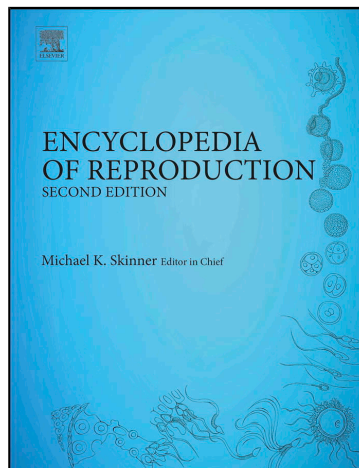


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COMPARATIVE MAMMALIAN MALE REPRODUCTION

Mammalian Reproduction Overview

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Glossary

Altricial Offspring that are hatched or born in a very immature and helpless condition so as to require parental care for some time.

Delayed implantation Delayed implantation or embryonic diapause is a reproductive strategy used by approximately 100 different mammals in seven or eight different orders. In embryonic diapause, the embryo (blastocyst) does not immediately implant in the uterus after sexual reproduction has created the zygote, but is maintained in a state of dormancy.

Eutheria Is the taxonomic name for the main group of living mammals. This taxon contains the placental mammals, of which humans are one species.

Marsupials Mammals of an order whose members are born incompletely developed (i.e., altricial) and are typically carried and suckled in a pouch on the mother's belly. Marsupials are found chiefly in Australia and New Guinea, and also in America.

Metatheria Is a mammalian clade that includes all mammals more closely related to marsupials than to placentals. It is a slightly more inclusive group than the marsupials; it contains all of the living mammals with abdominal pouches (most female marsupials) as well as their more primitive ancestors and relatives.

Monotreme Any member of the Monotremata, the most primitive order of mammals, characterized by certain birdlike and reptilian features, such as hatching young from eggs, and having a single opening for the digestive, urinary, and genital organs. Platypus and echidnas are the only extant monotremes.

Phylogeny The evolutionary history of a group of organisms, especially as depicted in a family tree.

Prototherian Primitive oviparous mammals belonging to the order Monotremata.

Introduction

The diversity of reproductive strategies and mechanisms exhibited by mammals is bewildering and complex. This is not surprising as there are estimated to be more than 5400 species of mammals worldwide (Wilson and Reeder, 2005), subdivided into 1229 genera (groups of species that are highly related and share common phylogeny). These species have evolved to occupy multiple ecological niches, and therefore exhibit a huge amount of life history variation. Detailed evolutionary studies of mammalian origins have produced some contentious outcomes, partly because phylogenetic trees can be derived using both DNA and protein sequences, as well as paleobiological data interpreted by a diverse array of statistical approaches. However, a relatively recent publication in Science (Meredith *et al.*, 2011) presented a credible attempt to reconcile these divergent views and these authors published a helpful mammalian phylogeny based on data from 164 species.

As a group, mammals are distinguished from other species by their ability to support their newborn offspring with milk, which is produced by the female's mammary glands during lactation. Milk is a rich source of important nutrients, including fatty acids, proteins, vitamins and growth factors, but it also provides newborns with a range of important immunologically active compounds that protect against infections during early postnatal development (Blum and Baumrucker, 2008; Oguchi *et al.*, 1997). Lactation is thought to be an ancient process that evolved in a clade of amniotes (synapsids, or mammal-like reptiles (Kemp, 2007)) which may have existed before the first appearance of mammals on earth (Ofstedal, 2012). Owing to its important role in neonatal development, lactation has persisted in all forms of mammals, but the interactions between mothers and their offspring are highly variable between species. Monotremes (prototheria), i.e., platypus and echidnas, are the only egg laying mammals and yet their neonates still receive milk from their mothers. Likewise, the marsupials (metatheria), whose neonates are still in a fetal and poorly developed condition (altricial) when born are provided with milk for prolonged periods after birth. The placental mammals (eutheria), which constitute the overwhelming majority of mammalian species, despite having evolved placental function to support their offspring during embryonic and fetal growth, still lactate and thus provide their neonates with an important additional source of nutrition in early life. These differences, based on the various ways in which neonates are supported during early postnatal growth, represent a useful criterion for dividing the mammals into three distinct classes with different evolutionary histories. It is, therefore, worth beginning this review by making some general observations about the reproductive mechanisms that characterise these three mammalian groups.

