

Estrous Cycle of Induced Ovulators: Lesson From The Camel – A Review

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ABSTRACT:

Camel, rabbit, cat, ferrets, minks, koala and meadow moles are induced ovulators requiring copulation to trigger the ovulatory process and the estrous cycle differs from that of other domestic animals. The estrous cycle in these animals composed of follicular recruitment, follicular growth, follicular maturity and follicular regression phase. These animals are variously reared as companion, fur-bearing and meat animals. Among these, the camel is the most valuable and classical induced ovulator which is rear not only for milk and meat, but as work animal and contributes effectively to the welfare of people in harsh and difficult environments. As a classical induced ovulatory, camelid has cycling receptivity with distinctive estrus but requires mating in order to ovulate. The other classes of induced ovulators like cats and ferrets require both the presence of male to achieve behavioral estrus and actual copulation to ovulate. The camel has good prospects of survival as a suitable livestock for projects of sustainable agriculture and animal production under harsh desert or arid conditions. However the reproductive nature of camels presents a huge challenge to camel husbandry. The natural constraints include the long period of attaining puberty, limited breeding season, difficulties in induced ovulation, long gestation period and inter-calving intervals. Efforts to improve the reproductive efficiency of the female camel are closely related to a better understanding of the folliculogenesis or follicular wave pattern. Many investigators might not be aware of the peculiar reproductive information available about this animal species. A working knowledge of ovarian function or estrous cycle will be of immense importance to the application of assisted reproductive technologies (ARTs) and enhancements of reproduction in camelids. This work presents the overview of estrous cycle in camel as a classical example of induced ovulators with the aim of providing current knowledge to the reader and to stimulate wider research interest in camel research and reproduction.

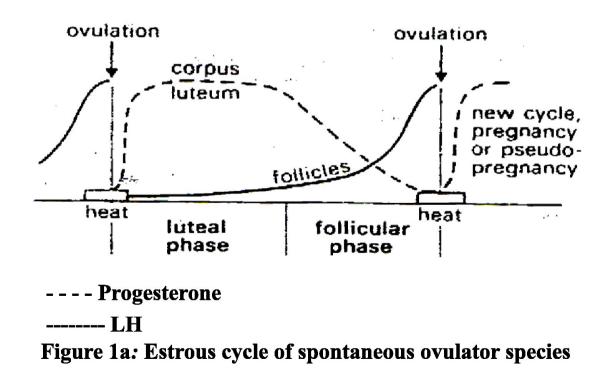
*Corresponding Author: E Mail: yahidauda@gmail.com Tel: +2348037811882 **Key Words:** Camel, Estrous cycle, Follicular wave, Induced ovulators, Reproduction

INTRODUCTION

Estrous cycle is defined as the period extending from one estrus to the next successive estrus [1,2]. In other words, it is a combination of physiological events which begins at one estrus and ends at next [3, 4]. The estrous cycle of spontaneous ovulators species such as sheep, goat and cattle is generally divided into two broad phases: the follicular phase and the luteal phase. This is further subdivided into a number of phases which include pro-estrus, estrus, metestrus and di-estrus [5, 6, 7, 3, 4]. Unlike spontaneous ovulators, the estrous cycle of induced ovulators is characterized by repetitive waves of follicular growth and regression usually referred to as follicular wave pattern [8, 9, 10, 11] (Figures 1a & 1b). Hence induced ovulators do not have a true classical estrous cycle. The estrous cycle or follicular wave

pattern in these animals notably composed of recruitment, follicular growth phase, mature phase and regression phase [10, 11, 12].

The induced ovulators or reflex ovulators, such as the camel, rabbit, cat, ferrets, minks, koala and meadow moles require the act of copulation to trigger or stimulate the ovulatory process [13, 7, 14, 15, 16, 17]. These animals are usually reared as companion, fur-bearing and meat animals. Coitus triggers signals that stimulate release of gonadotrpin releasing hormone (GnRH) which leads to release of LH and induces ovulation. In classical induced ovulators like camel and rabbits, sexual receptivity occurs in cycles that are spontaneous, but ovulation does not occur without copulation or simulation [13, 18]. In others like mink and ferret, presence of male is also require to come into behavioural estrus and to ovulate [15].





