also responsible for nutrient and gas exchange, which is accomplished using a combination of active transport and passive diffusion to move solutes from maternal circulation into fetal circulation and vice versa. As such, each fetus develops its own

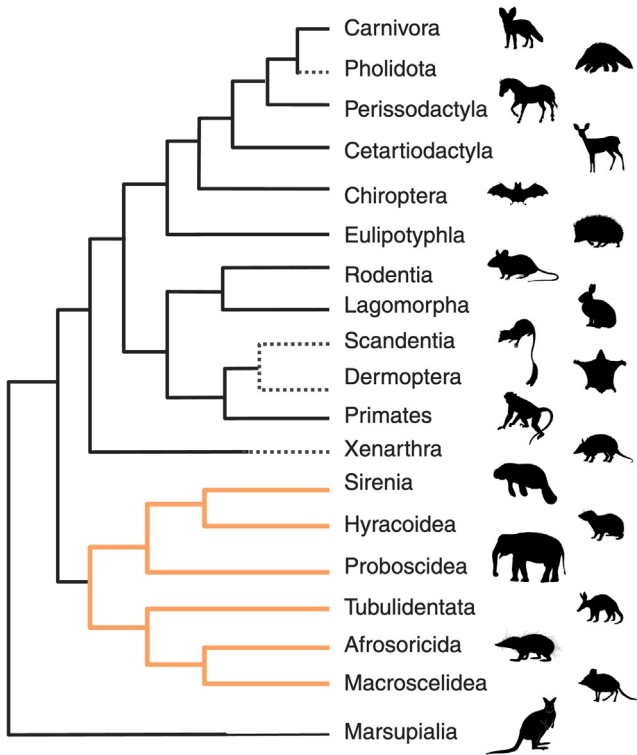


FIG. 1 Phylogeny of eutherian mammals showing relationships among orders discussed in this chapter. Orange lineages are discussed under the broad superorder Afrotheria. Dashed tips indicate orders where little information is available on gestational endocrinology. (Created with *Biorender.com*.)

placenta (except in the case of monozygotic multiples), which ensures each fetus is sufficiently supported. In general, the placenta does not begin to perform nutrient and gas exchange until mid-to-late gestation. As such, early development of the placenta generally focuses on functional maturation of endocrine structures and structural development of exchange structures, whereas later gestation emphasizes remodeling and expansion of these exchange structures. As such, the placenta continually changes across gestation.

The endocrine function of the placenta is primarily directed at modifying the physiology of the gestating parent, which is similarly dynamic. During the first half to two-thirds of gestation, the parental-fetal unit can be characterized by anabolism within the parental compartment. The gestating parent usually experiences dramatic growth and remodeling of major organs (including the liver, spleen, and gut) in preparation for the intensive final period of fetal growth and postnatal development (Napso et al., 2018). The second one-half to one-third of gestation is generally catabolic for the gestational parent; energy is mobilized and targeted to the fetus for rapid growth. Placental and (during late gestation) fetal hormones play a major role in driving these changes. As such, we expect variation in the duration of gestation and relative development at birth to be associated

with variation in the pattern of hormone production across gestation, as well as placental development dynamics. For example, the more altricial house mouse (*Mus musculus*) placenta near term resembles the more precocial human placenta during the second trimester, at least in its transcriptional landscape (Roberts et al., 2016). When comparing gestational physiology and endocrinology across groups, these developmental differences are thus important to keep in mind.

Beyond functional variation tied to development at birth, placental structure is highly variable among eutherian mammals (Fig. 2). In general, the factors that have driven diversification in eutherian placental structure are poorly understood (Schulkin & Power, 2012). However, variation in placental structure corresponds to some important functional variation (including immune function and cancer risk) (Wagner et al., 2022), and thus, we call attention to this diversity and discuss key terminology here.

The first axis of variation among placentas is in their macro-level structure. Eutherian placentas can be discoid (similar to humans), zonary (in which the placenta extends in a band around the entire fetus), cotyledonary (in which the placenta consists of many small cotyledons which superficially resemble mini discoid placentas), or diffuse (in which the entire chorion is vascularized and performs placental functions) (Fig. 2). Bidiscoid placentas, in which species have two, discoid placentas, are relatively common as well although it is not considered a distinct “type.” These macro-level structural variants are less important for determining the degree of immune interactions and other lineage-related traits; however, they are often phylogenetically concordant with microstructural terms discussed later and thus may be useful starting points for understanding placental development and structure among species.

The second and third axes of placenta diversity describe levels of placental “invasion,” either referring to the extent to which fetal cells erode maternal cell layers (i.e., epithelial and endothelial cell layers) and thus come into direct contact with maternal blood (as shown in Fig. 2), or the degree to which fetal cells enter and alter maternal tissues. The erosion of maternal cell layers is generally prerequisite to more significant invasion and remodeling of maternal tissues. Guinea pigs and humans display extensive invasion by fetal cells, which enter and remodel deep uterine vasculature. The extent to which similar invasion and remodeling occurs is more limited among other rodents, including mice and rats, and more extreme in primates. The discoid, hemochorial placenta, where in maternal blood is in direct contact with fetal tissues and thus significant immune suppression is required, is thought to be the ancestral placenta type among eutherian mammals (Roberts et al., 2016; Wildman et al., 2006).