Monotremes

The four extant species of echidna within the order *Tachyglossidae*, together with the duck-billed platypus (*Ornithorhynchus anatinus*) are the egg laying mammals, and show many reproductive characteristics reminiscent of birds and reptiles. These species are geographically restricted and occupy different habitats; echidnas are terrestrial mammals and are found only in Australia and New Guinea while platypus are aquatic, living in the river systems of eastern Australia and Tasmania. Genome research has suggested that monotremes diverged from the other mammalian lineage (therian mammals; which later further diverged, forming the marsupials and the placental mammals) about 166 million years ago. Detailed studies of platypus and echidna reproductive biology have only been conducted over the last few decades (see, e.g., Grant and Temple-Smith, 1998; Morrow and Nicol, 2009) and given that these species are secretive and until recently (Wallage *et al.*, 2015) have not been easy to breed in captivity, knowledge about their general biology is still rather rudimentary (Johnston and Keeley, 2015). In fact, some aspects of their biology seemed highly improbable to earlier generations of scientists, and indeed, when the first description of a platypus was sent to the Royal Society in London in the early 19th century (Home, 1802), it was widely regarded as a hoax!

Echidnas and the platypus are both seasonal breeders, and it is worth noting here that seasonality is an important reproductive adaptation for many, if not most, mammals. For detailed information on comparative mammalian reproductive biology the reader should consult the encyclopaedic book by Asdell entitled "Patterns in mammalian reproduction" (Asdell, 1965) and a subsequent revision of the same book, which presents further detailed information (Hayssen, 1993). The monotremes are testicond mammals, which means that the males' testes are situated inside the body cavity, rather than in a scrotum. The spermatozoa are filiform and bear more resemblance to avian and reptilian spermatozoa than to spermatozoa of other mammals; during sperm maturation in the epididymis, the spermatozoa become organized into bundles of approximately 100 cells, which swim together in synchrony. The microanatomy of the epididymis has been likened to that of birds and reptiles (Bedford and Rifkin, 1979; Carrick and Hughes, 1982). Monotreme yolky oocytes are fertilized within the female's oviduct where they meet the spermatozoa (Grutzner *et al.*, 2008). It is also worth noting that, as with marsupials (with the exception of some planigales), and, unlike eutherian mammals, the amino acid sequence of protamine 1 of monotreme spermatozoa does not include cysteine residues (Retief *et al.*, 1993). The sperm heads are thus considered rather fragile as there is no capacity for the formation of stable crosslinked nuclear protein-DNA complexes. Presumably platypus and echidna spermatozoa typically ascend the female tract as motile bundles (Johnston *et al.*, 2007; Nixon *et al.*, 2016), and although relatively little is known about fertilization mechanisms, it is interesting to see that the platypus genome encodes each of the four proteins of the human zona pellucida. Field and captive observations of echidna reproduction (Nicol and Andersen, 2007; Rismiller and McKelvey, 1996) have shown that the egg is incubated in the pouch for approximately 10 days after a pregnancy of about 3 weeks, whereupon the female eventually deposits the young in a nursery burrow. As neither the platypus nor the echidna possess nipples, the offspring suckle directly from mammary lobules that empty into an invagination of skin surrounding a hair follicle (Grant and Temple-Smith, 1998).

Remarkably, it appears that only the left side of the female platypus reproductive tract is functional, while that of the echidna has two functional ovaries. The male echidna does not urinate through the penis, but via urogenital papillae. The echidna penis itself is most bizarre, being about a quarter of the animal's body length when erect and terminating in two sides, each side possessing a glans penis taking the form of 2 rosettes. The urethrae terminate on the surfaces of the rosette in a series of openings through which the semen emerges (Johnston *et al.*, 2007); the platypus penis is equally bizarre and appears adapted for securing this organ into the urogenital sinus of the female during mating, which occurs in the water column.

Marsupials

Recent genomic data (Nilsson *et al.*, 2010; Warren *et al.*, 2008) suggest that marsupials diverged from eutherian mammals 130–150 million years ago, and since then they have colonised both central and south America as well as Australia and New Guinea. The marsupials, which include about 330 extant species, show huge variation in terms of their ecology and reproductive characteristics. This remarkable diversity is, however, often underestimated by those not familiar with the group as a whole (Johnston and Keeley, 2015; Johnston and Holt, 2001; Tyndale-Biscoe and Renfree, 1987). In contrast to the popular belief that all marsupials possess a pouch and lack a placenta, some of the carnivorous dasyurid species (e.g., phascogales and antechinus) possess only a marginal pouch that does not cover the mammary area, while the Peramelidae family (e.g., bandicoots) even develop an invasive chorioallantoic placenta during pregnancy. The majority of marsupials are also seasonal breeders, and some species, including macropods (kangaroos and wallabies) and the honey possum (Oates *et al.*, 2007; Renfree, 1981), exhibit embryonic diapause, where the embryo remains in the uterus for up to several months without showing any development; development can be rapidly initiated by changes in day length or the loss of pouch young. The occurrence of embryonic diapause is not restricted to marsupials as it has also been recognized in a range of eutherian mammals (Mead, 1993) as a strategy for the temporal separation of mating events and subsequent embryonic development. While it is impossible to describe in this short review how reproductive systems vary between marsupials, it is worthwhile attempting to summarise a few key differences, as well as emphasising how some of their characteristics differ from eutherian mammals.

