The ovarian follicular wave pattern and induction of ovulation in the mated and non-mated one-humped camel (*Camelus dromedarius*)

J. A. Skidmore[1,2], M. Billah[1] and W. R. Allen[2]*

[1]*The Camel Reproduction Laboratory, Nakhlee, PO Box 11808, Dubai, UAE; and* [2]*TBA Equine Fertility Unit, Mertoun Paddocks, Woodditton Road, Newmarket, Suffolk CB8 9BH, UK*

Ovarian follicular wave patterns were studied ultrasonographically in three groups of dromedary. Group 1 camels ($n = 20$) were teased daily with a vasectomized male but mating was prevented; group 2 camels ($n = 8$) ran freely with a vasectomized male camel for 10 h each day and group 3 camels ($n = 8$) were kept completely separate from any males. In a second experiment ($n = 63$), when the diameter of the dominant follicle reached 0.5–0.9 cm, 1.0–1.9 cm, 2.0–2.9 cm or > 3 cm, the camel was given one of three treatments to induce ovulation: (i) natural mating; (ii) 20 µg of the GnRH analogue, buserelin; or (iii) 3000 iu hCG. The ovaries were re-scanned regularly to monitor ovulation, and daily blood samples were assayed for progesterone and oestradiol concentrations. The follicular cycle was divisible into a growth phase (10.5 ± 0.5 days), a mature phase (7.6 ± 0.8 days) and a regression phase (11.9 ± 0.8 days). The dominant follicle reached a mean $\pm$ SEM maximum diameter of 2.0 ± 0.1 cm (range 1.5–2.5 cm) in 34 cycles (52%) before it began to regress. In the other 32 cycles (48%), however, the dominant follicle continued to grow to 4.2 ± 0.2 cm (range 4.0–6.0 cm) before regression commenced. Group 2 camels were mated when their follicles reached 1.3 ± 0.1 cm in diameter and the mean interval between successive matings was 13.8 ± 1.0 days. Mean $\pm$ SEM serum concentrations of oestradiol reached peak values at 39.0 ± 1.8 pg ml^{-1}, when the dominant follicle measured 1.7 ± 0.1 cm and, after ovulation, mean serum concentrations of progesterone reached peak values at 2.6 ± 0.3 ng ml^{-1} on day 8, before decreasing to < 1 ng ml^{-1} by day 10 or 11. When the dominant follicle measured 0.5–0.9 cm in diameter, 70%, 60% and 60% of them ovulated in response to mating, or treatment with buserelin or hCG, respectively. These ovulation rates increased to 85% (mating), 81% (buserelin) and 67% (hCG) when the follicle measured 1–1.9 cm, but they decreased again to 12.5% (mating), 29% (buserelin) and 13% (hCG) when the diameter had increased to 2.0–2.9 cm at the time of treatment. No follicles measuring > 3.0 cm ovulated in response to any of the treatments. These results indicated that the optimum time to mate or attempt to induce ovulation in the female dromedary is when the growing follicle measures 0.9–1.9 cm in diameter.

Introduction

Camelids of the New World (e.g. llama and alpaca) and the Old World (dromedary and bactrian camel) are seasonal breeders and induced ovulators (Fernandez Baca *et al.*, 1970; Musa and Abusineina, 1978; Adams *et al.*, 1990; Bravo *et al.*, 1990). Original studies on the follicular wave pattern in dromedaries were based on ovaries obtained from an abattoir and on serial palpations of the ovaries *per rectum* in small numbers of camels. From these surveys the duration of the follicular wave was reported to range from 17.2 to 23.4 days in India (Joshi *et al.*, 1978), and to have a mean duration of 24.2 days in Egypt (Wilson, 1984) and 28 days in Sudan (Musa and Abusineina, 1978). In bactrian camels, Chen and Yuen (1979) reported a

mean follicular wave duration of 19 days, with a range of 14–21 days. More recently, realtime ultrasonography has been used to monitor day-to-day ovarian follicular changes in large animals such as cows (Savio *et al.*, 1988; Sirois and Fortune, 1988), sheep (Ravindra *et al.*, 1994), horses (Pierson and Ginther, 1987; Sirois *et al.*, 1989) and llamas (Adams *et al.*, 1990; Bravo *et al.*, 1990). In cows, large antral follicles grow in two (Ginther *et al.*, 1989) or three (Savio *et al.*, 1988; Sirois and Fortune, 1988) waves, each of which is characterized by the simultaneous emergence of a cohort of follicles from a pool of small follicles and the establishment of a dominant follicle that continues to develop while apparently suppressing the growth of the other follicles (Fortune *et al.*, 1988; Pierson and Ginther, 1988; Savio *et al.*, 1988).