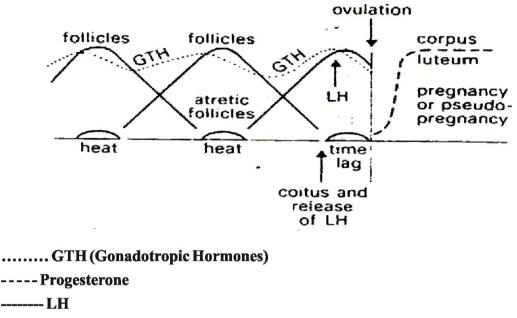


Figure 1b: Estrous cycle of induced ovulator species Adapted and modified from [9]

Females ferret reach puberty at the age of 8-12 months. The ferret is usually monoestrous, but can present a transition to the polyestrous subject to male effect. Copulation usually last from 45 min to 1 hour while ovulation usually occurs 30-40 hours after copulation. Ovulation is induced by pressure on the cervix associated with copulation [16]. The mink has similar estrous cycle pattern with the ferret but slightly differs in the ovulation period which occurs 28–72 hours after copulation [14, 17].

The female rabbits have periods of sexual receptivity every 4-6 days and the estrus period lasts about 14 days. Ovulation occurs within 10 hours of coitus. However, visual in conjunction with acoustic and olfactory contacts with an intact male could play a role in estrus and ovulation [19]. Like female rabbit (doe), cat queens are capable of multiple pregnancies within a single reproductive season, making them one of the most prolific domestic species.

On average, queens reach puberty or experience their first estrous cycle between 5 and 9 months of age [20]. Queens are seasonally polyestrous [21]. On average, queens display estrous behavior every 2 weeks during the season unless pregnancy or pseudopregnancy occurs [20].

Among the induced ovulator species, the camel is the most valuable animal and the classical induced ovulator that is being reared, not only for milk and meat, but as work animal and contributes effectively to the welfare of people in harsh and difficult environments. Camels belong to the family camelidae. The family Camelidae comprises of two subfamilies namely: Camelinae (Old World Camelids) and Laminae (New World Camelids). The genus Camelus has two species namely one humped camel (*Camelus dromedaries*) found in Africa, Arabia, Iran, Afghanistan and India and twohumped camel (*Camelus bactrianus*) found in Central Asia, Mongolia and Western part of China. The old World camelids are the bactrianus and the New World camelids include the llama (*Lama glama*), the alpaca (*Lama pacos*), the guanaco (*Lama guanacoe*), and vicuana (*Vicugna vicugna*) [22, 23, 24]. Dromedaries in Nigeria are concentrated in the semi-arid northern part of the country [24]. Pastoral groups that originate from the Chard and Niger Republic own most of the camels in northern Nigeria [25].

The camel has always been known as an indispensable bulwark against the frequent droughts and devastating famines that regularly afflict people living in the most formidable deserts and arid areas of the planet [26]. Khanvilkar et al. [27] described camels as a desert-friendly animal and important component of desert ecosystems. In the past, the primary use of the camel was for the transportation of goods and passengers in desert and semi-desert areas, while wool, milk, skin and meat were by-products [28, 29]. It used to be an irreplaceable part of the socioeconomic structure of these areas, but the advent of modern transportation system and automobiles has reduced this role and contributed to the camel's economic eclipse [30]. In addition to the wide use of the camel as draught animals, there has been increase in the use of camel as a source of milk, meat wool, race, tourism, agricultural work and beauty contest [31]. No other domestic animal is able to provide such a variety of uses to human populations. This is not unconnected with the fact that the camel is being considered as a multipurpose animal providing much of the food needs in the desert and semi-desert areas compared to cattle which are severely affected by heat and scarcity of water and feed [32]. Kadim [33] also reported that the camel is a good source of meat especially in areas where the climate adversely affects the performance of other meat animals. It is now apparent that in order to survive the new reality of more frequent drought pose by continual desert encroachment and climatic change, the inhabitants of these areas needs more camels. For these reasons, Faye [31] emphasized the need for increase camel production in the areas around the globe affected by climatic changes.

