REVIEW

REPRODUCTION IN CAMELIDAE

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Summary. Sexual activity in Camelidae appears to be acyclic and ovulation is induced by copulation. The duration of sexual activity is variable. When a rutting season exists, it is probably elicited by influences similar to those which induce the advent of oestrus in the female. The pattern of the reproductive cycle appears to relate to the harsh environment in which the camel progenitors evolved. Only calves born in a restricted period of the year had any chance of survival. Selection has, thus, been towards a type of animal with a breeding season coinciding with the most favourable time of the year. In areas with better environmental conditions, sexual activity does not follow such a restricted pattern.

Fertility rate is low compared with other domestic mammals.

Mating behaviour follows a fairly complex pattern of olfactory and/or visual stimuli.

All Camelidae have a similar type of placenta. It is diffuse and epithelio-chorial in nature, much as in the horse.

INTRODUCTION

The Fossil record indicates that the Camelidae family originated and developed in western North America, spread by way of land bridges into Asia and South America and finally became extinct in its original homeland. In the old world, we find the Genus *Camelus* represented by two extant species; the Bactrian camel or *Camelus bactrianus* (two-humped camel) and the Arabian camel or *Camelus dromedarius* (one-humped camel). These two species are much larger in size than any of the four species of the Genus *Lama* (or *Auchenia*) that live in South America: the llama (*Lama glama*), alpaca (*Lama pacos*), guanaco (*Lama guanicoe*) and vicuna (*Vicugna vicugna*).

The two-humped camel is found primarily in Central Asia and the one-humped dromedary lives mostly in South-Western Asia and Northern Africa. In both areas, as 'ships of the desert' these animals are of great value to the people who inhabit the drier portions of Asia and Africa. The primary uses of

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camels are for transport of goods and passengers in desert and semi-desert areas. Wool, milk, skin and meat are by-products of this main function.

The four species of the Genus *Lama* resemble one another in structure but they differ in size, range, pelage, temperament and usefulness to man. The llama is in common use by highland natives from northern Peru to northern Chile and Argentina for carrying burdens. Trains of llamas travelling long distances over the Andean highlands, descend westward to the arid coast and eastward to the low humid jungles. Llamas vary much in size, but the usual weight is about 200 lb, considerably more than an alpaca and twice as much as a vicuna. Alpacas resemble llamas in colour and they are kept primarily as producers of wool, though they are of importance in meat production. They thrive only in Peru and Bolivia and only at elevations above 12,500 ft, the level of lake Titicaca.

In contrast to the llama and alpaca, which have been domesticated for centuries, the vicuna and guanaco are wild animals. Guanacos look much like llamas but the colour of their coat is a fairly uniform reddish-brown. Although guanacos range from the highest grasslands to sea level, they are rather scarce throughout the range of the other *Auchenia* and are most abundant near the southern tip of South America. Adults are of little commercial value but the hides of the very young are prized by the natives for the manufacture of robes.

The phylogenetic classification of the *Auchenia* seems to be indeterminate, at least on the basis of structural criteria. Of the group, the llama and guanaco are the most similar, but the vicuna, although resembling the alpaca in some characteristics, is the most distinct. It has been variously classified as specifically subgenerically or generically separate from the other *Auchenia*. The characteristic, unique among living artiodactyls, that best supports generic separation of the vicuna is its peculiar lower incisors. These are very long and parallel-sided, with enamel only on one face, and an open root (Miller, 1924). In contrast to these rodent-like incisors, those of the llama are short and wedge-shaped with enamel on both faces and a closed root.

Another characteristic that distinguishes the vicuna from the other *Auchenia* is the bib of long hair which hangs from its brisket. This hair is white, like the rest of the under parts and contrasts strongly with the dark buffy-brown hue of the upper parts. As their wool is the finest known, and as their hides and meat are prized by the natives of the Andean highlands, vicunas have been hunted for centuries and the species is threatened with extinction in many parts of its range.

Very little attention has been paid to the breeding of these species and many aspects of reproduction are awaiting research. Maintenance of a high level of reproduction in livestock is essential not only for profitable production but also for maximum opportunity for selection. Thus, the breeding of these animals is extremely important for economic reasons, and its improvement can greatly contribute to the health and economy of the people living in the Camelidae area.

The literature concerning reproduction in Camelidae is reviewed here. The information available has been pieced together in as logical an order as

possible, but knowledge of individual species is incomplete and non-existent in some cases. An attempt has been made to correlate some reproductive phenomena in the Camelidae with those of other domestic animals.

REPRODUCTIVE LIFE CYCLE

PUBERTY

Leonard (1894) mentioned that the female camel was not put to a male until she was 3 years of age. According to him, one female camel could produce nine to ten calves at intervals of about 2 years. Ywema (1960) agreed with Leonard regarding the age of puberty in the female camel. Leese (1927) and Williamson & Payne (1959) believed that, although the female could come into season at about 3 years, service was usually allowed only when she reached 4 years. The male might breed when he was 3 years old but full reproductive power was not developed until some 6 years of age; he could then serve up to fifty females in a season and, if he was very well fed and cared for, he could cover up to seventy (Leese, 1927). According to Yasin & Wahid (1957), in Pakistan, the female camel first mated at 4 years of age and would breed until she was 30 years old; the males were used for breeding at 6 years and continued to 15 to 20 years. In Somaliland, the male camel usually arrived at the age of puberty when 5 years old (Mares, 1954).