Reproductive Features of Marsupials

Species diversity among marsupials is as multifaceted as diversity among eutherian mammals. Some species, such as the Tasmanian devil (*Sarcophilus harrisii*), which is the largest of the dasyurids, are carnivorous, while others, such as the macropodidae are herbivores. Marsupials have also evolved multiple and diverse reproductive strategies and as a consequence the details of their reproductive biology are also highly varied. In an effort to classify and make sense of the different reproductive strategies found among marsupials, Tyndale-Biscoe and Renfree (1987) proposed that four distinct categories could be identified. However, because more knowledge of marsupial reproduction and its complexity has become available over the last 30 years, this simple classification needed further refinement (Johnston and Keeley, 2015).

Understanding reproductive anatomy in female marsupials is also challenging in itself, being different from that of the eutherian mammals (Fig. 1(D)). The caudal region of the female reproductive tract possesses two lateral vaginae, each of which opens into a urogenital sinus that also receives the urethra (Tyndale-Biscoe and Renfree, 1987). The differences arise during organogenesis owing to a difference in the migration of the embryonic urinary and genital ducts. The ureters pass medially to the Wolffian and Mullerian ducts, rather than laterally to them, as in eutherians. As a result, the female Mullerian ducts are prevented from fusing medially so that the uteri and vaginae on either side remain separate, except where the ducts fuse medially at the junction of the developing uterine and vaginal sections (Mackay *et al.*, 2004; Renfree *et al.*, 1996).

Prior to parturition, it is thought that most marsupials develop a new birth canal; this joins the posterior margins of the vaginal cul-de-sac to the anterior end of the urogenital sinus (Johnston and Keeley, 2015). In most species that have been examined, the connective tissue closes and repairs quite rapidly while in others (e.g., Honey possum, kangaroos and wallabies) it remains patent.

At the time of copulation, semen is deposited into the cranial portion of the urogenital sinus, from where it moves through the lateral vaginae, a vaginal complex or cul-de-sac, cervix and into separate uteri and oviducts. Although this is the general scheme, there is considerable anatomical variation between and within species (Tyndale-Biscoe and Renfree, 1987), which sets considerable challenges to the development of artificial insemination and embryo transfer technologies, where both semen and embryo deposition require both anatomical and temporal precision.

Inter-male competition is prevalent in many species, for example, wallabies (Jarman, 1991) and some researchers have used testis weight as a predictor of this reproductive strategy; in principle, it is likely that species engaging in male-male competition would benefit from high sperm production capacity and hence a high testis/body weight ratio (Rose *et al.*, 1997). Some species, especially the dasyuridae, combine such competitiveness with a more complex phenomenon known as semelparity (Naylor *et al.*, 2008). This strategy involves the almost complete death and ecological disappearance of males after mating combined with a heavy reliance on sperm storage in oviductal crypts within the female reproductive tract (Taggart *et al.*, 1999; Taggart and Temple-Smith, 1991).

The morphology and physiology of marsupial spermatozoa are highly variable between species (Breed, 1994), but it is notable that sperm morphology within a single species can either be highly pleiomorphic, as in the koala (*Phascolarctos cinereus*), or show very little variability (e.g., macropodidae). The new world marsupials have evolved an unusual reproductive specialization whereby their spermatozoa become "paired" during maturation in the epididymis (Krause and Cutts, 1979; Temple-Smith and Bedford, 1980); the pairing involves very specific and stable interactions between the flattened surfaces of the two sperm heads, and the end result appears to provide both of the spermatozoa with synchronized and rapid motility (Moore and Taggart, 1995; Taggart *et al.*, 1993). Experiments (Rodger and Bedford, 1982) have shown that the two spermatozoa become separated shortly before meeting the egg, but detailed studies of marsupial sperm capacitation and acrosome reaction have yet to be conducted.