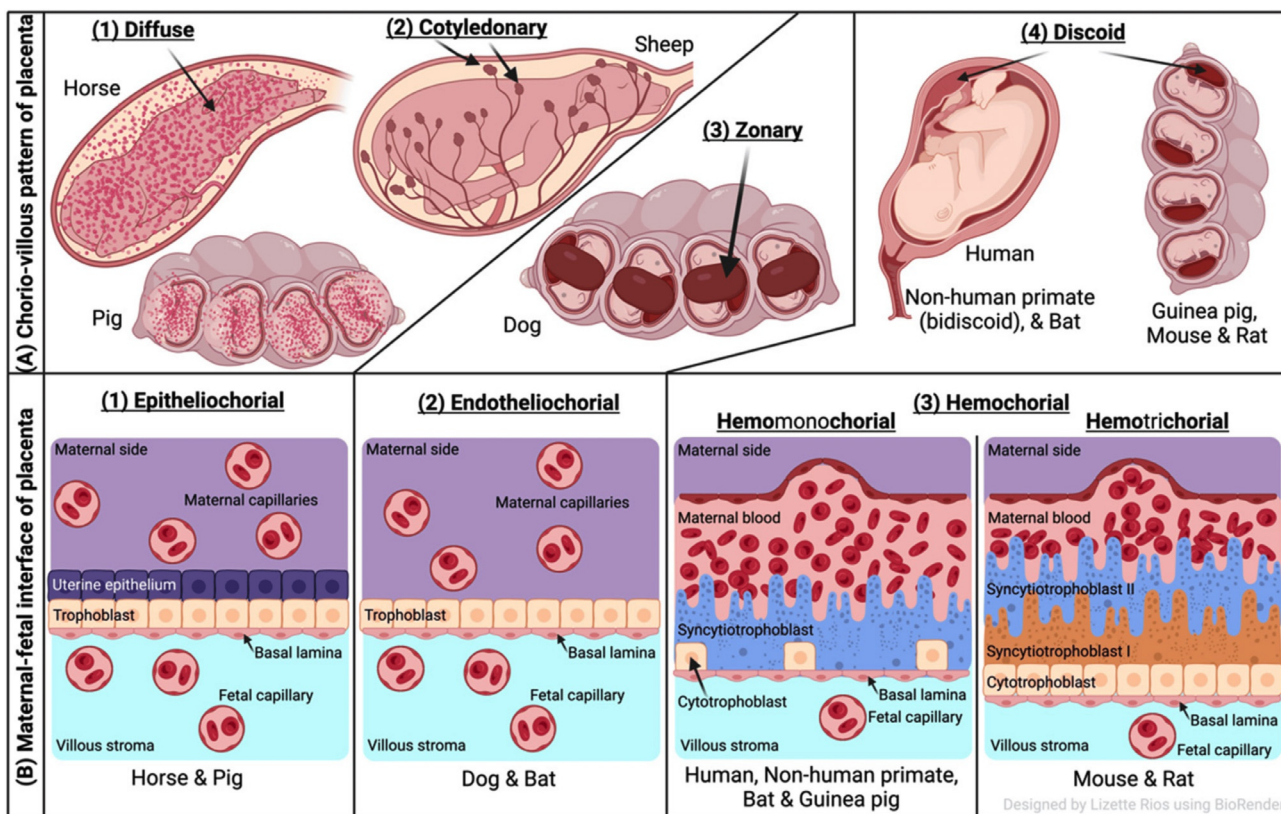


FIG. 2 A visual diagram illustrating placental diversity among eutherian mammals. See text for explanation of placental types. (Reprinted from Avalos-Borges, E. E., Rios, L. E., Jiménez-Coello, M., Ortega-Pacheco, A., & Garg, N. J. (2022). Animal models of *Trypanosoma cruzi* congenital transmission. *Pathogens*, 11(10), 1172.)

The portion of the placenta responsible for endocrine hormone production varies with placental structure. Single-nuclei sequencing and other new technologies are still discovering and resolving the many unique placental cell types that contribute to endocrine and immune regulation, and there appears to be significant variation across eutherian mammals (Davenport et al., 2023; Liu et al., 2018; Marsh & Blelloch, 2020). However, the major hormones are similar and thus we can cogently discuss the endocrinology without focusing on the complexity of the many cell types responsible for their production.

2.2 The major hormones of pregnancy

In line with the common endocrine organs of pregnancy, there are several key hormones that perform broadly conserved functions, are derived from similar structures, and display similar profiles across gestation in eutherian mammals. Bazer and Spencer (2011) included extensive details about the molecular mechanisms by which these hormones modify maternal tissues and fetal development. Here, we focus on the biological role of these hormones and their general patterns across gestation.

2.2.1 Sex steroids (progestogens and estrogens)

Progestogens and estrogens are the two primary groups of sex steroids involved in gestational endocrinology. The primary progestogen is usually progesterone (often abbreviated as P₄), which is essential for pregnancy progression as its action is usually permissive for many of the other hormones that coordinate broader physiological changes. For example, progesterone is a major product of placental steroid hormone synthesis, and it is essential to maintain gestational physiology (Morel et al., 2016; Noyola-Martínez et al., 2019). Progesterone is thus typically maintained at elevated concentrations (relative to those found in nonpregnant females) during gestation, with a peak in progesterone occurring during late gestation just prior to degradation of the placenta.

Progesterone is initially derived from corpora lutea (CLs) and/or accessory structures in the ovary, with a transition to placental progesterone later in gestation. The timing of this transition is highly variable among mammals, with some species requiring ovarian progesterone throughout gestation. Estrogens generally follow progesterone, increasing across gestation and transitioning to predominant

production from the placenta later in the gestation. Although not considered essential in the same way that progesterone is, estrogens contribute to the maintenance of the uterine lining, fetal growth and development, and mammary development and maturation during late gestation. In humans, the placenta predominantly produces estriol (often abbreviated as E_3), which is otherwise undetectable in nonpregnant individuals. Although estriol has relatively weak estrogenic activity compared to estradiol (often abbreviated as E_2), it also interacts weakly with binding globulins (particularly sex hormone-binding globulin) relative to estradiol, and thus, estriol exerts greater biological activity during gestation. Assessments of estrogens other than E_2 in nonhuman mammals are rare.

2.2.2 Relaxin

Relaxin is a peptide hormone related to insulin and the insulin-like growth factors (IGFs) and is produced by the ovary (particularly the CL) and the endometrium throughout pregnancy. However, its abundance in circulation increases predominantly during late gestation. Relaxin is best known for its role in relaxing the pubic symphysis for labor (Jelinic et al., 2018); however, relaxin has also been implicated in pregnancy establishment, blood volume expansion, and osmoregulatory adaptations to pregnancy (Choi et al., 2009; Doan et al., 2022; Marshall et al., 2017). Most of these effects are also supported by steroid hormones such that the absence of relaxin (via genetic knockout) does not cause gestational failure, at least in rodents (Samuel et al., 2005). Increased relaxin during late pregnancy also contributes to maturation of the mammary glands (e.g., in rats, mice, pigs, and humans) (Goldsmith, 2013; Hurley, 2019; Klein, 2016; Sherwood, 2004).

2.2.3 Placental lactogens

Placental lactogens, also termed chorionic somatotropins in some groups, are related in structure and function to growth hormone and prolactin, depending on the species (reviewed in Kelly et al., 1991; Nicoll et al., 1986; Soares, 2004). As implied by their name, placental lactogens are produced by the placenta. These hormones play a broad role and are involved in maintaining CLs in some mammals, modifying the metabolic state of the gestating parent during pregnancy to facilitate transfer of nutrients to the conceptus, and mammary gland maturation (Ben-Jonathan et al., 2008; Soares et al., 2007). The actions of placental lactogens are mediated by prolactin and growth hormone receptors, which may form homo- or hetero-dimers. Production of placental lactogens increases steadily throughout gestation in association with placental growth, with its peak production near parturition.

2.3 Putting the pieces together: Gestation as a dynamic physiological state

Now that we have introduced the major organs and hormones of pregnancy, we can discuss the significant endocrine events in pregnancy. The first step for successful gestation is the maternal recognition of pregnancy, wherein physiology of the gestational parent “recognizes” that viable blastocysts are present. Generally, this physiological recognition of pregnancy serves to preserve progesterone production by CLs in the ovary. However, the lifetime of CLs in the ovary is limited by production of an endometrium-derived hormone-like lipid, prostaglandins, which are produced in response to CL-derived progesterone. Through the process of luteolysis, prostaglandins drive the degradation of the CLs and thus determines their lifespan. The result of this feedback cycle is that CLs naturally degrade following ovulation, leading to progesterone and estrogen withdrawal in the uterine lining, which renders the uterine lining unreceptive to implantation and/or inhibits other changes that must occur to support early fetal growth. This cycle is highly effective at maintaining cyclicity in individuals that are not pregnant, but it necessitates some physiological recognition of gestation to interrupt the cycle and permit gestation.

In most mammals, physiological recognition of pregnancy occurs via blastocyst-derived signals that are either luteotropic (meaning that they act positively on the CL to promote its growth and function) or antiluteolytic (meaning that they counteract the activity of prostaglandins and instead inhibit degradation of the CLs). The end result is similar: CLs remain viable and steroidogenic. Luteotropic signals are usually pituitary-like hormones produced by the embryo and/or early placenta and are either placental gonadotropins (e.g., human chorionic gonadotropin, hCG) or lactogens (e.g., placental prolactins, in rodents). Antiluteolytic signals are usually blastocyst-derived estrogens and/or prolactins (many ungulates) or interferon tau (ruminants only) (Bazer et al., 2018).

As part of the physiological recognition of pregnancy, the uterine lining begins to become receptive to implantation. Uterine preparation for implantation and the onset of receptivity to a blastocyst (or early-stage embryo) is termed decidualization and involves progesterone and estrogen-dependent proliferation of the uterine lining (i.e., the endometrium). A more detailed anatomy of decidualization is shown in Fig. 3.