The factors that control ovulation in the camelids are not well understood. In bactrian camels, ovulation can be induced by deep intravaginal deposition of whole semen or sperm-free

seminal plasma (Chen *et al.*, 1985), as well as by i.m. injection of semen or seminal fluid (Zhao *et al.*, 1990). In dromedaries, ovulation is induced by mating with an intact or vasectomized male (Marie and Anouassi, 1987), but manual stimulation of the cervix or intrauterine injection of whole semen, seminal plasma, water or the prostaglandin F analogue, cloprostenol, does not stimulate the release of sufficient LH from the pituitary to cause ovulation (Musa and Abusineina, 1978; Sheldrick *et al.*, 1992). Efficient methods to induce and synchronize ovulation in dromedaries are now required as interest grows in the potential application of artificial insemination and embryo transfer to this species (Cooper *et al.*, 1992). However, mating to a vasectomized male is not acceptable because of the potential for spreading venereal diseases. This leaves treatment with an LH-like gonadotrophic hormone at the optimal time in the follicular growth cycle as the most practical alternative.

The purpose of the present study was twofold. First, to define accurately the patterns of follicular growth and regression in dromedaries by means of repeated realtime ultrasonographic examinations of the ovaries, and to relate these morphological events to changes in behaviour and steroid hormone concentrations in peripheral blood. Second, to compare the efficacy of two forms of gonadotrophin therapy to induce ovulation in non-mated camels and to determine the optimal time in the follicular wave cycle for their application.

Materials and Methods

Animals

A total of 73 mature female dromedaries aged 5–14 years was used in two experiments. They were maintained in groups of 8–30 animals in fenced pens, each of 0.002–0.004 km² area. They were fed a diet of mixed concentrates and lucerne hay once a day and were given water *ad libitum*. Thirty-six camels were used in Expt 1 (1 December–31 January, 1993–1994) and 60 were used in Expt 2 (12 November–30 March, 1993–1994).

Ovarian examinations

The ovaries of every camel were examined on alternate days throughout the defined experimental periods by transrectal ultrasonography as described by Skidmore *et al.* (1992). An Aloka Model 500 realtime scanner with a 5 MHz linear array transducer (Al Carmal Ltd, Dubai, UAE) was used and all follicles ≥ 0.5 cm in diameter and corpora lutea present in both ovaries were counted, measured using the internal electronic calipers and photographed using a Sony Model UP 860CE videoprinter (Al Carmal Ltd) interfaced with the scanner.

Blood sampling and hormone assays

Samples of jugular vein blood (8 ml) were recovered daily from all camels throughout the experimental periods. They were kept at room temperature (19–23°C) for 1–2 h before being centrifuged at 1500 *g* for 5 min. The serum was decanted and stored at − 20°C until subsequent assay for progesterone and oestradiol. Owing to a limited supply of antibody and
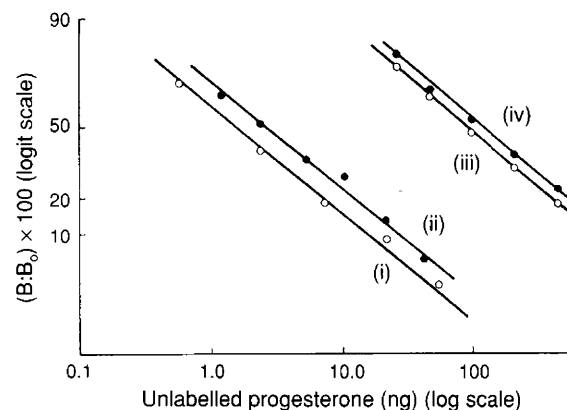

Fig. 1. Typical standard curves for the progesterone assay: (i) standards made up in human serum supplied in the assay kit; (ii) standards made up in charcoal-stripped male camel serum; (iii) and (iv) serial dilutions of a sample of camel serum containing a high concentration of progesterone diluted in either (iii) human serum or (iv) charcoal-stripped male camel serum. Results are plotted as log–logit linear transformations.

other materials for the oestradiol assay, the sera from only eight camels could be assayed for oestradiol concentration. These animals were selected randomly from Group 1 of Expt 1.