The variations in spermiogenesis and epididymal sperm maturation result in significant differences in sperm morphology between marsupials (Rodger and Mate, 1993; Temple-Smith, 1994). These represent wonderful sources of information for researchers interested in the comparative evolution of reproductive biology; however, the relevant literature is far too detailed and rich to describe here. The reader is advised to consult J. M. Bedford's thought provoking reviews (Bedford, 1996, 2004, 2008, 2014) on gamete form and function.

Fertilization and embryonic development in marsupials show many differences from the same processes in the eutherian mammals; the main points of these differences are well summarized in two excellent reviews (Baggott, 1992; Selwood, 2007). Marsupial oocytes are much larger (150–200 μm diameter) than those of the eutherians (typically about 100 μm diameter), and after fertilization the zygotes exhibit visible polarity as an early indication of embryonic cell commitment. The polarity predicts the eventual separation into two cell types, pluriblast (equivalent to the inner cell mass of the mouse), the trophoblast, and ultimately the alignment of the body axis.

Assisted Reproductive Technologies and Marsupials

Like animal populations everywhere, the unique fauna of Australia is under threat from many directions, including land management, industrial development and environmental pollution, habitat fragmentation, disease and invasive species. Many of the marsupials are therefore endangered and under imminent threat of extinction. However, there are also many conservation schemes that attempt to counter these problems. Almost all of the conservation measures are based around habitat protection and the mitigation of direct threats, but some researchers have argued that these policies should be backed up by the use of assisted reproductive technologies (ART), such as artificial insemination and the cryobanking of genetic resources (Czarny *et al.*, 2009; Johnston and Holt, 2001) that could be used for genetic management. Unfortunately, these technologies are still very underdeveloped with respect to