The timing and extent to which this occurs differs between menstruating and nonmenstruating mammals. In nonmenstruating mammals, decidualization primarily occurs after physiological recognition of pregnancy has occurred. In contrast, among menstruating mammals, decidualization

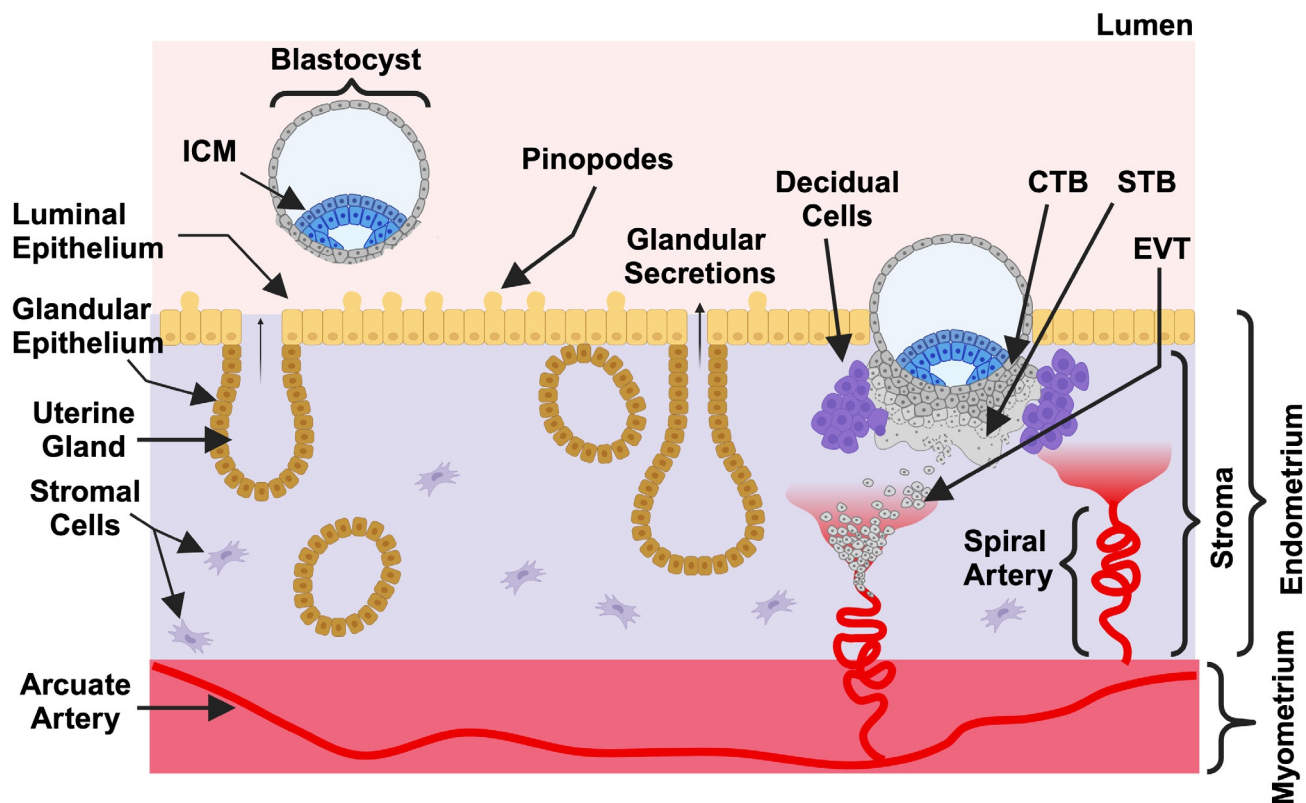


FIG. 3 A general diagram illustrating the early processes of decidualization and blastocyst implantation in the uterus. Following initial entry into the uterus, the blastocyst is supported by histotrophic nutrition via glandular secretions from the uterine glands. Eventually, the blastocyst will implant and degrade the luminal epithelium (yellow). In mammals that do not exhibit spontaneous decidualization, decidualization will occur at the site of implantation. Decidualized cells are derived from stromal cells (shown in purple) in the endometrium. As part of implantation, extravillous trophoblasts (EVT), a specialized cell type derived from the blastocyst, will begin to invade into the endometrium and syncytiotrophoblasts (STB), another trophoblast subtype from the blastocyst, will begin to remodel local vasculature via the spiral arteries. The fetus will arise from the inner cell mass (ICM). Cytotrophoblasts (CTB), which will develop into other portions of the placenta, are also shown. (Created with [Biorender.com](https://www.biorender.com).)

is spontaneous and thus begins immediately following ovulation without needing signals from a viable blastocyst. The physiological recognition of pregnancy instead serves to preserve this lining; without a viable blastocyst producing factors that drive maternal recognition of pregnancy, the decidualized endometrium experiences hormonal withdrawal as estrogen and progesterone production of the CL decreases, and the lining is shed (i.e., menstruation). Although relatively rare, menstruation is found across the mammalian phylogeny, including in primates (including humans and some Old World and New World monkeys), elephant shrews, bats, and spiny mice (Bellofiore et al., 2017; Emera et al., 2012; Rasweiler IV, 1991; Rasweiler & De Bonilla, 1992; Siriwardena & Boroviak, 2022; Zhang et al., 2014).

Successful decidualization is essential for successful implantation, in which the blastocyst engages with and may “invade” endometrial tissues. Successful implantation usually involves careful local regulation of the gestational parent’s immune system, by both parental and fetal factors, to prevent rejection of the embryo (Fujiwara et al., 2016;

Yoshinaga, 2008). Once implantation is complete and pregnancy recognition is established, placental development can accelerate. However, the process of placentation, or placental development, still takes considerable time. Thus, this major organ responsible for supporting fetal growth does not usually begin to facilitate circulatory system-mediated nutrient exchange until nearly halfway through gestation. Instead, early growth of the conceptus (both prior to, during, and following implantation) is supported by histotroph secreted from the endometrial glands (Burton et al., 2020) (Fig. 3). Although historically thought to be limited to some eutherian groups, it is now generally accepted that histotrophic nutrition is a feature of early conceptus development in all mammalian pregnancies (Burton et al., 2020). Histotroph secretion is dependent on a combination of placental lactogens, progesterone, and estrogens, and thus, the endocrinological milieu produced by the blastocyst and CLs (if still functional) directly supports nutrient transfer to the developing conceptus.

Once the implantation site is established and the placenta has developed endocrine capacity, the placenta usually

takes over progesterone production from CL. In some mammals, this is relatively early in gestation; however, others require CL progesterone production throughout gestation (see Section 3 for examples). Placental development and maturation also generally leads to a broader increase in circulating hormone concentrations in the gestational parent, which serves to remodel parental physiology as

mentioned in Section 2.1. However, it is worth reiterating that gestational endocrinology remains dynamic and it varies considerably across mammals. For example, the peak of progesterone in the circulation of the gestating parent may occur during early, middle, or late gestation, depending on the species (Fig. 4). In some cases, the biology that underlies these species-specific dynamics are known,