Progesterone assay. Progesterone concentrations were measured directly in 25 µl aliquots of sample or standard in a commercially available assay kit (Amerlite Progesterone Assay: Kodak Clinical Diagnostics, Amersham) which used a competitive immunoassay technique based on enhanced luminescence (Whitehead *et al.*, 1983). The suitability of the assay for use with camel serum was tested by comparing the parallelism of the standard curves produced by standards made up in charcoal-stripped male camel serum and the human serum provided in the assay kit. In addition, a sample of pregnant female camel serum with a high progesterone concentration was diluted serially in male camel serum and human serum and run against the standard curves in the assay. All the curves were parallel with the kit standard curve (Fig. 1), indicating that camel serum did not interfere with binding in the assay. The minimum detection limit of the assay was 0.11 ng progesterone ml^{-1} serum and the intra- and interassay coefficients of variation, calculated by the method described by Dighe and Hunter (1976), were found to be 7.5% and 8%, respectively. The crossreactivities of the anti-progesterone serum used in the assay were stated by the manufacturers to be 5.2% with 5α-pregnane-3,20-dione, 4.17% with 5β-pregnane-3,20-dione and 1.1% with 20α-dihydroprogesterone.

Oestradiol assay. Concentrations of free oestradiol were measured in selected sera recovered in Expt 1, using a radioimmunoassay based on the method described by Heap and Hamon (1979). The anti-oestradiol serum was raised in a rabbit immunized with oestradiol-6-(CMO) conjugated to bovine serum albumin (E002; Steranti Research Ltd, Herts) and it showed stated crossreactivities of 0.55% with oestrone and 0.19% with oestriol. Aliquots (1 ml) of serum were extracted with 5 ml diethyl ether before being assayed in duplicate. To measure procedural losses during the extraction process, 0.1 ml
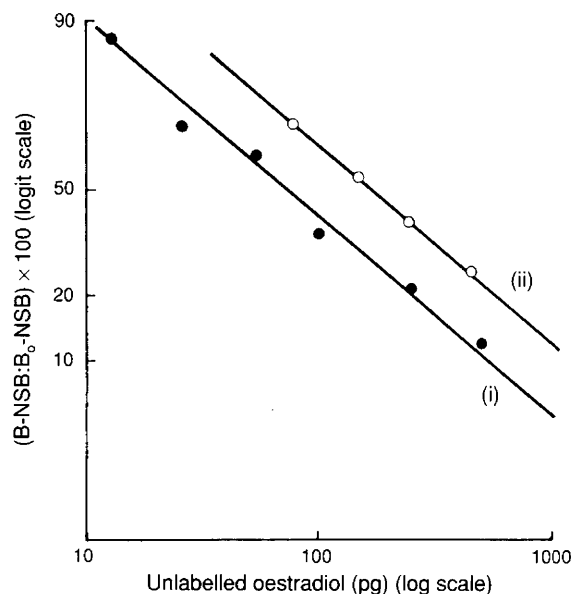
Fig. 2. (i) A typical standard curve for oestradiol and, (ii) a serial dilution curve of a sample of camel serum known to contain a high concentration of oestradiol. Results are plotted as log–logit linear transformations. NSB: nonspecific binding.

of the tritiated oestradiol ([2,4,6,7-H]oestradiol; specific activity 3.15 TBq μmol^{-1}; Amersham Life Sciences, Bucks) was added to 1 ml of charcoal-stripped male camel serum and extracted as above. This gave a mean recovery rate of $82.0 \pm 1.7\%$.

The assay was validated for camel serum by measuring the recovery of oestradiol added to a sample of male camel serum to give concentrations of 25, 100 and 250 pg oestradiol ml^{-1}; the mean recovery of this cold oestradiol was $109 \pm 6.9\%$. In addition, a sample of camel serum containing a known high concentration of oestradiol was diluted serially and assayed against the standard curve. This gave a parallel curve, thereby indicating that camel serum did not interfere with binding in the assay (Fig. 2). The intra- and interassay coefficients of variation were 6.2% and 10.1%, respectively, and the mean minimum detection limit was 8.3 pg ml^{-1}.

Experimental design

Experiment 1. The 36 camels in this experiment were divided into three groups. Group 1 animals ($n = 20$) were kept in one pen and were teased daily with a vasectomized male camel for at least 30 min in the early morning. Signs of oestrus (following the male, stradling the hind legs, lifting the tail and urinating when being examined by the male) were recorded but mating was not allowed. Group 2 ($n = 8$) camels were kept in another pen in which a vasectomized male was allowed to run freely for 10 h each day. They were observed constantly for signs of oestrus and any matings that occurred were recorded and timed. Group 3 ($n = 8$) camels were kept together in an isolated pen that was out of the sight, sound and smell of any male camels so that their follicular wave patterns could be monitored in the complete absence of any male influence.