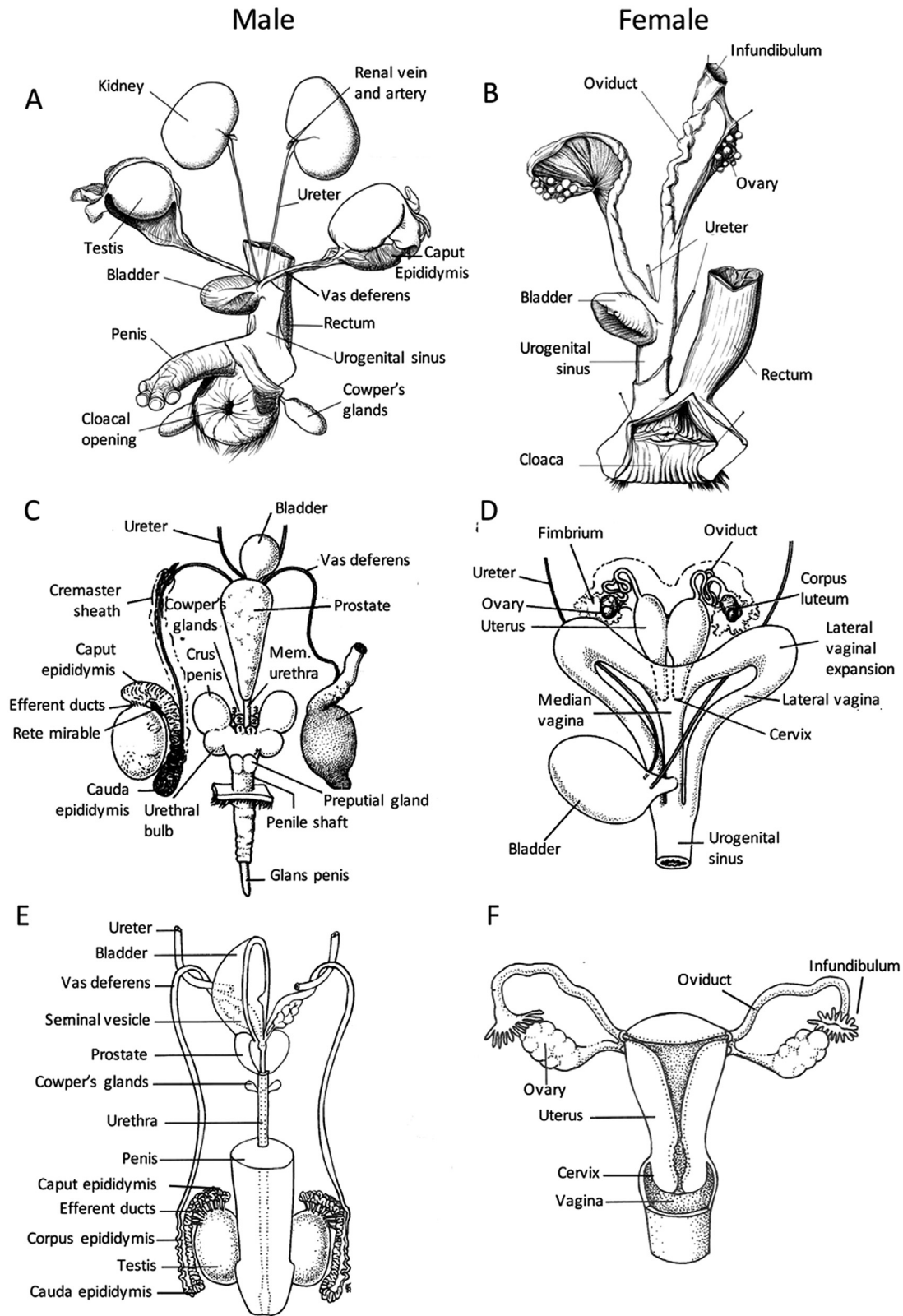


Fig. 1 Comparative mammalian reproductive anatomy. (A) Male prototheria – Echidna; (B) female prototheria – Echidna; (C) male metatheria – Tamar Wallaby; (D) female metatheria – Tamar Wallaby; (E) male eutheria – Human; (F) female eutheria – Human. A and B modified from Augee, M.L., Gooden, B., Musser, A., 2006. *Echidna: Extraordinary Egg-Laying Mammal*. Collingwood, VIC: CSIRO Publishing. C and D modified from Renfree, M., Shaw, G., 1999. Marsupials. In: Knobil, E., Neill, J.D. (Eds.), *Encyclopedia of Reproduction*. London: Academic Press, pp. 104–114. E and F modified from Lombardi, J., 1998. *Comparative Vertebrate Reproduction*. Boston; Dordrecht; London: Kluwer Academic Publishers.

the marsupials, mainly because there is such a paucity of knowledge about the reproductive physiology of marsupials (Johnston and Holt, 2001). Using ART requires detailed knowledge of both male and female physiology, coupled with practical methods for semen collection, the control of ovarian cycles, semen cryopreservation and reproductive anatomy. All of these factors have proven extremely challenging in marsupials. Having pointed out the difficulties, it is worth mentioning that appropriate investment of effort does indeed produce results, and that artificial insemination has been successful in the koala (Allen *et al.*, 2008; Johnston *et al.*, 2003) and tammar wallaby (Paris *et al.*, 2005; Rodger *et al.*, 2009).

Reproduction in Eutherian Mammals

The eutherians account for the vast majority of extant mammals. Their shared reproductive characteristic is that they are all viviparous; that is, they all produce live offspring that have been nurtured via an invasive chorioallantoic placenta throughout pregnancy. Unlike the marsupials, the newborn offspring reach an advanced stage of development before birth and continue to receive maternal support after birth by suckling milk from the mammary glands. Placental function during pregnancy is supported by the secretion of progesterone, produced initially from the corpus luteum, formed within the ovary when the post-ovulatory Graafian follicle becomes luteinized, and later in many species by the placenta itself. Circulatory progesterone and its metabolites (known collectively as progestagens) can readily be measured after excretion into fecal samples and/or urine. In practical terms this is the basis for the non-invasive detection of oestrous cycles and pregnancy, a technique that can be used with many wild mammalian species (Brown *et al.*, 1994; Burgess *et al.*, 2012; Wasser *et al.*, 1996). Fig. 2 illustrates this principle, using data from a study of the Mohor gazelle (*Gazella dama mhorr*) (Pickard *et al.*, 2001).

One important role of progesterone in eutherian mammals involves transforming the lining of the uterus in order to allow implantation of the early embryo and the subsequent formation of the placenta. Prior to ovulation the ovary has been more concerned with oocyte development within the follicle, a process supported by the production of estradiol from thecal and