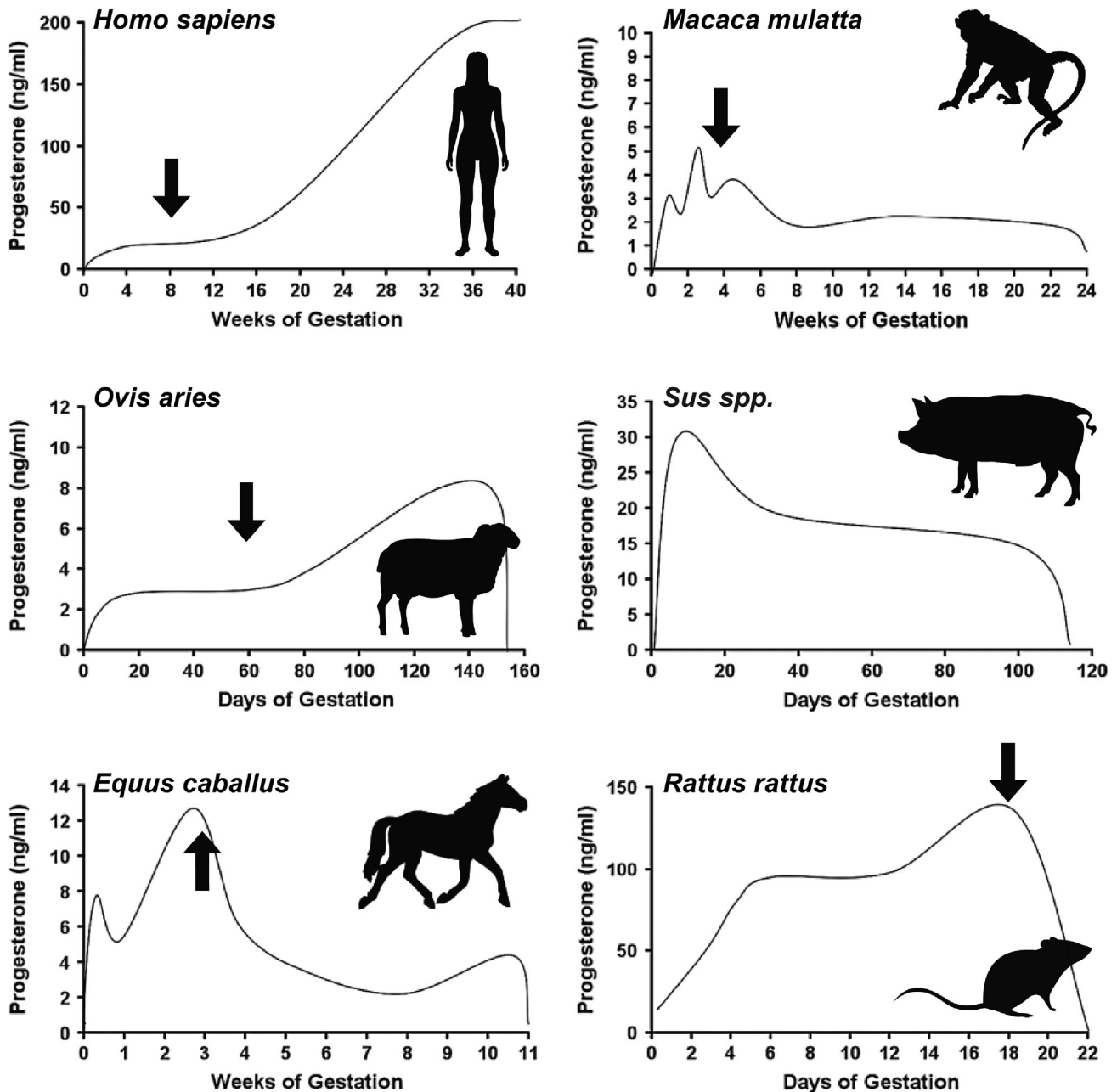


FIG. 4 Patterns of change in concentrations of circulating progesterone throughout pregnancy in different mammals. The scientific name of each species is indicated the top left of each panel. The *solid arrow* indicates the time at which progesterone is no longer predominantly secreted by the ovarian CL. (Adapted from Bazer, F. W., & Spencer, T. E. (2011). Chapter 5 - Hormones and pregnancy in eutherian mammals. In D. O. Norris & K. H. Lopez, eds. Hormones and reproduction of vertebrates (pp. 73–94). London: Academic Press. <https://www.sciencedirect.com/science/article/pii/B9780123749284100057> (17 August 2023).)

however in many groups these dynamics are not well-understood or relatively uncharacterized, pointing to opportunity for future study. These specifics are mentioned in Sections 3.1–3.10 in this chapter.

2.4 A note on pseudo-pregnancy

Pseudo-pregnancy describes a physiological state in which a functional CL persists in the absence of a viable blastocyst or conceptus, generating an endocrinological and behavioral profile similar to that observed during pregnancy. For mammals that are largely studied using noninvasive methods (particularly in zoos or conservation settings), pseudo-pregnancy creates significant challenges for identifying pregnancy and studying early development or gestational failure. The occurrence of pseudo-pregnancy among eutherian mammals is often associated with physical stimulation of the vagina or perineal area, and thus it is particularly common in induced ovulators, which require physical stimulation for ovulation.

3 COMPARATIVE ENDOCRINOLOGY OF PREGNANCY IN EUTHERIAN MAMMALS

In each of these groups, we describe the ovulation type (induced vs. spontaneous) and placental structure, when known, because these features are usually linked to variation in gestational endocrinology. In some cases, these associations are well-characterized. However, we include this information even when connections to gestational endocrinology are not known to provide readers with some direction for expected variation therein. We also include mention of offspring number and gestation duration, which also correlate with gestational endocrinological traits, as discussed in Section 2. After laying out these general traits, we focus on unique aspects of their gestational endocrinology or biology, including the signals involved in physiological recognition of pregnancy, and any ecological traits of the group that are relevant to considering their gestational endocrinology and physiology.

3.1 Primates

Ovulation among primates is generally spontaneous, and spontaneous decidualization (along with menstruation) is more common in this group than any other mammalian orders. Placentation is diverse among primates, particularly within Old World monkeys. In macaques and tarsiers, the placenta shape is discoid or bidiscoid, and placentation is hemochorial. In contrast, strepsirrhine primates generally have diffuse placentas (Carter & Pijnenborg, 2011; King,

1993; Martin, 2008). Most primates give birth to singletons; however, marmosets (and to an extent tamarins) (Sweeney et al., 2012) almost exclusively give birth to dizygotic twins or triplets (Leutenegger, 1979). Gestation duration ranges from just under 2–9 months, correlating with brain size, body size, and lactation duration (Dubman et al., 2012).

Maternal recognition of pregnancy is determined by gonadotropins produced by the conceptus and later the placenta. Chorionic gonadotropins (CGs) produced by primate blastocysts are thought to be the only maternal recognition of pregnancy signal. CGs provide luteotropic actions via the LH receptor expressed by CLs in the ovary (Bazer & Spencer, 2011). CGs also play a role in promoting additional decidual development beyond the spontaneous decidualization that occurs in many primates. Production of CGs increases to peak values in the first trimester and then decrease during late gestation in humans; however, these patterns vary among primates (Shimizu, 2005; Yoshida, 1999).

3.2 Rodentia

The order Rodentia is one of the most diverse eutherian orders and it includes many well-known and well-studied model systems, including murids (rats, mice, and hamsters) and caviae (guinea pigs). Ovulation is generally spontaneous (Dixon, 2021). Rodents have hemochorial, discoid placentas (Carter & Enders, 2004). Some rodents also display a subplacental organ (Davies et al., 1961; Fischer, 1971), which has the potential for steroid hormone secretion during early gestation. The subplacenta primarily produces estrogens and androgens (but not progestogens) (Migliano et al., 2021), though in rats, the subplacenta also produces a number of placental lactogens (Bu et al., 2016). Rodents generally give birth to larger litter sizes (>3 pups, generally), composed of altricial young, following relatively short pregnancies (<60 days, with many less than 1 month). Cavia species are an exception to this general rule—most cavia give birth to precocial young in relatively small litters (Hayssen & Orr, 2017). Rodents do vary considerably in litter size, even within relatively closely related species (Wilsterman & Cunningham, 2023), which presents opportunities for understanding how litter size and evolution thereof interacts with dosing of hormones produced by placentas.