On the basis of the alternate day scanning results, a growth and regression profile of the dominant follicle was plotted for each camel in the three groups. This was defined as a follicle that grew to at least 1.5 cm and exceeded the diameter of all other follicles. These individual dominant follicle profiles were started when the follicle was first detected at a diameter of 0.5 cm. The mean number of follicles present in both ovaries, from 20 days before to 20 days after a reference point, was tabulated in relation to the diameter of the largest follicle, to confirm that follicular growth occurred in waves. Because ovulation did not occur in group 1 and group 3 camels, this common reference point (day 0) was taken as the day on which the dominant follicle first reached its maximum diameter.

Experiment 2. The ovaries of all 60 camels included in the experiment were examined ultrasonographically on alternate days throughout the defined experimental periods. All follicles ≥ 0.5 cm in diameter were counted and measured and when the dominant follicle reached a diameter of 0.5–0.9 cm ($n = 30$), 1.0–1.9 cm ($n = 51$), 2.0–2.9 cm ($n = 48$) or > 3 cm ($n = 45$), the camel was assigned to one of three treatment groups to induce ovulation. These treatments were: (i) natural mating ($n = 61$); (ii) 20 μg of the GnRH analogue, buserelin (Receptal: Hoechst Animal Health, Milton Keynes) given i.v. ($n = 58$); or (iii) 3000 iu hCG (Chorulon: Intervet Laboratories, Cambridge), also given i.v. ($n = 55$). The ovaries were rescanned at 36, 48, 72 and 96 h after treatment to monitor ovulation, which was confirmed subsequently by measuring a rise in peripheral serum progesterone concentrations. Some camels were used more than once in the experiment but, in each case, at least one complete follicular cycle was allowed to occur between successive treatments.

Statistical analyses

To investigate possible associations between the number of follicles and the diameter of the largest follicle, the product moment correlation coefficient (r) was calculated. The result was confirmed by carrying out a periodic regression analysis using sine and cosine terms, as well as calculating the equivalent rank coefficient (Kendall's Tau). Student's t test was used to compare cycles in which follicles grew to 1.5–2.5 cm in diameter with those in which they grew to 2.6–6.4 cm in diameter, and differences were considered to be significant if $P < 0.05$. Fisher's exact test was used to compare the ovulation responses of follicles of different sizes. The relationship between oestradiol concentrations and follicle growth was emphasized by calculating the magnitude of the mean ($\pm$ SEM) differences between the time periods days -8–0, and days 0–$+8$.

Results

Experiment 1: follicular wave dynamics

Although the follicular wave pattern varied considerably between individual camels in both group 1 and group 3, it was none the less clearly divisible into three phases in all animals: a growth phase, a mature phase and a regression phase (see Table 1; Fig. 3). New follicles became visible and started to grow before the mature follicle had fully regressed, to give a

Table 1. Follicular growth patterns in cycles that resulted in dominant follicles of 1.5–2.5 cm maximum diameter versus follicles of 2.6–6.4 cm diameter

	Mean ($\pm$ SEM) duration (days) of		
Parameter	Growth phase	Mature phase	Regression phase
Cycles that resulted in a dominant follicle with a maximum diameter of 1.5–2.5 cm ($n = 34$)	10.5 ± 0.5^a	7.6 ± 0.8^b	11.9 ± 0.8^c
Cycles that resulted in an oversized follicle of 2.6–6.4 cm diameter ($n = 32$)	18.4 ± 0.8^a	4.6 ± 0.5^b	15.3 ± 1.1^c

Means with the same superscript are significantly different: [a]$P < 0.001$; [b]$P < 0.01$; [c]$P < 0.02$ (Student's *t* test).

mean interwave interval of 18.2 ± 1.0 days. The dominant follicle reached a maximum diameter of 2.0 ± 0.1 cm in 52% ($n = 34$) of the wave patterns studied before it began to regress (Fig. 4a). However, in the other 32 instances (48%), the follicle continued to grow beyond 2.0 cm until it reached a mean ($\pm$ SEM) diameter of 4.1 ± 0.2 cm (range 2.6–6.4 cm; Fig. 4b). These oversized follicles took significantly longer to attain their maximum diameter ($P < 0.001$), and then to regress to < 0.5 cm ($P < 0.02$), than did dominant follicles with maximum diameters of 1.5–2.5 cm (Table 1). During the regression process, the follicular fluid of the oversized follicles became increasingly echogenic owing to the development of free-floating echogenic strands, which later became organized into transecting fibrous bands (Fig. 4b). Nevertheless, these over-large follicles did not inhibit the growth of other follicles in the same or contralateral ovary, which would mature and ovulate if the appropriate stimulus was applied (Fig. 4a).