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However, the reproductive efficiency; of camels under natural pastoral conditions is low compared to other domestic animals [34, 35]. The reasons for this low reproductive efficiency include the short breading season, the long gestation period of thirteen month and the late age of reaching puberty [34, 35]. As the commercial and scientific interest in camel increases [36], it is now becoming desirable to develop methods for manipulating ovarian function in the female camel to maximize reproductive efficiency throughout the relatively short breeding season. The introduction of controlled breeding in camelids in recent years is a welcome development that can be used to exploit the reproductive potentials of the camelids and revolutionize camel industry. However, several problems associated with camel reproduction have to be considered and overcome. Firstly, the estrous cycle and estrus behavior in camel is very unique, and difficult to interpret. Secondly, all camelids are induced ovulators that normally ovulate only in response to mating [37, 38, 39, 40, 32]. Therefore, the ability to control ovulation in these species is of fundamental importance when alternative method of inducing ovulation such as the use of gonadtropin therapy is to be investigated [41]. In addition, the use of embryo transfer is becoming increasingly important, but involves the necessity to super-ovulate the donor and synchronize the recipient. This requires thorough knowledge of camelid estrous cycle and the ovarian kinetics in order to determine the exact time and period when the follicles can be responsive to such treatments. These and other scientific techniques that may emerge to improve camel reproduction require an adequate knowledge of reproductive physiology of the camelids. Therefore, a thorough knowledge of estrous cycle in camel is a key to successful and good management of such species and to the understanding of the fertility and rationalizing its treatment.

Ovarian activities and follicular wave pattern in camelids

Ovarian cycle activities and follicular wave pattern in camelids have been variously described by several authors [13, 10, 35, 11, 42, 12]. In the past, studies on the follicular wave pattern in camelids were based on ovaries obtained from an abattoir and on serial palpations of the ovaries per rectum in small numbers of camels. Nowadays, real time ultrasonography has been used to monitor and characterize day-to-day ovarian follicular changes in camelids [43, 44, 10, 35, 12].

Among the domestic animal species, the camel exhibits a unique reproductive pattern. As mentioned above, she-camel is considered to be an induced ovulator where ovulation is induced by coitus and the follicular growth occurs in regular waves during the breeding season [45, 42]. In the past, camels were considered as polyestrous, having estrous cycles all the year round [46, 47]. However, recent literatures affirm that camels are generally seasonal polyestrous species with marked peak of sexual activities usually seen or occur at certain time of the year (Table 1). Must [47] describe an allyear-round estrous in the female camel, but this was not found in natural habitat in any other literature or publication. Therefore, camels are now generally considered as seasonal polyestrous breeders whereby there are certain months during which the ovarian activity is very

low while, in others is very high [29, 48, 49, 50, 51].

Sexual activity in female camels has been reported to start between 3 and 4 years of age, but they are not usually bred until they are 5 years old when they reach their physical maturity at about 70% of their adult body weight otherwise abortion rate will increase [52, 53, 54, 55, 56]. The main triggers for sexual receptivity and ovarian activities in camels are low climatic temperature, rainfall and better grazing conditions [57, 58]. In addition, El-Harairy et al. [59] reported that environmental temperature, relative humidity and daylight length seemed to play a major role in the regulation of seasonal ovarian activity in the female dromedary camels. However, reports concerning the beginning and the length of the breeding season are rather conflicting in some quarters. Outside the breeding season, Skidmore [50] reported that mating activity ceases and the ovaries become inactive or only have few small follicles. On the other hand, Vyas et al. [60] reported that the she-camel is sexually active twice a year. It is now generally agreed that the breeding season differs in various climatic zones or countries. In Egypt for example, the session is from December to May [61]. In India, the breeding period is from November to March [62]. In the region of Pakistan, the breeding period is from December to March [9]. In Australia, it is June to September [63], while in Nigeria, the season is from October to December [24, 57] (Table 1).



