Reproduction Supplement **61**, 37–47

The main challenges facing camel reproduction research in the 21st century

J. A. Skidmore

The Camel Reproduction Centre, PO Box 11808, Dubai, United Arab Emirates

The reproductive efficiency of camels under their natural pastoral conditions is low. The reasons for this low reproductive efficiency include the short breeding season, the late age of reaching puberty and the long gestation period of 13 months. The introduction of controlled breeding programmes is important but several problems have to be considered. For example, oestrous behaviour is very vague and difficult to interpret, as it does not often relate to follicular development in the ovaries. In addition, all camelids are induced ovulators that normally ovulate only in response to mating, so alternative methods of inducing ovulation, such as injecting gonadotrophic hormones, have been investigated. The use of embryo transfer is becoming increasingly important but involves the necessity to superovulate the donors and synchronize the recipients so that they ovulate preferably 24 h after the donor. Superovulation can be achieved using exogenous gonadotrophins, although there is a high incidence of follicle luteinization before mating, of overstimulated ovaries and non-responsive females. The development of AI in camels is complicated by the difficulty of collecting semen and the gelatinous nature of the semen produced. However, diluting semen in Green Buffer and inseminating a minimum of 300×10^6 live spermatozoa has given encouraging results. The ability to control the follicular cycle of camels is leading to an improvement in reproductive efficiency.

Introduction

The family Camelidae contains two subfamilies (Camelinae and Laminae) divided into three recent genera (*Camelus, Lama* and *Vicuna*) with a total of six species. The genus *Camelus*, otherwise known as the Old World camelids, comprises two species, *Camelus dromedarius* the dromedary or one-humped camel, and *Camelus bactrianus* the Bactrian or two-humped camel. The New World camelids of South America include the domesticated llama (*Lama glama*) and alpaca (*Lama pacos*), and the wild guanaco (*Lama guanacoe)* and vicuna (*Vicugna vicugna*).

For many centuries camels have been important animals in the desert because of their ability to provide milk, meat and transport in harsh, dry conditions. Llamas and alpacas play a very important role in the economy of a large population of the Andean region,

Email: luluskid@emirates.net.ae

where they provide hair, meat, pelts and dung that is used as fuel and fertilizer (Fernandez-Baca, 1993). However, as camels are generally used in less developed countries, organized attempts to apply breeding selection to improve characteristics, such as fertility and milk or meat production, are lacking. In the Middle East, the development of camel racing has markedly increased the value of the racing dromedary camel and, thus has led to more research in the area of reproduction and the desire to improve reproductive efficiency of camels.

The reproductive efficiency of camels under natural conditions is generally considered to be low. For example in Tunisia, Djellouli and Saint-Martin (1992) reported an overall calving rate of approximately 40% for 30 herds and a mortality rate between birth and 1 year of age of 17%. Saley (1990) reported calving rates as low as 45% in East Central Niger and mortality rates of 10–25% at 0–6 months of age. The reasons for these low reproductive rates could include: (i) a relatively short breeding season; (ii) delay in the onset of puberty; (iii) a gestation period of 13 months; (iv) a prolonged (8–10 months) period of lactation-related anoestrus leading to a long interval between births; and (v) lack of use of assisted reproductive technologies, such as embryo transfer and AI. The last reason is due partly to religious beliefs but also to the lack of availability of veterinary expertise in such specialized techniques (Arthur, 1992). This review investigates the reasons behind some of these problems.

Breeding season

Both the dromedary and Bactrian camels are generally regarded as induced ovulators and seasonal breeders (Chen and Yuen, 1979; Wilson, 1984). For the dromedary camel, a rather short breeding season occurs between December and March in Pakistan (Yasin and Wahid, 1957), between December and April in Egypt (Shalash, 1965) and from November to March in most of Arabia (Abdel Rahim and El-Nazier, 1990). For the Bactrian camel in China, the breeding season occurs between the middle of January and the middle of April (Chen and Yuen, 1979).