There was a strong inverse relationship between the number of follicles in the ovaries and the diameter of the largest follicle. The product moment correlation coefficient for this relationship was calculated to be $r = -0.0627$ ($P < 0.003$) and Kendall's coefficient of rank correlation confirmed the conclusion ($\tau = -0.467$, $P < 0.004$). The very pronounced cyclical pattern was investigated further by carrying out a periodic regression analysis, using sine and cosine terms. A highly significant correlation was detected for both variables ($r = 0.823$ for follicle number and $r = 0.883$ for follicle diameter). The data therefore provided strong confirmation of the cyclical variation in number of follicles and diameter of the largest follicle.

In group 2, the vasectomized male mated with the female camels when the mean ($\pm$ SEM) diameter of their dominant follicle was 1.3 ± 0.1 cm. Mating therefore significantly shortened the interwave interval from 18.2 ± 1.0 (group 1 and group 3 camels) to 13.8 ± 1.0 days ($P < 0.01$). Ovulation in the mated camels was followed in 3–4 days by the development of a spherical, echogenic corpus luteum that grew from a diameter of 0.7 ± 0.2 cm on day 3 to 2.2 ± 0.1 cm by day 9 (Fig. 4c). It exhibited a secretory lifespan of 8.5 ± 0.5 days, as reflected by the serum progesterone profile. Concentrations remained low (< 0.5 ng ml^{-1}) for the first 3–4 days after ovulation and then rose to reach a mean peak of 2.6 ng ml^{-1} on day 8. They decreased again sharply on days 9 and 10 to reach baseline values of < 0.5 ng ml^{-1} by days 10–12. Progesterone concentrations in the non-mated camels in group 1 and group 3 remained low (0.1–0.4 ng ml^{-1}) throughout the experimental period. New follicles became visible 5.1 ± 0.5 days after a first mating and they took 8.3 ± 1.0 days to mature to a diameter of 1.3 ± 0.1 cm when the camel was remated by the vasectomized male.

An increase in both mean serum oestradiol concentrations ($+ 14.2 \pm 1.5$ pg ml^{-1}; $P < 0.001$) and follicle growth ($+ 0.76 \pm 0.12$ cm, $P < 0.001$) occurred between days -8 and day 0 as the follicle grew to a diameter of 1.7 ± 0.1 cm (Fig. 5). Between day 0 and day 8, however, oestradiol concentrations decreased (-11.9 ± 1.6 pg ml^{-1}; $P < 0.001$), while follicle growth continued to increase ($+ 0.69 \pm 0.18$ cm, $P < 0.01$). Signs of oestrus in group 1 and group 2 females were highly variable and seemed to bear little relationship to follicle maturity. Individual camels would often show apparent oestrus when approached by the male, including stradling the hind legs, raising the tail and urinating, when there was little follicular activity in their ovaries. Only twice was a female observed to submit instantly to the male which, more often, would select a female that was definitely not showing visible oestrus. He would chase her around the pen biting her hump or hind legs until she submitted and allowed him to mate. Copulation in these group 2 camels lasted from 5 to 15 min.

Experiment 2: induction of ovulation

Ultrasound scanning of the ovaries, combined with daily peripheral serum progesterone measurements, showed that of the 30 camels with a follicle of 0.5–0.9 cm in diameter, 7 of 10 (70%) ovulated in response to mating, 6 of 10 (60%) ovulated in response to buserelin and 6 of 10 (60%) in response to hCG. However, reappraisal of the data revealed that of the 19 group 1 camels that ovulated, 16 (85%) had a follicle of 0.9 cm in diameter and only three (15%) had follicles between 0.5 and 0.8 cm. Thus, it would appear that 0.9 cm is about the minimum ovulatory diameter of the Graffian follicle in dromedaries.