Country	Breeding Season	References
Egypt	December – May	Shalash, 1987 [61]
India	November – March	Matharu, 1966 [62]
Tunisia	December – March	Vyas et al., 2001 [60]
Mali	February - March	Bono, 1979 (80)
Morocco	May – June	Wilson, 1989 (9)
Pakistan	December – March	Wilson, 1989(9)
Somalia	June – September	Wilson, 1989(9)
Australia	June – September	McKnight, 1969 (18)
Saudi Arabia	October – April	Abdel-Rahim and El-Nazier, 1990
Sudan	March – August	Wilson, 1989(9)
Israel	December – March	Yagil, 1984 (48)
Nigeria	October – December	Abdussamad et al., 2011 (51)

Table 1: Variations in the onset of breeding seasons of camel in some countries of the world

Estrus behavior, copulation and ovulation

Sexual activity is usually manifested by sexual behaviors characterize by signs of estrus or heat whereby the female is sexually receptive. The she-camel accepts the male only during this stage [29]. She-camel on heat usually becomes restless, bleat continuously and prefer to associate with males and often aggressive in manner. Tails are usually lifted up and flapped, urinate frequently; the vulva is usually swollen and discharge from the vulva frequently seen. Mounting other females, straddling of the hind limbs, copious foul smelling vaginal mucus discharges which are repulsive to human but presumably powerful and attractive stimuli for the male camels are some of the estrus behavioral signs [52, 65, 65, 66, 9, 64].

Receptivity to male culminates in lying in crouched position to be descended upon by male and the actual coitus usually takes place in crouched position [52, 65]. Copulation usually lasts for 15 - 20 minutes [64, 27]. If there is no copulation or ovulation in an induced ovulator, estrus may continue for few days (2 - 3 days)[67, 68, 35] followed by the regression of the dominant follicles and the follicular phase starts all over again until copulation and ovulation occur. Without mating or ovulation there is no luteal phase [65, 69]. In the event of actual mating or copulation, ovulation usually occurs 24 to 36 hours following copulation [70, 71]. The actual heat or estrus lasts for 3-4 days [67, 65,69].



There seems to be inadequate and conflicting reports on the mechanisms and factors that control ovulation in camels. Because the detail mechanisms that controls ovulation in naturally mated camel is not well understood, studies on alternative methods of inducing ovulation are being carried out particularly treatment with gonadotropin releasing hormones (GnRH) to induced ovulation [72].

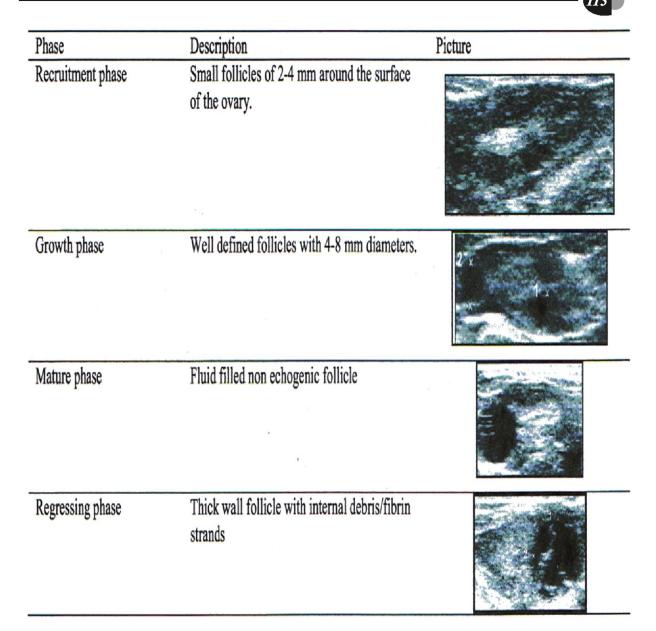
Like other induced ovulating animals, copulation in camel stimulates the cervix and afferent pathways via the hypothalamus, causing release of luteinizing hormone (LH) from the anterior pituitary. The hypothalamus controls the pituitary secretion of LH as well as follicle stimulating hormone (FSH) through the decapeptide gonadotropin releasing hormone (GnRH) which is usually produced in the region of arcuate nuclei, and possibly in the preoptic anterior-thalamic region.