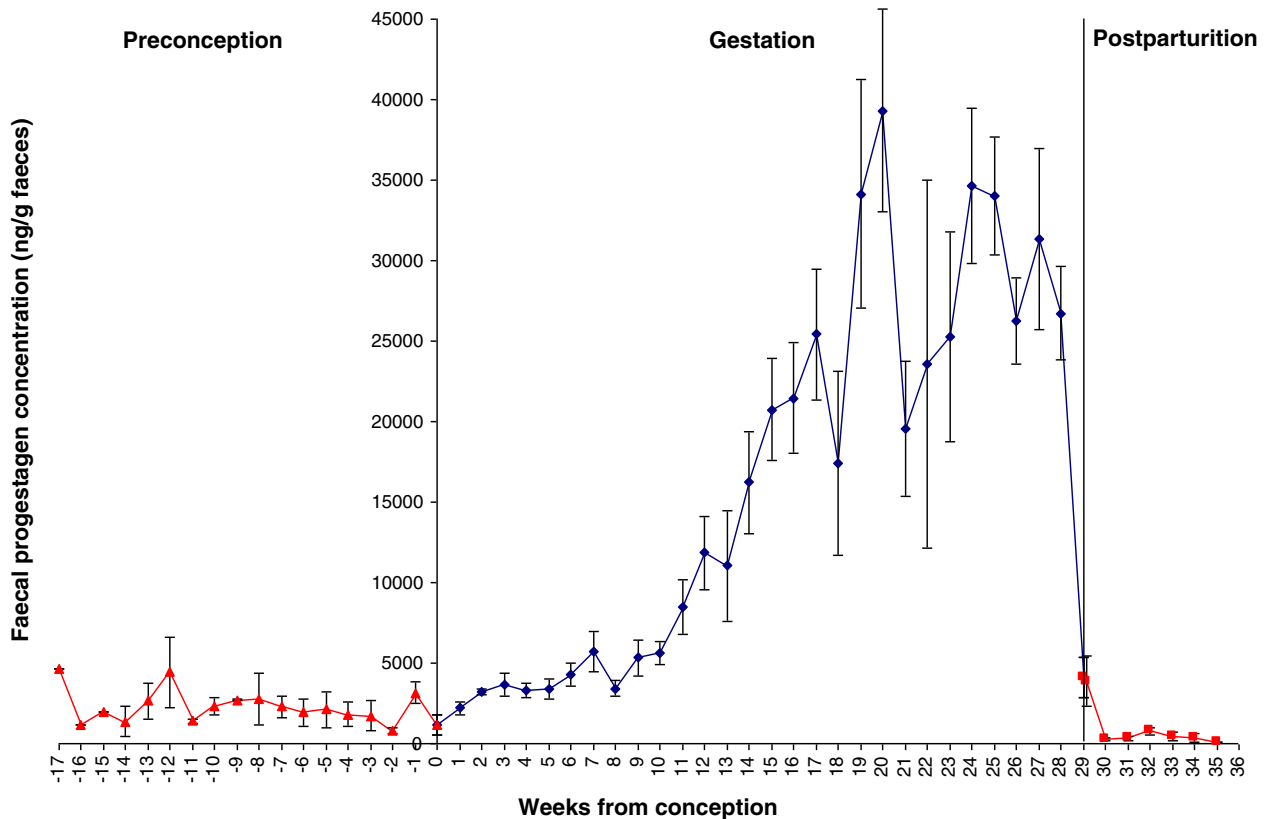


Fig. 2 Faecal progestagen concentrations (mean \pm SEM; $n=7$ females) before conception (red triangles), during gestation (blue diamonds) and after parturition (red squares) in the Mohor gazelle (*Gazella dama mhorr*). The first vertical line indicates the date of insemination and the second vertical line indicates the date of parturition. The progestagen concentrations do not increase significantly until about 9 weeks after insemination, whereupon they rise steeply and remain high until shortly before parturition. Reproduced with permission from Pickard, A.R., Abaigar, T., Green, D.I., *et al.*, 2001. Hormonal characterization of the reproductive cycle and pregnancy in the female Mohor gazelle (*Gazella dama mhorr*). Reproduction 122, 571–580.

granulosa cells that line the follicle itself. These two sequential processes, which together result in the basic features of the estrous cycle (follicular and luteal phases), have been moulded by evolutionary processes in ways that are adapted to assure optimal reproductive success in different habitats and climates.

Control of the estrous cycle and its relationships to environmental factors such as photoperiod is exerted via the neuroendocrine system. These physiological processes are governed by the pulsatile secretion of gonadotropin-releasing hormone (GnRH) from nerve endings in the hypothalamus which are then released into portal vessels connected to the anterior pituitary. The pituitary responds by a highly synchronized release of two gonadotropins (luteinizing hormone (LH)) and follicle stimulating hormone (FSH), which together and in association with inhibin and activin from the ovary, control gonadal function (i.e., both in the ovaries and the testes). In some mammals (e.g., human, cattle, pigs) the estrous cycle occurs regularly and spontaneously until it is interrupted by pregnancy, but it is important to note that in many species (e.g., rabbits, ferrets, cats, camelids, often grouped together and known as “induced ovulators”) there are sophisticated control mechanisms that help to ensure either that births occur at a favourable time of year, or that ovulation only takes place when a female is likely to encounter a male. It would, for example, be a waste of energy for females with solitary lifestyles to ovulate regardless of the likelihood of being mated. In many species, ovulation can be induced, often by physical stimulation of the female genitalia during mating, but also by the presence of ovulation-inducing hormones in seminal plasma (e.g., Adams and Ratto, 2013, Camelidae).