This variation in both the onset and the duration of the breeding season demonstrates that local environmental factors must initiate sexual activity. One view is that changes in daylength stimulate seasonality (Williamson and Payne, 1978; Chen and Yuen, 1979) but, obviously, in dromedaries situated near the equator, factors such as rainfall (Bono *et al.*, 1989), pasture condition and nutrition are more important (Merkt *et al.*, 1990). Observations in the United Arab Emirates indicate that well-fed, well-watered female dromedary camels show ovarian activity throughout the year and the determinant factors of the observed seasonality in conception dates are due to a decrease in libido in the male and an increase in early embryonic death during the summer months. When males were kept in a cooler, controlled environment (temperatures $\leqslant 30^{\circ}C$ and humidity $< 40\%$), breeding was possible during the extreme heat (45–48°C) and humidity (80–100%) of August in the United Arab Emirates. However, all the females that conceived experienced early embryonic death and resorption within the first 45 days of gestation (Tibary and Anouassi, 1997). The effect of heat and humidity on embryo survival is also well illustrated by embryo transfer results. In a study by McKinnon and Tinson (1992), no pregnancies were obtained after transfer of embryos during July and August.

It is still unclear whether the seasonal trend of reproduction in the dromedary camel is due to the failure of the female to come into oestrus or to the failure of the male to mate. The answer could be found in performing an endocrinological study of ovarian activity but there is very limited information on the endocrinological aspects of seasonality in the

dromedary camel. Plasma concentrations of oestradiol vary considerably from one month to another but do not demonstrate any association with breeding activity (Bono *et al.*, 1989).

The major endocrinological change in male camels during the rutting season is the increased secretion of androgen, especially testosterone. In Nigeria, Gombe and Oduor-Okele (1977) reported a monthly variation in testosterone concentration in the dromedary camel with a negative correlation with the temperature : humidity ratio. In the Negev and Judian desert too, androgen concentrations in the male dromedary were found to increase tenfold during the rutting season. During this period, males began to show the typical rutting behaviour and increased interest in females (Yagil and Etzion, 1980).

Puberty

Puberty in female camels usually occurs at about 3 years of age in both the dromedary and Bactrian species (Chen and Yuen, 1979; Yagil, 1985), but the first mating is generally delayed until the female has nearly reached her mature physical size at 4 years of age (Yasin and Wahid, 1957), which results in the first calving at $\geqslant$5 years of age. Several factors, including nutritional status and breed or type of camel, can affect the age of onset of puberty, age at first conception and consequently the age at first parturition. In one study, age at first conception and age at first calving were 31.7 and 43.7 months, respectively, for females that were adequately fed (that is reared on an experimental farm), whereas females on lower planes of nutrition (that is, traditionally reared) did not conceive until 45 months of age (Kamoun and Wilson, 1994).

Yagil and Etzion (1984) and Rai *et al.* (1990) were able to advance the onset of puberty in young female camels by injecting them with a total dose of 2000–6000 iu equine chorionic gonadotrophin (eCG; Folligon, Intervet Laboratories, Cambridge) administered over 2–3 days. Although all the camels that received treatment showed signs of oestrous behaviour at 3–5 days after the last injection, only one of the nine camels treated by Rai *et al.* (1990) that subsequently mated carried a pregnancy to term. None of the camels treated by Yagil and Etzion (1984) conceived on the first mating after treatment.

The male camel may first show rutting behaviour as early as 3 years of age (Novoa, 1970; Chen and Yuen, 1979), which is long before physical maturity is attained. Therefore, young bulls would have little chance of mating with females in a large mixed herd, so their rut may be suppressed until full reproductive potential is reached at 5–6 years of age (Wilson, 1984). Physiological breeding capacity increases up to 10 years of age and, thereafter, remains at a fairly constant level until 18–20 years (Yasin and Wahid, 1957).