The LH upsurge causes the concentration to rise sharply which stimulates the matured follicles to rupture and ovulate (Figures 1a & 1b). It was reported that only matured follicles of size between 0.9 cm and 2.9_cm ovulate while those below 0.9 cm, as well as those above 2.9 cm do not ovulate [10]. The granulosa cells of these ovulatory matured follicles contain LH, prolaclin and the hormone inhibin. The hormone inhibin preferentially suppresses pituitary secretion of FSH. This subsequently results in shift in LH/FSH ratio in favor of LH which leads to sharp increase in LH surge and subsequent ovulation [73]. In dromedary camels, LH concentration was reported to increase within one hour after mating reaching a peak of $3-10 \text{ ngm}^{-1}$ after 2-3 hours and then decreased in 6 hours later. Estrogen level however has been reported to remain low at basal concentration level during this period [74, 71].

Follicular Phase

As previously mentioned above, camels are induced ovulators and normally ovulate only in response to mating. Follicles tend to grow, have a period of maturity during which are capable to ovulate, and then regress if ovulation is not induced [65, 12]. The non-mated, nonovulatory cycle is characterized by repetitive waves of follicular growth and regression follicular wave pattern (Figures 1a & 1b). Thus the changes in the ovarian follicular dynamics in dromedary camels are described as a follicular wave pattern. Early studies on follicular wave pattern in camels were based on postmortem examination and palpation of the ovaries per rectum. However, nowadays studies are done using real time ultrasonography to monitor day-to-day ovarian follicular changes more accurately. Each follicular wave is divided into four phases namely follicular recruitment phase, follicular growth phase, follicular maturity phase and follicular regression phase [10, 11, 35] (Table 2).





The concept of establishment of dominant follicles and regression of subordinate follicles is likely to be the result of the effect of increasing inhibin production by the follicles. This is supported by an experiment by Tibary and Anouassi [42] which showed an increased number of follicles from the same ovarian walls reaching sizes greater than 1.0 cm 'after immunization of dromedary female against inhibin. The ovarian follicles under the influence of FSH grow and attend normal maturity during which time they are capable of

being ovulated and thereafter regress if mating and ovulation does not take place [65, 12]. Serial studies and field observations showed that the duration or length of estrous cycle or follicular wave interval in camelids range from 17-23 days [67, 68, 10].

Follicular recruitment phase

The follicular recruitment phase is the phase whereby a number of follicles from the ovarian pool are recruited under the influence of follicle stimulating hormone (FSH). The follicular recruitment phase corresponds to the start of a new follicular wave. During this phase the FSH secretion provides the fundamental signals for the recruitment. The follicular recruitment is characterized by the presence one or more follicles from the ovary and begin to grow and could be recruited in this phase [76]. The initial sizes of the emergent follicles were reported to vary between 2-4 mm diameters on the surface of the ovaries [10, 35, 76, 75]. The follicular recruitment phase usually takes about 2-4 days [11, 10, 75].

Follicular growth phase

The period of follicular recruitment is usually followed by the period of follicular growth of about 3 - 4 follicles, under the influence of FSH. This is followed by the establishment of one or more dominant follicles. The dominant follicles usually grow to a mean diameter of 4 - 8 mm while the other subordinate follicle regress [11, 10, 35, 75]. Follicular growth is usually accompanied by increased in estrogen levels as well as increased in testosterone concentration. The estrogen level usually rises to a peak of $25.0 - 29.0 \text{ pgml}^{-1}$ before declines to the basal level of 1.0 - 2.5 pgml⁻¹ where it remains until the next wave of follicular growth [10, 77]. The follicular growth phase usually lasts between 6 - 10 days [11, 10, 35, 75]. The growing follicular stage is equivalent to pro-estrus stage [78].