Chinchillia species in the genera *Lagidium* and *Lagostomus* (commonly referred to as viscacha and including guinea pigs and chinchilla) display an interesting ovulation strategy that shapes gestational progression and litter size. In each reproductive cycle, 200–800 eggs are ovulated, but only 10–12 will implant, and only 1–2 embryos actually make it to term (Roberts & Weir, 1973). The reason for this

multiple ovulation strategy is not clear (Flamini et al., 2020), but the resorption of most embryos appears to be linked to local variation in vasculature in the endometrium (Acuña et al., 2022).

The CL must produce progesterone through three-quarters of most murid gestations (Soares et al., 2007). During early gestation, twice-daily (diurnal and nocturnal) surges of prolactin from the pituitary that are luteotropic and protect CL-derived progesterone from metabolism into an inactive form. Behind the scenes of these surges of prolactin is puromycin-sensitive aminopeptidase, without which the CLs of pregnancy do not mature (Osada et al., 2001). Importantly, vaginal stimulation during copulation is required to trigger these twice-daily prolactin surges. During the latter half of gestation, placental lactogenic hormones supersede pituitary prolactin to act as luteotropic hormones.

3.3 Lagomorpha

Order *Lagomorpha* consists of two families: *Leporidae* (rabbits and hares) and *Ochotonidae* (pikas). The gestational endocrinology of rabbits and hares is well-described, whereas pikas are relatively poorly understood. Nonetheless, we do know that all lagomorphs are induced ovulators (Bazer, 2015; Caillol et al., 1989; Flint et al., 1990; Hilliard, 1973; Kirkpatrick & Satterfield, 1973; Stoufflet & Caillol, 1988), and (in association with this trait) lagomorphs frequently display pseudopregnancy. Lagomorphs have discoid, hemochorial placentas (Chavatte-Palmer & Tarrade, 2016; Dharmarajan et al., 2004), and litter size can range from 2 to 8 offspring (Caravaggi, 2022). Gestation duration is generally shorter (1–2 months). However, within this variation, rabbits and hares differ in the degree to which offspring are developed at birth; whereas rabbits are highly altricial, hares are generally precocial (González-Mariscal & Rosenblatt, 1996). Of additional note, rabbits are able to superfetate, meaning that they can carry a secondary fertilized ovum within the uterus that is gestating a second litter, such that the two pregnancies are occurring concomitantly (Flux, 1967; Heldstab, 2021). The endocrinological dynamics of superfetation are not understood to our knowledge.

Immediately following mating in rabbits, oxytocin release from the pituitary increases, which may have a role in facilitating movement of sperm toward the oocytes (Bazer, 2015). Maintenance of the CL is generally luteotropic and may involve the neuropeptide kisspeptin (Maranesi et al., 2019). An additional luteotropin is responsible for maternal recognition of pregnancy in lagomorphs (Caillol et al., 1989; Flint et al., 1990; Gadsby, 1989; Hashem & Aboul-ezz, 2018; Marcinkiewicz & Bahr, 1993), and it is thought to be derived from the placenta (Dharmarajan et al., 2004; Hashem & Aboul-ezz, 2018). Progesterone production

throughout pregnancy is primarily secreted via the CLs and not the placenta (Dharmarajan et al., 2004; Greep, 1941; Hilliard, 1973).

The CLs are notably long-lived in pikas. Whereas parturition and the commencement of lactation is associated with deterioration of the CLs in most mammals, the CLs persist during lactation in pikas (Kirkpatrick & Satterfield, 1973). The mechanisms by which the CLs are maintained and the degree to which they secrete steroid hormones is unclear (Kirkpatrick & Satterfield, 1973).

3.4 Cetartiodactyla

Cetartiodactyla includes four groups of even-toed ungulates and cetaceans (see also Chapters 16 and 17, this volume): pigs and peccaries (Suina), Old World and New World camelids (Tylopoda), Bovids (which includes Bovidae, Cervidae, Mochidae, Giraffidae, Tragulidae, and Antilocapridae), and hippopotamuses and cetaceans (Cetancondonta, formerly Whippomorpha).

Cetartiodactyla are generally spontaneous ovulators (Bazer & Spencer, 2011; Brown, 2000; Flacke et al., 2017; Pomeroy, 2011; Skidmore, 2015), except for camelids, which are induced (but see Bravo & Sumar, 1989; Fernandez-Baca et al., 1970a), and whales, in which facultative induced ovulation has been suggested (Atkinson & Yoshioka, 2007; Flacke et al., 2017; Marsh, 1985; Pomeroy, 2011; Steinman et al., 2012). Pseudopregnancy is uncommon among Cetartiodactyla (but see Atkinson et al., 1999; Brown, 2000; Combelles, 1995; Flowers et al., 1999; Steinman et al., 2012; Stieger-Vanegas & McKenzie, 2021). Cetartiodactyla placentas are either diffuse (e.g., in camelids and pigs) or cotyledonary (Carter, 2019), and they generally produce one or two offspring following a longer gestation (>100 days and up to 330 days in some ruminants) (Korzekwa et al., 2016; Mithileshwari et al., 2016; Umopathy, 2017). Pigs (Suidae) offer an interesting exception to these patterns; some species in the this group can have up to 10 offspring (Bazer & Spencer, 2011). Most Cetartiodactyla offspring are precocial.

Maternal recognition of pregnancy in most of Cetartiodactyla is associated with blastocyst-dependent production of estrogens (Bazer & Johnson, 2014; Skidmore et al., 1994). In pigs, blastocyst-dependent production of estrogens also promotes decidualization and remodeling of the endometrium. This remodeling redirects luteolytic prostaglandins from the uterine venous drainage, where they would otherwise lead to luteolysis of the CL, into the uterine lumen (Bazer et al., 2008; Bazer & Johnson, 2014). Additional secretions from the developing conceptus further modulate adhesion and secretory activity of the

endometrium to permit implantation (Blitek et al., 2012; Geisert et al., 2014; Green et al., 1995; Jaeger et al., 2005; Ka et al., 2018).

In contrast, the physiological recognition of pregnancy in most ruminants (Bovids) is interferon tau, a type I interferon that is produced by the conceptus. This interferon inhibits the pulsatile release of prostaglandins from the endometrium in most ruminants (Bazer et al., 2020). Bovid placentas also secrete a pregnancy-associated glycoprotein, which can be used as a reliable marker of pregnancy (Wallace et al., 2015; Wooding, 2022). Bovids also are unique in that relaxin has not been implicated in parturition or mammogenesis in this group (Hooley & Findlay, 1981).

The majority of camelid pregnancies occur in the left uterine horn of a bicornuate uterus, which in some cases involves migration of the fertilized egg (Agnew, 2018; Carter, 2019). The luteolytic activity of the left uterine horn is able to act locally and systemically, whereas the right uterine horn is only local in its effect (Del Campo et al., 1996; Fernandez-Baca et al., 1979). These features are associated with embryonic loss in camelids (i.e., insufficiency of the right ovary; Fernandez-Baca et al., 1970b; Fernandez-Baca et al., 1979).

Finally, hippos are differentiable from other Cetartiodactyla for their CL dynamics following ovulation. In hippos, several accessory luteinized follicles persist in the ovary (in addition to the ovulatory CL), and these accessory luteinized follicles appear to increase in number across gestation (Eltringham, 1999). Although one might assume that these ovarian structures are involved in progesterone secretion and likely derived from anovulatory follicles, their endocrinological role is unclear. However, waves of estrogen have been observed during pregnancy and lactation in captive hippos, suggesting that follicular development continues during gestation (Flacke et al., 2017).