Oestrous behaviour

Oestrous behaviour can be vague, highly variable and difficult to relate to follicular activity in the ovaries. Often the male follows the female around the pen, sniffing her poll gland and then her vulva before exhibiting the flehmen reaction. In response, the female straddles her hind legs, lifts her head and tail into the air and periodically urinates even though there is no follicular activity in her ovaries. However, more often the male stands quietly in the centre of the female herd before suddenly selecting one female which he then chases, biting her hump or hind legs, until she finally submits and allows herself to be mated. Subsequent scanning of the ovaries of the selected female would show a mature follicle in one of her ovaries (Skidmore *et al.*, 1995). Arthur *et al.* (1985) also showed that a determined bull camel

would mate with a female even during early pregnancy or the luteal phase that follows a sterile mating. Therefore, oestrus detection remains a major problem in female camels.

Ovarian follicular kinetics

All camelids are induced ovulators and, therefore, if mating does not occur, follicles tend to regress after initial periods of growth and maturity and, for this reason, it is more appropriate to use the term 'follicular wave pattern' than oestrous cycle (Musa and Abusineina, 1978; Adams *et al.*, 1990; Skidmore *et al.*, 1996). Studies using ultrasonography of the ovaries to monitor the follicular wave pattern have shown that it varies considerably between camels, but can be divided into three phases: the growth phase of 10.5 ± 0.5 days, a mature phase of 7.6 ± 0.8 days and a regression phase of 11.9 ± 0.8 days. In approximately 50% of the oestrous cycles studied, the mature follicle reached a maximum diameter of 2.0 ± 0.1 cm before it regressed as expected but in the other 50% of cycles the follicle continued to grow until it reached a mean diameter of 4.1 ± 0.2 cm. These oversized, anovulatory follicles attained maximum diameter in 18.4 ± 0.8 days, remained at the same size for 4.6 ± 0.5 days and then took 15.3 ± 1.1 days to regress completely. Nevertheless, these follicles did not inhibit the growth of other follicles in the same or contralateral ovary, which would grow, mature and ovulate if the appropriate stimulus was applied (Skidmore *et al.*, 1996).

Control of ovulation

It is well established that mating with an intact or vasectomized male will induce ovulation in camels but the detailed mechanism that controls it is not well understood. In Bactrian camels it is also thought that ovulation can be induced either (i) by deep intravaginal deposition of whole semen or sperm-free seminal plasma (Chen *et al.*, 1985) or (ii) by i.m. injection of semen or seminal fluid (Pan *et al.*, 1992). This ovulation inducing effect of the seminal plasma is retained after mild heating and treatment with acid or alkali, but is destroyed by trypsin digestion, indicating that there is an active protein or polypeptide in camel semen that can express GnRH-like activity (Zhao *et al.*, 1992; Pan *et al.*, 2001). However, in dromedaries, manual stimulation of the cervix, intrauterine injection of complete semen, seminal plasma, water or cloprostenol does not stimulate the release of sufficient LH from the pituitary gland to cause ovulation (Sheldrick *et al.*, 1992).

Alternative methods for inducing ovulation have been investigated because when animals are being prepared for AI or as recipients for embryo transfer, mating to a vasectomized male or insemination with camel seminal plasma would be impractical because of the risk of spreading venereal infections and the difficulty of collecting the seminal plasma from male camels (Billah and Skidmore, 1992). In addition, because of the common occurrence of oversized, unovulated follicles, it is important to determine the limits, in terms of follicular growth and maturation, as to when the dominant follicle is most responsive to such therapy.

Studies have been carried out to investigate the reliability of treatment with GnRH or gonadotrophic hormones as a means of inducing ovulation in female camels exhibiting follicles of various sizes. Camels were treated with 20 μg of the GnRH analogue, buserelin (Receptal; Hoechst Animal Health, Milton Keynes) or 3000 i.u. hCG (Chorulon; Intervet Laboratories), or were mated (controls) when the follicles were of different sizes. The results showed that ovulation did not occur if the follicle was <0.9 cm in diameter, but ovulation increased to 85% if the follicle grew to 1.0–1.9 cm in diameter. However, the ovulation rate decreased to <30% if the follicle had grown to 2.0–2.9 cm in diameter and none of the camels ovulated when the follicle was >3.0 cm in diameter (Skidmore *et al.*, 1996).