The mature phase

The mature phase starts when one or two growing follicles under the influence of FSH grow and become dominant to attend normal maturity during which time they are capable of being ovulated. This phase encompasses the time when the diameter of the dominant follicle could continue increasing to reach maximum



diameter of between 1.5 - 2.0 cm and capable to ovulate [10, 35, 76].

In an experiment, using 36 matured female camel exposed to male each day for 27 days, Skidmore *et al.* [10] reported that 85% of the female that ovulated had follicles of diameters 0.9 cm; while the 15% had follicles between 0.5 - 0.8 cm. Thus, it would appear that 0.9 cm is about the minimum ovulatory diameter of the mature camelid graaffian follicle.

In another similar experiment ovulation rates were reported to rise sharply in mated camels with follicular diameter of between 1.0 - 1.9 cm, and then decreased sharply in camels with lower follicular diameter between 0.9 - 1.3 cm, indicating peak ovulatory diameter of about between 1.4 - 1.8 cm which also corresponds to the peak estrogen level [10]. Some oversized follicles with diameter of >2.9 cm were also noticed in the experiment [10]. Earlier, Bravo and Sumar [79] also reported similar incidence of oversized follicles which they ascribed to pathological cysts on the basis of size alone. Skidmore et al. [10] observed that the oversized follicles were anovulatory and concluded that the oversize follicles in camelids do not ovulate. However, they do not inhibit the growth and responsiveness to ovulatory stimulus of other follicles in the same or contra-lateral ovary Luteum [10, 11]. The reported incidences of oversized follicles could be due to continuing basal secretion of luteinizing hormone (LH) from the pituitary gland, but in the absence of true ovulatory (LH) surge. The mature phase usually lasts on the average 7 - 10 days [10, 76]. The matured follicular stage is equivalent to the estrus or heat stage (78).

Regression phase

The follicular regression phase occurs after the

mature phase and is due to the absence of mating or ovulation inducing treatment. In the absence of mating or induced treatment, the matured follicles regress in 7 - 8 days [10, 11, 35, 76]. As follicular growth is followed by increased estrogen production which reaches peak when follicles reaches its maximum diameter, increased inhibin production by the follicles also follows as the follicles grow to maximum size. Increased circulating levels of inhibin and estrogen have a negative feedback effect on pituitary secretion of FSH. Follicle stimulating hormone (FSH) deprivation results in follicular atresia and regression [73]. Some of the regressed follicles become thickened wall structured containing strands of blood clot. Nevertheless, like the oversized follicles, the matured follicles were reported to be non inhibitory to the growth of other follicles in the same or contra lateral ovary [10, 11, 35, 76]. New growing follicles are usually visible on the ovary before the matured follicle fully regressed to give an inter-wave interval of 17-23 days [67, 68, 10].

Luteal phase

As there is no spontaneous ovulation in the camel [45] there is no luteal phase without mating or stimulation that induces ovulation [65, 69]. In the event of sterile mating or copulation and ovulation, short luteal phase is usually observed [77, 10]. The luteal phase in the camelid is highly variable. The length of the luteal phase is not only shorter that of other livestock species, but varies greatly among the females from 2 - 10 days [71, 10, 77]. It is characterized by luteinization of the epithelial lining of the ruptured follicles and development of corpus luteum and subsequent progesterone production. As reviewed above, ovulation usually occurs 24 to 36 hours following copulation or stimulation [70, 71] and this is followed by either luteal phase or pregnancy.

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Corpus luteum usually develops following ovulation. The corpus luteum usually develops within few days (2-3) after ovulation grow to a peak, then plateau and finally regresses by day 6 - 10 if pregnancy has not occurred [71, 10, 35, 41, 77]. If pregnancy occurs, the progesterone concentration is maintained between 3 - 5 ngml⁻¹ [43, 10, 77].