The ovulation rates rose, although not significantly, to 85% (17 of 20), 81% (13 of 16) and 67% (10 of 15), respectively, in the animals that were either mated or treated with GnRH or hCG when they had a 1.0–1.9 cm diameter follicle in their ovaries. The ovulation rates then decreased again sharply ($P < 0.001$) when the diameter of the follicle had increased to 2.0–2.9 cm at the time of treatment (2 of 16, 12.5% for mating; 5 of 17, 29% for buserelin and 2 of 15, 13% for hCG), and
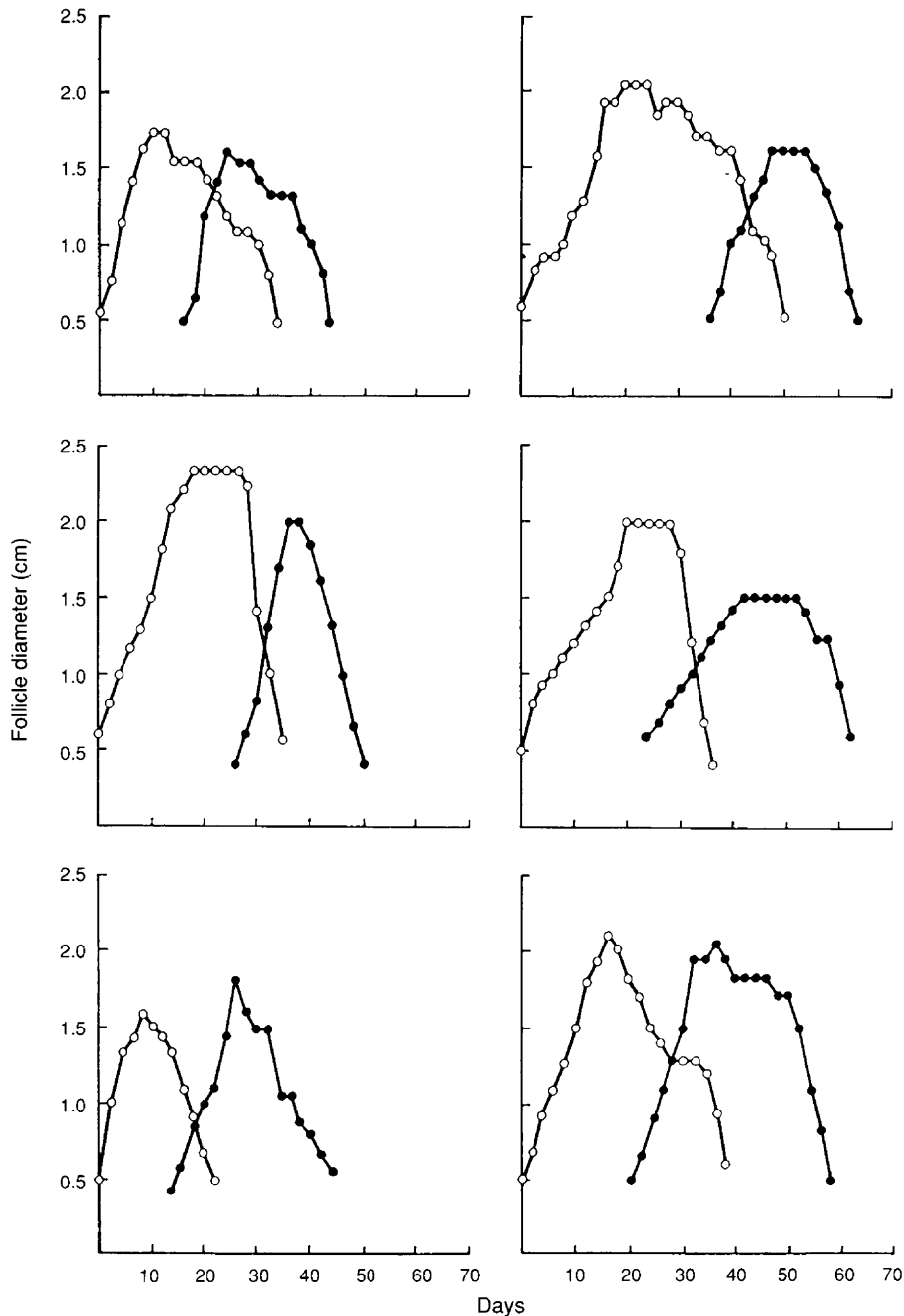
Fig. 3. Typical follicular wave profiles recorded in 6 unmated camels that did not develop overlarge follicles.

when the follicle had grown to > 3 cm, none of the camels mated or treated with gonadotrophic hormones ovulated ($P < 0.01$).