Hormone profiles in non-pregnant camels

In unmated camels, progesterone concentrations remain low at $<1\,ng\,ml^{-1}$ throughout the entire follicular wave pattern. However, oestradiol concentrations initially increase with the increase in follicle diameter to reach maximum values of approximately $40\,pg\,ml^{-1}$ when the follicle reaches a diameter of 1.7 ± 0.1 cm. Although the follicle may continue to grow to >2.0 cm in subsequent days, the concentration of oestradiol decreases to basal concentrations of about $20\,pg\,ml^{-1}$ and remains at this concentration until the next wave of follicles start to grow (Skidmore *et al.*, 1996).

If the camel is mated, ovulation occurs 24–36 h later but progesterone concentrations in peripheral serum remain low (<1 ng ml) for the first 3 days after mating. Progesterone concentrations increase to reach maximum values of about $3\,ng\,ml^{-1}$ by day 8 or day 9 after mating before decreasing rapidly to basal concentrations of $<1\,ng\,ml^{-1}$ again, in the non-pregnant camel, by day 11 or day 12 (Marie and Anouassi, 1987). The corpus luteum has a very short luteal lifespan in comparison with other domestic species, and this has to be taken into consideration when preparing animals as embryo transfer recipients.

Maternal recognition of pregnancy

In all domestic farm animals the developing conceptus has to produce a biochemical message to the maternal animal that prevents the release of $PGF_{2\alpha}$ and, thereby, extends the lifespan of the corpus luteum. In camels, this signal has to be released before day 8, which is much earlier than in other species, if it is to prevent the occurrence of luteolysis. In cattle and sheep, this maternal recognition of pregnancy signal is thought to be interferon tau (IFN-τ; Godkin *et al.*, 1982, 1988), whereas embryonic tissues from horses and pigs do not secrete IFN-τ, but instead possess high aromatase activity and can synthesis large amounts of oestrogens from as early as day 10 of gestation. This finding indicates that oestrogens are involved in maternal recognition of pregnancy in these species (Perry *et al.*, 1973; Heap *et al.*, 1982).

The camel ruminates like cattle and sheep but has an epithelial chorial placenta like horses and pigs. However, incubation of camel conceptus tissue between day 10 and day 60 has shown no evidence of the production of IFN-τ, but has shown high aromatase activity and the ability to produce large amounts of oestrogens from as early as day 10 of gestation. This finding may indicate that fetal oestrogens are involved in maternal recognition of pregnancy in camels (Skidmore *et al.*, 1994).

Use of assisted reproductive technology in camels

As mentioned previously, opportunities to improve the reproductive efficiency of camels are limited not only by the long gestation period, production of only one calf at a time and the short breeding season, but also by the continuing use of traditional systems of reproductive management in most breeding herds. The techniques of AI and embryo transfer could be used to overcome some of these problems and provide the opportunity to produce more offspring from desirable combinations of sire and dam.

Embryo transfer

There are certain essential prerequisites for successful embryo transfer programmes: (i) induction of superovulation in the donor animals by exogenous gonadotrophin therapy and (ii) simple methods for preparing groups of synchronized recipients.

