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Reproductive cycle of the elephant☆

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ABSTRACT

The combination of a few factors, including poor captive reproduction, secession of importation from the wild and advances in hormone detection and ultrasonography, has contributed to the current knowledge on the elephant reproductive cycle. Several reproductive features in elephants differ markedly from other mammals. These include the urogenital tract anatomy, length and structure of the reproductive cycle, the formation of multiple corpora lutea and the type and secretion pattern of reproductive hormones. Being 13–18 weeks in length, the elephant estrous cycle is the longest amongst all studied non-seasonal mammals to date. Progesterone increases 1–3 days after ovulation, indicating the start of the luteal phase, which lasts 6–12 weeks. This is followed by a 4- to 6-week follicular phase that is concluded by two, precisely spaced and timed, LH surges. In general, the first, anovulatory LH surge occurs exactly 19–21 days before the second, ovulatory surge. Normally, a single follicle is ovulated. However, beside a corpus luteum (CL) forming on the site of ovulation, multiple accessory CLs can be found on the ovaries. Unlike many other species, the predominant progestagen secreted by luteal tissues is not progesterone, but rather its 5-alpha-reduced metabolites. The currently known aspects of the unique estrous cycle in Asian and African elephants, covering estrous behavior, circulating hormones, ultrasonography and anatomy of the reproductive organs as well as hormonal manipulation treatment possibilities, will be reviewed here.

1. Introduction

In the past, few zoological institutions were successful in breeding elephants. Unable to sustain captive populations due to cessation of imports from the wild and insufficient captive offspring production and the decline of elephant numbers in their natural habitats, have prompted research on the reproductive physiology of these magnificent creatures. These efforts were coupled by advances in hormone detection techniques in serum, urine and fecal samples and the utilization of ultrasonography as a non-invasive tool to help understand reproductive events such as the onset of puberty, ovarian cycle activity and reproductive senescence in elephants.

The order proboscidea contains only one family of living animals – the elephantidae, which includes the genera Loxodonta with two species and Elephas with a single species. This separate taxon position makes the comparison of the elephant reproduction physiology with models of related animals difficult. Thus, research on these animals, primarily in their natural habitat, provides us with knowledge of new, and apparently successful, reproductive strategies within the animal kingdom (Rasmussen et al., 1982; Hildebrandt et al., 2006). The reproduction of elephants, as our largest and most charismatic land mammal, has interested many researchers. During the large culls in African from the 1950s to the 1980s the understanding of reproductive physiology increased due to post mortem investigations (e.g. Perry, 1953; Short, 1966; Hanks and Short, 1972). Advances in the use of ultrasonography and radio- and enzyme-

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immunoassays in wildlife medicine played a decisive role in the progression of reproductive understanding and management in both elephant genera.

In general, the reproductive processes within the family elephantidae are believed to be similar (Hodges, 1998), however, when compared, slight differences in the hormone profiles, especially during pregnancy, are apparent (Brown et al., 2004; Meyer et al., 2004). The growing database on reproduction biology of elephants has led to the development of assisted reproduction technologies (Hildebrandt and Schnorrenberg, 1996; Hildebrandt and Göritz, 1998) and enhanced birth rates in captivity (Saragusty et al., 2009). However, there are still some gaps in knowledge.