3.5 Perissodactyla

Perissodactyla includes all odd-toed ungulates. Odd-toed ungulates are generally spontaneous ovulators, though induced ovulation has been observed in Sumatran rhinos (Roth, 2006). Odd-toed ungulates have epitheliochorial, diffuse placentas. In general, these ungulates bear a longer gestation and give birth to one, but occasionally two, precocial young (Carter & Martin, 2010; Mess & Carter, 2006).

Gestation duration can be highly variable in some species of odd-toed ungulates. For example, gestation duration in donkeys ranges from 11 months to as long as 14 months (Graubner et al., 2017, 2020; Paulson & Comizzoli, 2021). This variation may be associated with the sex of the fetus, with male gestations lasting longer than female

gestations (Miragaya et al., 2018), or based on photoperiod. In the latter case, conceptions that occur earlier in the breeding season are associated with longer pregnancies such that parturition is relatively synchronized even when conception is more variable (Carluccio et al., 2015; Galisteo & Perez-Marin, 2010). Similar patterns are observed in rhinos (Schwarzenberger & Hermes, 2023). Though this variation is undoubtedly controlled by endocrine systems, which also mediate seasonal timing in vertebrates generally (Wilsterman et al., 2018), the mechanisms remain poorly understood.

Maternal recognition of pregnancy in Equids (including horses) depends on antiluteolytic factors secreted by the fetus (Bazer et al., 2009; Swegen, 2021). Although equine embryos secrete estrogens and interferon delta very early in gestation, these factors apparently are not linked with maternal recognition of pregnancy (Tayade et al., 2008). Instead, placental cells produce a chorionic gonadotropin (equine chorionic gonadotropin, eCG) (Carter, 2022; Wooding et al., 2001). eCG stimulates secondary follicle development, resulting in a secondary CL and accessory CLs that maintain adequate progesterone levels during mid-pregnancy. Other Equidae species also have CGs, respectively referred to as donkey chorionic gonadotropin (dCG) or zebra chorionic gonadotropin (zCG). However, zebras lack the secondary CL that supplements progesterone (Allen et al., 2017). In contrast, maternal recognition of pregnancy remains unclear in rhinos and tapirs. No CG has been found in rhinos, but prolactin may play a role (Ramsay et al., 1994; Roth, 2006; Sherman et al., 1997). In Tapirs, a CG has been identified, but very little about it is known (Brown, 2018).

3.6 Carnivora

Several major groups make up Carnivora that differ significantly in their gestational physiology. Here, we make distinctions among felids and hyenids, canids, ursids, mustelids, and pinnipeds. Many species within Carnivora are considered induced ovulators (Jewgenow & Songsasen, 2014). However, ovulation also occurs in the absence of copulation in domestic cats and lions (Dixon, 2021), and therefore, many Carnivora species may also be facultative ovulators (Concannon, 2009; Concannon et al., 2018). Some species within Carnivora display delayed implantation, where fertilized embryos do not implant immediately. It is not clear whether the CL remains active during delayed implantation (Amstislavsky & Ternovskaya, 2000). The Carnivora placenta is endotheliochorial and zonary. Offspring are generally altricial and born after variable gestation durations; this variation is tied in part to uncertainty around delayed implantation and/or flexibility in gestation duration.

Persistent CLs, in which the CLs remain present and steroidogenic throughout gestation and sometimes past pregnancy, are extremely common among carnivores. The evolutionary function of the persistent CL across Carnivora is not well understood, but its sustained progesterone production may contribute to early pregnancy maintenance and/or to suppress follicular growth to achieve highly seasonal reproductive cycles. Lynx express perhaps the most extreme example of persistent CLs, which can remain in the ovary for up to 2 years following ovulation (though it likely does not maintain progesterone secretion for this duration) (Painer et al., 2014). The persistent CLs contribute to sustained pseudopregnancies in many Carnivore species. For example, pseudopregnancy in pinnipeds can last up to 210 days (Boyd, 1991).

CL persistence is also associated with seasonality in Carnivores. Among bears and mustelids, this seasonality and its impact on gestational endocrinology is particularly notable. In both bears and mustelids, copulation and embryo implantation are significantly separated in time (up to months in some bears). In bears, this delay coincides with what appears to be partial luteinization of the CL, where the CL is maintained and capable of producing progesterone but maintains low levels during the delay. It is not until postimplantation that CL production of progesterone increases dramatically (Hellgren et al., 1991; Tsubota et al., 1998). Although the delay is not as dramatic, postimplantation is also associated with a dramatic increase in progesterone in mustelids (Amstislavsky & Ternovskaya, 2000; Corner et al., 2015).

In minks, the increase in progesterone that is required for implantation may in fact be determined by the photoperiod such that implantation is determined by time of year, not copulation date (Amstislavsky & Ternovskaya, 2000).

In some Carnivora species, the persistent CL is so extreme that a blastocyst-derived signal for physiological recognition of pregnancy may not be necessary; hormonal signals from pregnancies and pseudopregnancies are indistinguishable (meaning no physiological recognition cue from the fetus is required to support CL steroidogenic activity) (Flint et al., 1990). This assertion oversimplifies the role of hormonal signals and two-way communication between the gestational parent and developing fetus for normal development, but it effectively summarizes the degree to which CL persistence and pseudopregnancy is displayed within this group, and it crystallizes the pervasive challenge of distinguishing pseudopregnancies from pregnancies using routine hormonal measures (particularly progesterone) among Carnivora species.

Receptivity of the uterus to embryo implantation in carnivores is driven by ovarian steroids (progesterone and estradiol), though estradiol is relatively unimportant in Canids (Paulson & Comizzoli, 2021). In canids, decidualization also requires prostaglandins (Graubner et al., 2017,

2020; Paulson & Comizzoli, 2021). In felids and mustelids, progesterone and estradiol are sufficient to drive functional decidualization (Mead, 1981; Wilsterman et al., 2019), suggesting that prostaglandins may also be important in these other groups.

The source of hormones of interest (particularly progesterone) across gestation is not well-defined outside of domestic cats and dogs. There are some assumptions that extended life of the CL is involved in maintaining progesterone, suggesting that placental progesterone production is insufficient for much of pregnancy, but there is no experimental or observational data to support this idea.

Bears and pinnipeds display a few notable traits related to gestational endocrinology that are worth highlighting further here. Bears are unique for their use of torpor (hibernation) coincident with gestation. In most animals, torpor expression is incompatible with reproduction, whereas hibernation is a routine and potential requisite part of gestational physiology for some bear species (McAllan & Geiser, 2014). For example, although hibernation duration decreases dramatically at low latitudes in male black bears, female black bears that are reproductively active appear to maintain a denning period consistent with hibernation in these same locales (Wilsterman et al., 2019). Thyroid hormones play a critical role in controlling torpor expression and energetic balance across hibernation, although gestational status does not appear to impact thyroid hormone production in black bears (Tomasi et al., 1998). More generally, pseudopregnancy and pregnancy have similar physiological profiles during hibernation in other bears (Shimozuru et al., 2013). These physiological changes are coincident with differential regulation of body temperature during gestation and hibernation, and thus are likely to confer energetic costs to females (Tøien et al., 2011).

Pinnipeds display strongly synchronous breeding along with delayed implantation (Boyd, 1991). The delay in implantation appears to be sensitive to environmental factors (Boyd, 1991). The physiological factors that influence the timing of implantation in pinnipeds remain unknown, though manipulating sex steroids does not appear to modify the implantation delay (Boyd, 1991). The function of the delay in pinnipeds is likely tied to their unique life histories, which require a terrestrial or pagophilic (ice-bound) period during reproduction (Boyd, 2009; Cassini, 1999).