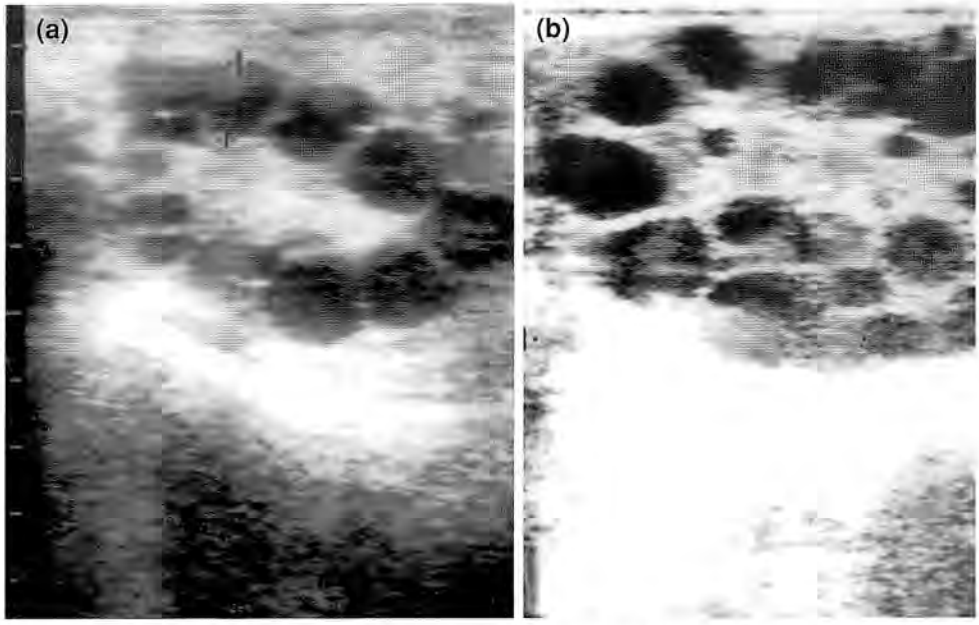

Fig. 1. Ultrasonographic images of ovaries of superovulated dromedary camels: (a) on day 9 after the start of treatment (a total dose of 2500 iu equine chorionic gonadotrophin (eCG) administered as a single i.m. injection on day 1 of the treatment protocol, and 400 mg porcine FSH injected twice a day in decreasing doses over 4 days, also beginning on day 1) showing several mature follicles and (b) an overstimulated ovary with multiple generations of follicles.

Induction of superovulation. Early attempts to induce superovulation in camels used doses of 2000–6000 i.u. eCG, 20 i.u. ovine or 400 mg porcine FSH and these treatments resulted in the recovery of 2–12 embryos (Skidmore *et al.*, 1992; McKinnon *et al.*, 1994). More recently, other methods using a combination of eCG and porcine FSH have shown more potential. A total dose of 2500 i.u. eCG administered as a single i.m. injection on day 1 of the treatment protocol, and 400 mg porcine FSH injected twice a day in decreasing doses over 4 days, also beginning on day 1, was used and 19.7 ± 5.3 follicles were produced in the ovaries (Fig. 1a) (Skidmore *et al.*, 2002).

However, there are several problems associated with superovulation treatments in Camelidae. For example, approximately 20–30% of females treated do not respond to the hormones and it has also been noted that in FSH-treated animals there is a high incidence of premature regression of the follicles, which could be due to inappropriate dosage of the hormones or method of delivery. In addition, there is a high incidence of follicle luteinization before breeding, which is particularly prevalent in eCG-treated females, and could be due to the LH activity of the hormone. In addition, in some females the ovaries become 'overstimulated' and contain many generations of follicles of different sizes, not all of which will be mature enough to ovulate when the camel is mated (Fig. 1b). Dromedary camels can also become refractory to the superovulation treatment with FSH and eCG which may be caused by immunization against these hormones. A complete arrest of ovarian activity has been noted in some females that have been repeatedly treated with these superovulation hormones over a few years (Tibary and Anouassi, 1997). More studies are needed on follicular dynamics and its intra-ovarian and hypthalamo–pituitary regulation to address these problems.