2. Anatomy of the reproductive tract

Formerly, most of the knowledge on the reproductive organs in elephants is derived from culls of African elephants (e.g. Perry, 1953) and single specimens of Asian elephants (e.g. Balke et al., 1988a). Thus, historically, basic information has mostly relied on findings in African savannah elephants and from them applied to the other species. These pioneers provided the groundwork for understanding of elephant reproduction. Possibly the most striking characteristic of the female elephant reproductive tract is its size. Being about 3 m in total length, it is the longest amongst all land mammals (Balke et al., 1988a,b). The vestibule (canalis urogenitalis) has an average length of 1.3 m and it opens at the vulva between the hind legs. This tube-like structure runs caudo-vertical from between the hind legs towards the tail, where it curves cranially around the pelvic bone to form a 20- to 40-cm long horizontal sac. At its cranial end, the hymeneal membrane is found, leaving only a tiny opening of about 4 mm × 2 mm to the vagina. This vaginal os is guarded left and right by two blind pouches of similar size. The hymen will rupture during the first delivery and not during copulation, as is the case in other species. The vagina extends to a length of up to 50 cm and its internal surface is folded into longitudinal folds. The lumen of the vagina is filled with mucous which increases markedly during the transition from the luteal to the follicular phase. The mucous gradually dissolves between the first and second LH surges and is excreted during urination. The mixture of urine and mucous contain specific pheromones that act to attract the breeding bulls to the female in estrus (Rasmussen et al., 2008). The folded cervix is about 15 cm long with a prominent cone-shaped portio cervicalis. The bi-corneal uterus includes a *corpus uteri* (about 15 cm long) that splits into two long uterine horns. The endometrium lining the uterine body and horns show longitudinal rugae. Each pregnancy leaves permanent damage on the endometrium that is repaired by scar tissue so that the number of pregnancies can be determined during autopsy by counting these scars (Laws, 1967). The comparably small ovaries, averaging 55–65 mm (Short, 1966; Kidson et al., 1995), of adult females are completely enveloped in a serosal pouch which forms the oviductal infundibulum and is incorporated into the two ovarian bursae (Amoroso and Perry, 1964). Physiologically, the ovaries always contain functional structures such as small follicles during the follicular phase, in addition to a preovulatory follicle at estrus, and multiple corpora lutea at all times, however the progestagen concentration remains at baseline during the follicular phase (Smith and Buss, 1975; Hermes et al., 2000). Between 6 and 42 corpora lutea have been recorded on both ovaries (Laws, 1969), with larger number recorded in younger, pregnant cows (Hanks and Short, 1972).

3. Ovarian cycle

Elephants are considered to be non-seasonal, polyestrous breeders although the issue of seasonality has been challenged (see section on sociosexual behavior). In the wild, females reach maturity at an age of 10–12 years (Perry, 1953; Sukumar, 1994), whereas in captivity pregnancy was reported to occur at an age as young as 3.5 and 7 years for Asian and African elephants, respectively. The elephant exhibits the longest spontaneous estrous cycle of any mammal studied to date: 13–18 weeks in duration, with a 6- to 12-week luteal phase and 4- to 6-week follicular phase (First reports, Asian: Hess et al., 1983; African: Plotka et al., 1988). This suggests that females may express only three to four fertile cycles per year. Free-ranging animals, however, are either pregnant or in lactational anestrus, thus multiple non-conceptional cycles seem to be rare in the wild (Hildebrandt et al., 2006).

Elephants are monovular species, however multiple CL are present in every reproductive cycle. The origin of the accessory CL stayed unresolved for a long time, leaving room for speculations. The fact that elephants are primarily uniparous (twins occur in approximately 1% of the births, Niemuller et al., 1998) and the finding of only one recent ovulation in an African elephant female shot shortly after copulation (Short, 1966), led to the assumption that elephants must be monovulatory. It was not until the introduction of ultrasonic technologies for reproduction monitoring (Hildebrandt et al., 1996, 2000; Hermes et al., 2000) that it was possible to prove this theory to be correct.

Changes throughout the cycle were studied in African elephants by Hermes et al. (2000). The study demonstrated two ovarian follicular waves within the inter-luteal phase. Only the second wave bore a dominant follicle that ovulated. For an animal of such a body size, the ovulatory follicle ruptures at a comparatively small diameter of about 21 ± 0.5 mm, 12–24 h after the ovulatory LH peak. The maximum follicular diameter around the first, anovulatory LH surge, for comparison, is 13.7 ± 0.7 mm. Even before estrus, luteinization of non-ovulatory follicles can be regularly seen after the first LH peak. The ovulatory CL reaches a diameter of 22.5 ± 0.8 mm shortly after ovulation, and it can no longer be distinguished from the other CLs after that. No follicular growth takes place throughout the luteal phase (Hermes et al., 2000). Follicles start forming as soon as concentrations of progesterone have reached baseline (unpublished data).

The endocrine status has distinctive influence on the uterine texture. Under estrogen dominance, during the late follicular phase, the cross-section of the endometrium becomes enlarged (35.4 ± 0.2 mm) and the horns become more convoluted than during the luteal phase (Hildebrandt