Pinnipeds also produce a placental CG relatively early in pregnancy (Browne, 2004; Hobson & Wide, 1986). Pinniped CG appears to be derived from a luteinizing hormone-like gene, similar to primates. Any role for CG in supporting CL function or progesterone production has not been proven. Unlike other carnivore species discussed, postpartum estrus is common in pinnipeds, in line with their life history, which involves a concentrated period of reproductive activity and interaction with other individuals.

3.7 Chiroptera

Chiroptera (bats) is divided into two main groups: Yinpterochiroptera (formerly Megachiroptera) also known as the megabats and Yangochiroptera (formerly Microchiroptera) known as the microbats. Intense adaptive radiation has produced a high degree of diversity in reproductive habits, structures, and mechanisms within Chiroptera (Crichton & Krutzsch, 2000; Rasweiler IV, 1993); however, knowledge of gestational hormones in bats is limited to a few species, the majority of which are found within Yangochiroptera.

Differences in menstruation in distinct groups could indicate it as a more widespread and variable character in Yangochiropterans. Menstruation can be periovulatory or preovulatory, and could allow for successive pregnancy cycles (Crichton & Krutzsch, 2000; Rasweiler, 1970; Rasweiler & De Bonilla, 1992). Most bats are spontaneous ovulators, though induced ovulation has been reported in some captive species (Badwaik et al., 1997; Pakrasi & Tiwari, 2007; Rasweiler, 1970, 1972, 1979; Rasweiler & Badwaik, 1997; Rasweiler & De Bonilla, 1992). Following ovulation, estrogens appear to be supplemented by the adrenal glands in Yinpterochiropterans (Crichton & Krutzsch, 2000; Ifuta et al., 1988; Martin et al., 1995; Towers, 1988: 19; Towers & Martin, 1985).

Pseudopregnancy has not been explicitly described, but elevated progesterone levels occur in nonpregnant females of several yangochiropteran species, suggestive of pseudopregnancy. Although the ovary is suspected to be responsible for progesterone levels, adrenal progesterone content exceeds ovarian progesterone production in nonpregnant and postpartum animals (Crichton & Krutzsch, 2000), suggesting the adrenal glands are broadly important for gestational endocrinology in bats.

Implantation occurs in specific locations along the uterine horns in many bats and is facilitated by ovarian hormones acting on localized sections of the uterus via intricate and localized vasculature termed “tufts” (Badwaik & Rasweiler IV, 1998; Rasweiler & Badwaik, 1999). This highly localized receptivity to implantation may limit litter sizes (Badwaik & Rasweiler IV, 1998; Crichton & Krutzsch, 2000). Delayed implantation is relatively common among bats and is mediated by low progesterone and estrogens.

In many yangochiropterans, the CL is present through all of gestation, though it only maintains steroidogenic function for the first third to half of gestation in most species (Beguelini et al., 2020, 2021; Greville et al., 2022; Santiago et al., 2020; Stukenholtz et al., 2018). Among yinpterochiropterans, most species experience CL regression in early or midpregnancy, and thus, progesterone production for the latter half of gestation is placenta-dependent (Gopalakrishna & Badwaik, 1989; Jerrett,

1979; Kennedy, 1993; Meenakumari et al., 2009; Towers & Martin, 1985, 1995).

There are two different placental types present in extant chiropterans: endotheliochorial and hemochorial (Dudley et al., 2021; Enders & Carter, 2004). Some of this variation is ontological, such that the placenta transitions from endotheliochorial to hemochorial midway through gestation (Badwaik & Rasweiler, 2000; Cukierski, 1987; Enders & Carter, 2004). Placentas in bats may be discoid or bidiscoid (Carter & Enders, 2016; Carter & Mess, 2008). In the yangochiropteran *Miniopterus schreibersii*, a single discoid placenta first develops, and as gestation progresses, it regresses and is replaced by a pair of discoid placentas on either side of the first placenta (Chari & Gopalakrishna, 1984; Kimura & Uchida, 1984; Malassine, 1970). In other bats, the single discoid placenta “divides” in two to form two discoid placentas later in gestation (Bhiwgade, 1977; Gopalakrishna, 1958; Gopalakrishna & Moghe, 1960).

Hormone production from the placenta across gestation is fairly typical among bats. Of notable interest though, *Myotis nigricans* lacks the expression of aromatase in the placenta, a key enzyme for the production of estrogens, and thus any estrogens necessary for gestation must be derived from other endocrine organs or structures. Although the ovaries are a likely source of these estrogens, the adrenal glands may also be an important source (Beguelini et al., 2021).

Chiropterans typically have one offspring, but in some groups like Vespertilionidae, two to four is normal (Crichton & Krutzsch, 2000). Gestation length varies greatly between species of bats, and can sometimes vary greatly within a species due to differential developmental delays, some of which are implicated in hibernation in several species (Gopalakrishna & Badwaik, 1993; Hayssen et al., 1993; Kawamoto, 2003; Racey & Swift, 1981; Rasweiler & Badwaik, 1997).

3.8 Eulipotyphla

Three major families make up the Eulipotyphla: Soricidae (shrews), Talpidae (moles), and Erinaceidae (hedgehogs). Most of these species are induced ovulators (Bedford et al., 2004), except for hedgehogs (Deanesley, 1934), which are spontaneous ovulators. Insectivores tend to give birth to large litters of altricial young after a short gestation period (Carter & Martin, 2010; Mess & Carter, 2006). All of the insectivores studied have epitheliochorial placentas (Carter & Enders, 2009; Ferner et al., 2014), and they give birth to a small litter (2–8 offspring) after a short gestation (<6 weeks). Of note, hedgehogs display great variability in their length of gestation due to their use of torpor throughout pregnancy (Fowler, 1988; Ranson, 1941).

For most shrew species, the development of a postmating CL is dependent on the release of prolactin, which is

initiated by physical stimulation during copulation (Flint et al., 1990). However, in contrast to rodents, pseudopregnancy is not dependent on this physical stimulation (Inoue et al., 2022), suggesting that in shrews, pseudopregnancy is CL-independent. Implantation and gestation to term are not apparently dependent on CLs in shrews; females ovariectomized after Day 5 of pregnancy can still complete gestation (Hasler & Nalbandov, 1978). The CLs of shrews thus appear to be functionally redundant with other sources of gestational hormones for most of gestation (Inoue et al., 2022). Postpartum estrus in shrews is common and can persist up to 5–6 days after parturition (Hellwing, 1975: 1).

3.9 Afrotheria

Afrotheria, a superorder rather than a true order, contains the aardvarks (Tubulidentata), dugongs and manatees (Sirenia), hyraxes (Hyracoidea), elephant shrews (Macroscelidea), tenrecs, golden moles, and otter shrews (Afrosoricida), and finally elephants (Proboscidea). Afrotherians exhibit a range of unique gestational traits. Ovulation is generally spontaneous (Lumpkin et al., 1982). Fewer than four offspring is the typical in Afrotheria (Amaral et al., 2014; Lueders et al., 2012; Oduor-Okelo et al., 1983; Tripp, 1971: 19), though some tenrec species produce up to 32 pups in a single litter (Künzle et al., 2007).