Reproduction in mammals is modulated by subtle and sophisticated mechanisms, details of which are beyond the scope of this article. However, it is worth mentioning the relatively recent discovery that the production of leptin, a peptide hormone produced by adipose tissues and also by the placenta, is now seen as an important modulator of diet, body condition and the neural control of reproduction (Barb *et al.*, 2005; Daniel *et al.* 2013; Evans and Anderson, 2017). Extremes of body condition such as obesity or malnutrition are known to impact the success of reproduction in humans and other species (Hausman *et al.*, 2012; Perez-Perez *et al.*, 2015; Walzem and Chen, 2014).

Reproductive Seasonality

Seasonality has a major impact on reproductive processes and many eutherian mammals have adjusted their entire reproductive repertoire accordingly. For example, the breeding season of the harbour porpoise (*Phocaena phocaena*) and common dolphin (*Delphinus delphis*) is restricted to a short period in spring or summer (Neimanis *et al.*, 2000; Westgate and Read, 2006). Testicular weight during the summer months is approximately five times greater than in winter because, while spermatogenesis and sperm production are maximally active during the summer, they cease during winter and the testes undergo regression. Cycles of seasonally activated testicular activity followed by regression also occur in many other mammalian taxonomic groups, including various deer species (Lincoln, 1971), rodents and bats.

Many species align their reproductive physiology with environmental factors so that their offspring are born when environmental conditions are most favourable. Two common tactics for achieving this objective involve introducing a delay between mating and either fertilization itself, or the development and implantation of embryos (for review, see Orr and Zuk, 2014). One approach involves the prolonged storage of spermatozoa in the female reproductive tract (Holt, 2011; Holt and Fazeli, 2016); this is usually limited to several days in mammals, although sperm storage in some bat species can last several months (Krishna and Dominic, 1978; Racey *et al.*, 1987; Roy and Krishna, 2011). An alternative approach to the temporal uncoupling of mating and fetal development, known as delayed implantation (Fenelon *et al.*, 2014; Lopes *et al.*, 2004) has been adopted by at least 130 eutherian mammals. In species such as the seal (Pomeroy, 2011), badger (Yamaguchi *et al.*, 2006), Giant panda (Zhang *et al.*, 2009), armadillo and stoat (reviewed by Mead, 1993), the embryos do not develop for some weeks or even months, before the diapause ends and the pregnancy resumes. Sixteen species of mustelids exhibit long gestations ranging from 172 to 365 days, with embryonic development being arrested for most of this period (Mead, 1993). In these species, the fertilized embryo remains within the uterus until an external signal such as shortening day length stimulates the embryo to resume its development and undergo implantation. Mead (1993) pointed out that the distribution of this trait within a genus is not constant, and cited long-tailed weasels and stoats (*Mustela frenata* and *Mustela erminea*) as examples; these species exhibit delayed implantation, whereas the least weasel (*Mustela rixosa*) does not. Eastern and western spotted skunks (*Spilogale putorius*) may be even more closely related, yet only those from west of the continental divide exhibit embryonic diapause.

Mechanisms for the control of embryonic diapause in mammals are usually classified as either “facultative” or “obligate” (Fenelon *et al.*, 2014). Facultative diapause is induced by the metabolic stress of lactation, and implantation occurs when the stress is relieved. Examples include some of the marsupials, where the diapause is terminated immediately if lactation ceases (Renfree, 1981). Obligatory diapause is widespread among the mustelidae as described above (Mead, 1993), is rigidly controlled by factors such as photoperiod and occurs in every gestation. One of the mustelid species (the stoat, *Mustela erminea*) employs obligatory embryonic diapause in a very unusual way. Reproductive activity in this species, which is highly seasonal, involves the young female stoat reaching sexual maturity at about 6–8 weeks of age; she is mated while still in the nest and before she is weaned (Gulamhusein and Tam, 1974). Mating takes place in June or July, but the female does not give birth until the following April or May; in this instance, the delay of implantation is almost certainly necessary to ensure that the female is sufficiently mature to bear the stress of pregnancy.