Progesterone profiles during the luteal phase in the treated camels that ovulated were unaffected by the method used to induce ovulation. The mean peak concentrations of 2.5–3.0 ng ml^{-1} in the mated and GnRH-treated groups were not significantly different from the mean peak value of 4.5 ng ml^{-1} in the hCG-treated camels ($P > 0.1$). Serum progesterone concentrations remained low (< 1.0 ng ml^{-1}) in all the camels that failed to ovulate in all three groups.

Discussion

The occurrence of waves of follicular activity in camels was indicated in the present study by periodic increases in the number of follicles present in the ovaries, from which one would grow to a mean maximum diameter of 2.0 ± 0.1 cm or 4.1 ± 0.2 cm while the others regressed. Furthermore, there was an inverse relationship between the diameter of the largest follicle and the number of follicles present, which is consistent with the follicular wave theory proposed for cows by Ginther *et al.* (1989) and for llamas by Adams *et al.* (1990). The diameter
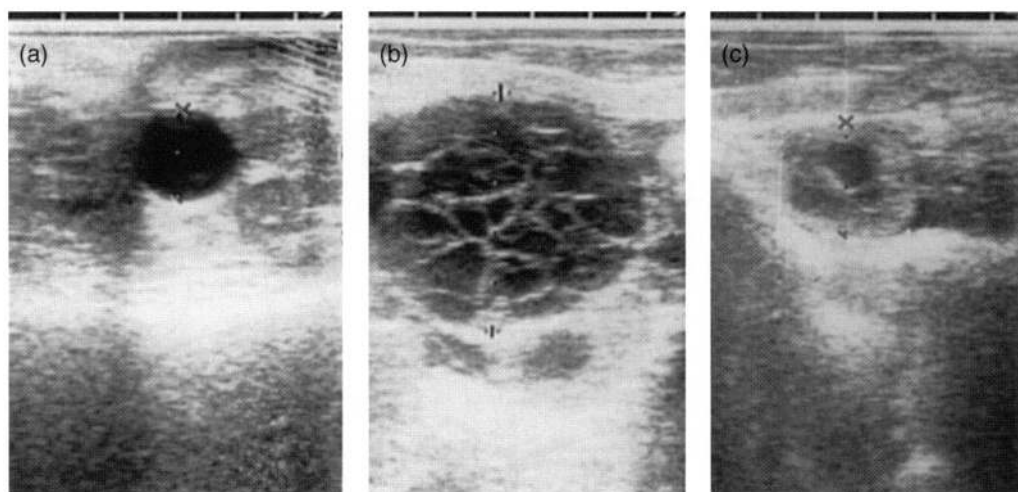
Fig. 4. Ultrasonographic appearance of (a) a normal mature preovulatory follicle of 1.7 cm diameter in the left ovary; (b) a large, overripe, unovulated regressing follicle of 4.8 cm diameter in the right ovary of the same camel, showing the characteristic echogenic transecting fibrinous strands in the follicular fluid; and (c) a typical echogenic corpus luteum with a persisting nonechogenic core on day 6 after ovulation.
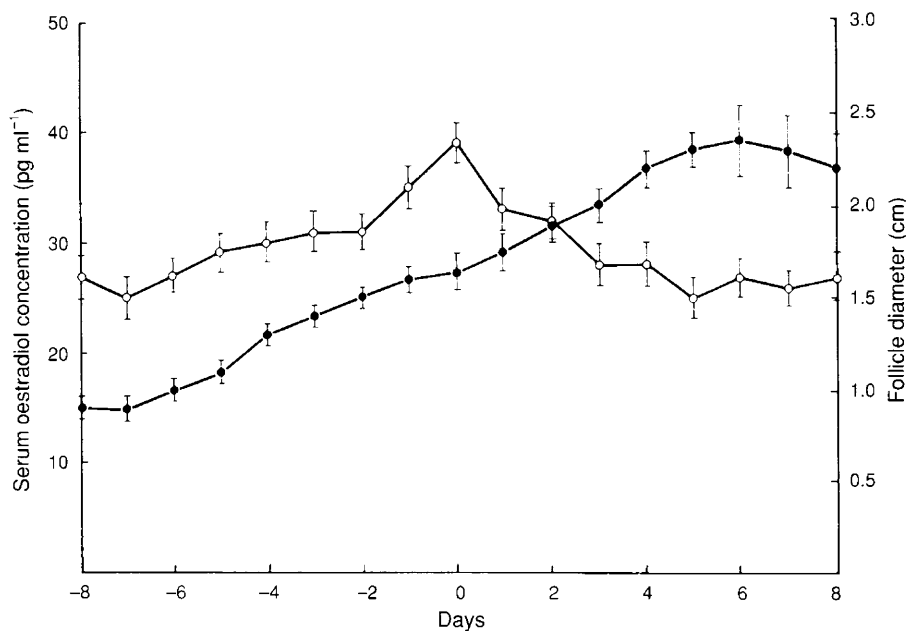