Synchronization of ovulation. When preparing camels for AI or embryo transfer it is necessary to be able to control follicular growth and synchronize ovulation in groups of animals. Results of embryo transfer in camels indicate that the best recipient to use should have ovulated on the same day as, or up to 48 h after, the donor (McKinnon *et al.*, 1994; Skidmore *et al.*, 2002). However, synchronizing ovulation and follicular growth poses particular problems in camels due to the absence of a cyclical corpus luteum that would be present in spontaneously ovulating species, such as the horse and cow.

Cows can be synchronized either by two injections of $PGF_{2\alpha}$ administered at an interval of 11 days (Cooper *et al.*, 1976) or by administration of exogenous progesterone or progestagens, with or without $PGF_{2\alpha}$ (Roche, 1976), but this treatment depends on the presence of an active corpus luteum in the ovaries. This method is unsuitable for camels because they are induced ovulators and, thus, normally have a corpus luteum in their ovaries only when they are pregnant (Musa and Abusineina, 1978). Therefore, it may be possible that the progesterone dominated background of dioestrus, which is thought necessary to provide 'priming' for the waves of follicular growth in other spontaneously ovulating species, is not necessary in camels. A sterile corpus luteum can be created by injecting GnRH when a mature follicle is present in the ovaries, and treatment with $PGF_{2\alpha}$ or one of its analogues will cause premature luteolysis if given after day 4 after ovulation but, because the lifespan of the corpus luteum is only 8 days on average, and because the interwave interval can be shortened only by 2 days when administering prostaglandin, the usefulness of this form of therapy to synchronize the follicular cycle of groups of camels is very limited (J. A. Skidmore, unpublished).

There are few published reports on the use of progestagens to control follicular growth in the dromedary camel. Treatment with progesterone releasing intra-vaginal devices (PRIDs) has been found to be unreliable because not only did several animals develop a vaginal discharge, but also only 39% and 28% of the females responded by ovulating after receiving 3000 iu hCG or 20 μg buserelin, respectively, after removal of the PRID. In addition, a high percentage of the females had high concentrations of progesterone before treatment with hCG or buserelin and were considered to have ovulated spontaneously after removal of the PRID (Marie and Anouassi, 1987; Cooper *et al.*, 1992).

Synchronization of ovulation between donor and recipient camels can be achieved using one of two methods, either selection of recipients from a random group or preparation of recipients using a combination of eCG and progesterone-in-oil to attempt to synchronize follicular development with the donor. In the first technique, a group of cyclic recipients is examined 24 h after the donor mates and all females that have a mature follicle in their ovaries are injected with GnRH or hCG (Skidmore *et al.*, 2002). However, this method of selection of recipients is time consuming and can be used only if the number of donors is limited and there is a large pool of recipients to chose from.

The best results of synchronization of ovulation have been obtained when recipients are induced to ovulate with hCG (3000 i.u.) or buserelin (20 μg) after a treatment combining progesterone and eCG (McKinnon *et al.*, 1994). The recipients are treated daily with progesterone-in-oil (100 mg day^{-1}) for 10–15 days followed by administration of 1500–2500 i.u. eCG. Progesterone treatment is scheduled to end on the day of injection of gonadotrophin in the donor and the eCG treatment guarantees the presence of mature follicles in the recipient at the same time or 24–48 h after the donor has ovulated. However, this method can be very time consuming as the camels need handling and injecting daily, as well as expensive when dealing with large numbers of animals.

Synchronization between embryo and uterus can also be obtained by progesterone treatment alone without induction of ovulation (Skidmore *et al.*, 2002). Progesterone (100 mg) is injected daily starting 1 day before expected embryo transfer but, as there is no corpus luteum

in the ovaries, progesterone treatment needs to be continued for the duration of pregnancy. Although pregnancies (44%) were established using this method, a treatment protocol requiring daily i.m. injections throughout the whole 13 month gestation period of a camel is not very practical. Further studies investigating other forms of progesterone or progestagen administration, such as the orally active progestagen allyl trenbolone (Regumate, Hoechst, Animal Health), which is capable of maintaining pregnancies in ovariectomized mares (McKinnon *et al.*, 1988), need to be performed.