Intriguingly, such observations of reproductive heterogeneity among closely related species tend to suggest that the mechanisms governing embryonic diapause and delayed implantation evolved independently. Using similar arguments, evidence that sperm storage mechanisms also show considerable dissimilarity between species leads towards the same conclusion (Holt and Lloyd, 2010). It seems reasonable to suggest that neither long-term sperm storage nor embryonic diapause required drastic genomic

and metabolic reorganization during evolution in order to introduce these reproductive modifications. Recent research on the expression and function of microRNA, short RNA molecules that are increasingly recognized as being significant regulators of development, suggests that they have an important role in controlling delayed implantation and embryonic diapause (Su *et al.*, 2010). This significant example of epigenetic regulation might explain how functionally important and highly targeted physiological differences could evolve so rapidly in closely related species.

Reproductive Adaptations in Eutherian Mammals

Evolution has led to a few unusual reproductive outcomes for eutherian mammals, and rather than try to provide here a detailed description of basic mammalian reproductive biology, which can be found in textbooks and reviews (Bronson, 1989; Doty, 1976), it is more interesting to point out how groups of species have adapted their reproductive patterns and physiologies to suit their specific needs. Eutherian mammals have colonized multiple habitats all over the world, and have evolved a dazzling variety of reproductive strategies and physiological mechanisms. Some species live in social groups while others are mainly solitary; some are tropical and others live in high latitudes where they have to cope with highly seasonal environments with differing day lengths, ambient temperatures, varying amounts of rainfall and availability of food.

African mole rats belong to a family of about 18 species of rodents whose lifestyle is, as their name suggests, mainly subterranean, and have evolved a very unusual social system that bears more similarity to that of bees and other social insects, than those of other mammals (Faulkes and Bennett, 2001). About 14 of these species live in socially well-organized colonies, where individuals within the colony have to fulfil specific functional roles such as foraging, digging tunnels or defending the colony. The ability to breed is restricted to a very small group of individuals, which includes a single female or “queen” and two or three breeding males. All other members of the colony are reproductively suppressed; consequently there is a high level of inbreeding within colonies (Reeve *et al.*, 1990). When a queen dies, one of the other females can take her place, thus showing that reproductive suppression is not irreversible. The non-reproductive males possess testes and produce spermatozoa, but they do not attempt to mate with the non-breeding females. In addition, species such as the Damaraland High Veldt mole rat *Cryptomys hottentotus pretoriae* (Rensburg *et al.*, 2002), are seasonal breeders, thus showing a rich repertoire of reproductive adaptations that provide a wealth of material for researchers interested in reproductive control mechanisms. This is not the only example of cooperative breeding in mammals; it also happens in some primates such as marmosets (*Callithrix jacchus*) (Mattle *et al.*, 2008; Yamamoto *et al.*, 2014; Ziegler, 2013), where a dominant female can suppress the reproductive capacity of other females in the group, as well as in canids (Moehlman and Hofer, 1996), beavers, mongooses and porcupines (for review, see Lukas and Clutton-Brock, 2012).

As pointed out more than four decades ago by Weir and Rowlands (1973), there are few, if any, reproductive mechanisms whose evolution can be directly attributed to either habitat or taxonomy. These authors based their argument on the premise that if two species of a genus are found to be different in any respect, then that particular factor is not a generic characteristic. This complicates our understanding of mammalian reproductive evolution and implies that some traits, such as delayed implantation and sperm storage in the female tract, have evolved independently several times. This possibility holds some promise for the survival of mammals in the face of current changes in climate and other environmental challenges as it indicates that they can adapt quickly when conditions change. In a review that was directed at considering the likely impacts of climate change, Bronson (2009) predicted that small rodents will probably adapt to new conditions with relative ease because of their short generation time; however, he also cautioned that large and long-lived species whose reproduction is rigidly controlled by photoperiod will find it more difficult to adapt, especially as they might shift their geographical ranges.

Conclusions

This short review emphasises that mammalian reproduction owes its widespread success largely to the way that a few physiological processes such as sperm production, ovulation and embryonic development have developed within a framework that can be modified by the demands of habitats. While the detailed neural mechanisms controlling the endocrine system, the cell biology of sperm formation or early embryonic development can be studied in isolation using experimental animals, a comparative overview between species demonstrates that nature has treated these fundamental processes as reproductive building blocks that can be engineered together in an endless number of permutations and combinations. That these permutations characterize the whole animal is a feature of biology that is frequently overlooked in an era when research tends to focus mainly on gene and protein sequences, without necessarily remembering that a mouse or rat is not the same as an elephant. This principle has been succinctly stated as “a cow is not the same as a cheetah” in numerous lectures and reviews by Wildt *et al.* (2001) of the Smithsonian Conservation Biology Institute, Centre for Species Survival in Washington, DC, United States.

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