In comparison with other domestic animals, the corpus luteum life span is relatively small and has early regression pattern in the absence of conceptus [41]. In the context of induced ovulators, it appears that the luteal phase of camelids estrous cycle differs from that of other induced ovulators like cats and ferrets, which become pseudo-pregnant and have extended luteal phase Camelids, therefore, have a reproductive advantage over this group of induced ovulating species, in that their much shorter luteal phase enables a more rapid return to a potentially fertile state.

Hormone secretions during camelids estrous cycle

The concentrations of Luteinizing Hormone (LH) were found to be higher during the breeding season compared to the non-breeding season [80]. These variations in LH concentration levels may explain why female camelids are seasonal breeders. The considerable variation in maximum ovarian activities and conception between seasons could be due to higher sensitivity of the pituitary to gonadotrophin releasing hormone (GnRH) and consequently their higher secretion of LH during the breeding season compared to the non-breeding season [81]. As induced ovulators, mating in camels is the stimulus for an LH surge needed for the completion of the final stages of follicular maturation and subsequent ovulation. As reviewed above, in the dromedary camels, LH concentration was reported to increase within one hour after mating reaching a peak of $3-10 \text{ ngml}^{-1}$ after 2-3 hours and then decreased in 6 hours later. Estrogen level however has been reported to remain low at basal concentration level during this period [74, 71]. On the other hand, high estrogen and testosterone concentrations during the follicular growth are probably the stimulus to behavioral estrus [78]. Regression of the follicles is usually followed by low estrogen and testosterone concentrations [82].

The main role of FSH in the estrous cycle of female farm animals is to stimulate the early stages of follicular development. Along with low levels of estrogen, FSH plays a part in the development of follicular LH receptors allowing follicles to become more responsive to the follicular increase in tonic LH secretion and thereby preparing them for ovulation and luteinization [83]. Follicle stimulating hormone in the female camelid tends to increase 3-4 days after mating compared to premating values [74, 84]. However, this increase is usually not significant [74, 83]. It is possible that this little rise in FSH secretion maybe needed for the development of the next wave of follicles if the previous mating did not end up with conception.

The primary source of progesterone in the female camelid is the corpus luteum, therefore, in the absence of mating and ovulation, progesterone plasma level remain very low throughout the follicular wave [78, 85, 86, 58]. However, after mating and ovulation progesterone concentrations start to rise reaching 3-5 ngml⁻¹ by day 7-8 [10, 41, 77]. If pregnancy occurs, the progesterone secretion is maintained [82, 43, 10, 77].

SUMMARYAND CONCLUSIONS

Camel is a classical induced ovulator species with cycling receptivity but requires mating in order to ovulate. The other classes of induced ovulators like cats and ferrets require both the presence of male to achieve behavioral estrus and actual copulation to ovulate. Unlike spontaneous ovulators, the coitus induced ovulators do not have a true estrous cycle. The ovarian activity during the cycle is strictly follicular without mating ovulation and the follicular growth occurs in regular wave pattern. Follicular wave pattern in the camelids consist of well defined, but individually variable, periods of follicular recruitment, growth, maturity and regression. The estrous cycle is therefore simply referred to as follicular wave pattern. The length of the estrous cycle or follicular wave interval in camelids ranges from 17 - 23 days. In the event of sterile mating or copulation, the luteal phase of camelids estrous cycle is short and differs from that of other induced ovulators like cats and ferrets, which become pseudo-pregnant and have extended luteal periods. Camelids therefore, have a reproductive advantage over these smaller induced ovulating species, in that their much shorter luteal phase enables a more rapid return to a potentially fertile state. The interest in applying modern reproductive technologies in camelids has increased over the last decade. This is due in part to their unique reproductive aspects and the possibility of utilizing their productive potential for commercial application (Faye, 2008). However, improving the reproductive efficiency still remains a challenging task under the present commercial production systems. More researches are needed to understand the kinetics of folliculogenesis and ovulation in the female camelid. This review, therefore, may likely stimulate further research interest in scientists

and be of considerable interest and value to camel owners as well as those who seek to support them through extension and other services.

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