Artificial insemination

As in other species, AI is an important technique not only to ensure rapid genetic progress in camels but also to enable more efficient use of genetically superior males, help prevent spread of venereal diseases, eliminate the need for transportation of animals and eliminate behavioural problems. The use of AI has been reported in camels and most studies have been carried out in Bactrian camels (Zhao *et al.*, 1994). In dromedaries, several workers have studied semen preservation but insemination trials are rare (Anouassi *et al.*, 1992). The lack of these studies could be due to the difficulty in collecting and subsequent analysis and handling of the semen.

Collection of semen. Semen can be collected in one of two ways: either by electroejaculation or by using an artificial vagina. For electroejaculation the male camel has to be fully anaesthetized and specialized equipment is necessary, so it is preferable to use the artificial vagina (Bravo *et al.*, 2000). However, not all males will use an artificial vagina especially if they are older and used to natural mating. Young males can be trained to the artificial vagina with time and patience but mating times are not as long as with natural mating and ejaculates may not be complete.

Semen analysis. Most studies on semen preservation in camels use sperm motility and acrosome integrity as the main parameters for the evaluation of semen. However, semen motility is very difficult to evaluate because of the gelatinous nature of the semen produced. Unlike in horses, this gel fraction cannot be separated from the sperm-rich fraction, which makes estimation of sperm motility very difficult and highly variable. It has been reported that semen will liquefy if left at room temperature for 20 min but again this can vary among ejaculates. In dromedary and Bactrian camels, semen is diluted at a ratio of 1 : 1 to 1 : 3 (semen : extender) depending on the concentration of spermatozoa (Anouassi *et al.*, 1992; Musa *et al.*, 1992) but thorough mixing is difficult due to the gelatinous nature of the semen.

More detailed studies are needed to determine which extender is the most effective and the minimum number of spermatozoa to be inseminated to establish pregnancies, but preliminary studies show that either Laiciphos or Green Buffer (I.M.V. L'Aigle) give the best results for extending the semen of camels, and pregnancies can be achieved by inseminating 300×10^6 live spermatozoa (Anouassi *et al.*, 1992; Bravo *et al.*, 2000). This number of spermatozoa could be reduced by more detailed studies on the timing of insemination in relation to time of ovulation as well as the method of insemination, that is, the conventional method, inseminating semen just through the cervix versus hysteroscopic insemination using a videoendoscope to deposit a much smaller number of spermatozoa directly on to the uterine tubule junction at the tip of the uterine horn. Morris *et al.* (2000) have developed this latter technique in horses and have shown that as few as 5×10^6 spermatozoa are required to establish a pregnancy.

Conclusion

Although camels are seasonal breeders and do not reach puberty until 3–4 years of age, the increasing necessity to improve camel production has led to the development of a more scientific management of these animals. Oestrous behaviour is difficult to interpret but ultrasonography can be used to monitor follicular growth in the ovaries. When mature follicles develop, ovulation can be controlled by using GnRH or gonadotrophic hormones if they are administered at the correct stage of follicular development. Superovulation can also be induced by using eCG or FSH, and embryos recovered by simple non-surgical means 8 days after the female camel is mated. Pregnancy rates of 65–70% can then be achieved if the embryos are transferred to recipients that have ovulated 24–48 h after the donor. Development of AI in Camelidae requires more research to develop reliable semen collection methods, to determine the appropriate frequency of collection and to develop reliable semen evaluation techniques. In addition, studies on the biochemistry of semen, especially with reference to liquefaction and the effect of seminal plasma on cryopreservation and its interaction with various extenders, needs further investigation.

These results show that with good management, controlled breeding and strategic use of hormone treatments it is possible to increase the reproductive efficiency of camels. However, there is still a large gap in the areas of nutrition and disease control and their relationship to production that needs to be filled to maximize the reproductive potential of these multipurpose animals.

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