Placentation in Afrotherians is generally endotheliochorial and zonary or discoid (Carter & Enders, 2009). Of course, several exceptions in this highly variable group exist: aardvarks have a diffuse placenta (Carter & Enders, 2004), and hyraxes, tenrecs, and elephant shrews have a hemochorial placentas (Carter, 2018; Carter & Enders, 2016; Oduor-Okelo et al., 2004). Afrotherians tend to have long gestations with most groups displaying gestations of 7 or more months. However, in association with smaller body sizes, elephant shrews and tenrecs have notably shorter gestations that last less than 2.5 months (Carter et al., 2004; Oduor-Okelo et al., 2004). Whereas some Afrotheria are precocial (elephant shrews, elephants; Medger et al., 2018), others are altricial (e.g., tenrecs; Eisenberg & Gould, 1970; Racey & Stephenson, 1996; Stephenson, 1993). In Sirenia and otter shrews, there is evidence of simultaneous lactation and ovulation or gestation, indicating that these endocrinological states are compatible in some Afrotheria (Pomeroy, 2011; Racey & Stephenson, 1996).

Many groups in Afrotheria display polyovulation in some form, despite retaining small to singleton litters. In dugongs and manatees, hyraxes, and afrosoricid species, this results in a large number of CLs (up to 60 in some manatees and 50 in elephant shrews). The functional role for these polyovulatory events is unclear. In dugongs and manatees, these multiovulatory events may be necessary for successful

implantation and gestation (Carter & Martin, 2010; Mess & Carter, 2006). Accessory CLs are required for gestation in hyraxes (Kirkman et al., 2001). A large number of CLs can accumulate in elephants, but the mechanism by which they accumulate is drastically different. Elephants are monovular (Allen, 2006; Short, 1966), and the CL persists past the estrous cycle in which it is produced. During their normal ovulatory cycles, elephants will display two LH peaks, the first of which produces luteinized unovulated follicles that then produce anovulatory CLs (Lueders et al., 2011). These anovulatory CLs secrete inhibins for dominant follicular selection, following which only the dominant follicle is ovulated (Lueders et al., 2011). Whether these anovulatory CLs are also involved in pregnancy maintenance is unclear.

Perhaps most distinctive in this group is the fact that progesterone is not required for early gestation and is not a good marker for pregnancy. Among hyraxes, tenrecs, and elephants, progesterone remains very low throughout gestation (Heap et al., 1975). In manatees and dugongs, progesterone does increase, but it remains extremely low relative to gestation-associated concentrations observed in other mammalian species, and it may not be involved at all in pregnancy maintenance in the West Indian manatee (Tripp et al., 2009). Instead, 5 α -reduced progestins (5 α -DHPs), which are secreted by the CLs (Kirkman et al., 2001), appear to perform functions similar to progesterone during early pregnancy (Hodges, 1998). 5 α -DHP may also be secreted by fetal gonads later in gestation, though it is not clear whether this contributes to the maintenance of pregnancy (Allen, 2006). Instead, there is thought to be some as-of-yet unidentified luteotropin or luteotropic molecule that supports the initial part of the persisting CL (Allen, 2006). Prolactin does increase later in gestation in elephants (Hodges, 1998; Meyer et al., 2004), and it may be luteotropic in this group (Yamamoto et al., 2017).

3.10 The understudied groups

3.10.1 Dermoptera

Dermoptera are comprised of colugos, an arboreal, gliding mammal related to primates. Essentially, nothing is known about gestational physiology and endocrinology among colugos. For example, estimates of gestation duration range from 1 to 5 months (Carter & Mess, 2017; Hayssen & Orr, 2017). Colugos develop a hemochorial discoid placenta to support a single developing offspring. Colugos are known to overlap gestation and lactation (Hayssen et al., 1993; Hubrecht, 1894; Medway, 1978; Wischusen, 1990), indicating that lactational endocrine requirements are compatible with gestational endocrinology in this group.

3.10.2 *Scandentia*

Scandentia species are divided into two families: family Tupaiidae (treeshrews) and family Ptilocercidae (the pentailed treeshrew) (Juman et al., 2021). Very little is known in general about these groups. Tree shrews exhibit delayed implantation, in association with postpartum estrus and concomitant lactation (Hendrickson, 1954; Luckett, 1968; Martin, 1968). Tree shrews develop an endotheliochorial, discoid, or bidiscoid placenta and give birth to two altricial young after a relatively short gestation of 1.5 months (Carter, 2020).

3.10.3 *Pholidota*

The order Pholidota is comprised of pangolin species. Reports on hormones and pregnancy in pangolins have been limited to several observations of individuals in captivity or captured gravid individuals. Variation in gestational durations have led many to suggest that pangolins may exhibit delayed implantation (Arora et al., 2023; Challender et al., 2019). Most pangolins produce epitheliochorial placentas (Carter, 2012), although one study identified the placenta of a black-bellied pangolin to be endotheliochorial (Heath & Amachree, 1967). One pup is typical (Hoffmann et al., 2020; Mahmood et al., 2016; Mohapatra, 2018; Yan et al., 2021). Lactation and gestation are known to overlap in some species (Challender et al., 2019; Fenelon & Renfree, 2018; Mead, 1993; Sweeney, 1974).

3.10.4 *Xenarthra*

Xenarthra include armadillos (Cingulata), sloths, and anteaters (Pilosa). Xenarthrans and Afrotherians are frequently grouped together for understanding the most basal models of eutherian reproduction. Delayed implantation is common in armadillos, and this delay appears to co-occur with inactivity of the CL(s) (Fenelon & Renfree, 2018; Mead, 1993). Such a delay may also occur in anteaters (Knott et al., 2013).

Armadillos and anteaters have hemochorial placentas, whereas sloths have an endotheliochorial placenta (Carter & Enders, 2004; Mess et al., 2012). In armadillos, the placenta developmentally begins as discoid but transitions to zonary later in gestation. There is less consensus on the form of the sloth placenta. Some sources mention that they begin as diffuse but later become discoid or bidiscoid (Carter & Enders, 2004). In other instances, the sloth placenta has been described as “multicotyledonary” as it can have up to 20 discs (also called “discoidal lobes”) (Accioly Lins Amorim et al., 2004). Gestation lasts up to a year in sloths (Hayssen, 2010) but lasts only 4–6 months in armadillos and anteaters (Luaces et al., 2011; Nakakura et al., 1982). In sloths and anteaters, one offspring is most common, whereas armadillos usually produce litters (Lara-Ruiz & Chiarello, 2005; Sibly & Brown, 2009; Superina & Loughry, 2012). In the nine-banded armadillo, the litter is invariably monozygotic quadruplets (Loughry et al., 1998).

4 FUTURE DIRECTIONS AND OPPORTUNITIES

The generalized mammalian pregnancy emphasizes that there are a broad set of generalizable traits and endocrinological features that are common to all mammals. However, various orders display considerable variation and there is much uncertainty in our understanding of diversity. Diversity among mammals provides a critical opportunity to discern the principles of eutherian gestational physiology, which is ultimately valuable for its ability to inform how we approach reproductive medicine in conservation, wildlife medicine, and biomedical contexts. There is significant opportunity for collaborative and zoo-led work to advance our understanding of the diversity in mammalian gestational physiology. The advent of noninvasive and minimally invasive sampling, as well as advances in proteomics, open up exciting opportunities to make significant improvements on the ELISA-based assays that have dominated our noninvasive understanding of gestational physiology to date. In particular, discovery-based proteomics offer significant potential to uncover diagnostic pregnancy markers and pregnancy recognition proteins, which remain unknown even among some well-studied groups. These kinds of advances are essential for conservation biology. Reproductive endocrinologists must understand principles and patterns in the gestational endocrinology of mammals if we are to conserve species through captive breeding programs and species conservation plans. Thus, gestational endocrinology research has a critical role to play in preserving mammalian diversity.

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