Fig. 5. Relationship between mean (± SEM) serum oestradiol concentrations ( ) and mean (± SEM) diameter of the dominant follicle (•) in 8 unmated camels. Day 0 was taken as the day of maximum oestradiol concentration.

of the dominant follicle in the mated camels in group 2 (1.3 ± 0.1 cm) was less than that of the dominant follicle in the non-mated camels in the other two groups, indicating that a follicle matures sufficiently to ovulate before it has reached maximum size. No overlarge follicle of > 3 cm diameter developed in any group 2 camels, presumably because they were mated when the dominant follicle reached maturity and this stimulated ovulation.

Similar oversized follicles that do not ovulate have been reported in llamas, and these all were the dominant follicle of a wave during which no copulatory stimulus had been applied (Adams *et al.*, 1991a). The development of follicles larger than

1.2 cm in diameter has been reported in alpacas by Sumar (1985) and Bravo and Sumar (1989), but these were considered to be pathological cysts on the basis of size alone. Clearly, these oversized follicles in both Old and New World camelids derive from the modern management practice of keeping male and female camels apart during the breeding season. However, the hormonal mechanisms that drive the development of such structures, and the reasons why they occur in only a proportion of unmated camels, have yet to be elucidated.

Follicular growth produced a peak of oestradiol in the serum but concentrations began to decline when the follicle grew to a diameter of more than 1.7 cm. This suggests that the follicle

was already beginning to undergo atretic changes, perhaps as a result of a commencing downregulation of LH receptors in the theca interna or granulosa cell layers. Alternatively, it could be argued that a continuing basal secretion of LH from the pituitary gland, but in the absence of a true ovulatory LH surge, may be the cause of the overgrowth of some follicles beyond a diameter of 2.0 cm.

The results of these experiments confirmed earlier observations of Marie and Anouassi (1987), Sheldrick *et al.* (1992) and Anouassi *et al.* (1992) that ovulation can be induced in dromedaries by a single treatment with GnRH or hCG. However, a significant finding of the present study was the marked reduction in the effectiveness of these hormone treatments and mating to induce ovulation when the diameter of the dominant follicle exceeded 2.0 cm.

Peripheral serum progesterone profiles in the non-mated camels in groups 1 and 3 of Expt 1 showed that no spontaneous ovulations occurred, even in those animals that were close to, but not mated by, male camels. Profiles in the mated camels in group 2, and in the camels in Expt 2 that ovulated in response to treatment, showed that luteolysis commenced between day 8 and day 9 after ovulation and was complete by day 11. These findings agree with previous reports for dromedaries by Marie and Anouassi (1987) and bactrian camels by Xu *et al.* (1985), as well as those for New World camelids such as llamas (Adam *et al.*, 1989; Adams *et al.*, 1991b) and alpacas (Fernandez-Baca *et al.*, 1970). It appears that the luteal phase of camelids differs from that of other induced ovulators like cats and ferrets, which become pseudopregnant. 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.

In this study it was impossible to relate oestrous behaviour shown by the female camels to follicular activity in their ovaries and steroid hormone concentrations in their blood. More often than not, animals in groups 1 and 2 were either mated (group 2), or the male made a determined effort to mate them (group 1), when they appeared to resent his attention. Conversely, females showing clear signs of oestrus were ignored by the male. Oestrous behaviour has been reported to be equally variable in other camelids. For example, England *et al.* (1971) found it impossible to discern any major differences in behaviour patterns between animals with corpora lutea in their ovaries and those without.

In summary, a follicular wave pattern was found in dromedaries to consist of well defined, but individually variable, periods of growth, maturity and regression. The size of the dominant growing follicle and the display of oestrous signs by the female seem to bear little relationship to the desire of the male to mate the female concerned. Nevertheless, ovulation can be induced by GnRH or hCG, as well as natural mating, and an optimum time to treat the animal is when the growing follicle is between 0.9 and 1.9 cm diameter.

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