In Russia, observations on the Bactrian camel showed that both males and females were first mated at 4 years. Each male served some ten females per year (Terentjev, 1951).

Domesticated vicunas were reported to be capable of reproduction at 1 year of age (Romero, 1927), but wild vicunas might not be fertile until they were several months older. Apparently the fertility of yearling females was low in the wild (Koford, 1957). Copulation by yearling vicuna males would rarely be successful in the wild for if one of them approached the females of a band he would be driven off by the dominant family male. In addition, because of his smaller size, a yearling male would seem to be unable to copulate efficiently with an adult female. Furthermore, the testes of a male about 16 months old were judged to be inactive but the testes of a 2-year-old were actively producing spermatozoa (Koford, 1957).

On haciendas in Peru, alpacas and vicunas are not usually bred until they are 2 years old. At la Raya (Granja Experimental de Auquenidos Puno-Peru), those females with faster growth rate are said to reproduce when they are 1 year old.

There is no information about factors affecting the age of puberty in Camelidae. In farm animals, on the other hand, the season of birth affects age of puberty mainly in seasonal breeders, in which reproduction is photoperiodically controlled. The age and body weight at which oestrus and conception first occur are less in sheep born in the spring and greater in the animals born in the summer (Hafez, 1952; Watson & Gamble, 1961). In pigs, the effect of season at birth on the age and weight at puberty is a controversial subject (Robertson, Crummer, Casida & Chapman, 1951; Self, Crummer & Casida,

1955) as a result of breed differences in the body weight at puberty, genotypic interactions in hybrids and differences in the degree of adaptability of the breeds. In general, spring-farrowed gilts tend to reach puberty earlier and to weigh more at puberty than do autumn-farrowed gilts (Sorensen, Thomas & Gossett, 1961; Zimmerman, Spies, Rigor, Self & Casida, 1960). Cattle reached puberty at an average age of 13 months at 27° C, and at 10 months at 10° C (Dale, Ragsdale & Chang, 1959). Delay in the puberty of farm animals in the tropics was attributed to a much slower growth rate, and it was suggested that puberty occurs at a certain threshold of body weight (Hafez, 1952).

BREEDING SEASON

Leonard (1894) quoted Aristotle to the effect that, in Arabia, the camel ruts in November and early December but his own observations suggested that the season was not fixed. The breeding season in Pakistan is from December to March (Yasin & Wahid, 1957). Female camels come into heat only during this period and this is also the rutting period of the male camels. In Somaliland, the male camel ruts in the spring (April to May) and at other times if grazing is good. Calves are usually born at the start of the dry season (October to March) as a result of mating in the autumn, and camels at the coast are always mated to calve then as it is the best time of the year for the coastal area (Mares, 1954). In India, sexual activity is from November to February (Singh & Prakash, 1964; Hira, 1947). The female camel remains in heat until she conceives.

Studies on the reproductive endocrine cycle of the male in Negeb-Israel (Bodenheimer, 1954), showed that camels have preserved a pronounced rutting season from January to March. Both birth and rutting seasons coincide with the season of luxuriant vegetation on the margins of the desert. In Morocco (Charnot, 1963a, b), the rutting season is in winter and spring. During this period, the male camel shows an important development of the interstitial testicular cells and an increase in one secondary sexual characteristic: the expansion of the soft palate, which protrudes from the mouth during sexual excitement.

Shalash (1965) studied the changes in ovarian functions in the camel during different months and seasons in Cairo and found a highly significant difference in the ovarian activity between months as well as between seasons. They concluded that the female camel showed a strong tendency to be a seasonal breeder rather than a breeder throughout the year since the highest ovarian activity occurred from December till May, although a sudden drop in ovarian activity occurred during February.

In the London Zoological Gardens, births of *Camelus dromedarius* have been recorded in February, April and September (Zuckerman, 1952-53).

Observations on the domesticated Bactrian camel in Russia (Bosaev, 1938) showed that this species was poly-oestrous, having cycles all the year round, but the wild Bactrian camel appeared to be a seasonal breeder. Bannikov (1945) studied the wild camel in the Djungari Gobi desert and found that the breeding season occurred during January and February. Other observations carried out by Prejevelsky (1876) in Mongolia showed that sexual activity in

Bactrian camels occurred early in spring. It is interesting to note that this is also the time when the Bactrian camel ruts in London (Heape, 1901). Moreover, all the Bactrian camels which have been bred in the London Zoological Gardens, were born in March and April (Zuckerman, 1952–53).

The literature concerning sexual activity in *Auchenia* is also conflicting. As in the camel, it varies with the area where the observations were performed. Thus in Argentina, according to Cabrera & Yepes (1940), *Lama glama* breeds during summer and early fall (November to May), *Lama guanicoe* breeds at the end of spring (November), and *Vicugna vicugna* throughout the year, but mostly during April and June. Koford (1957) reported that, in Peru, the sexual activity of wild vicuna was from mid-February to April. Studies conducted by San Martín (1961) in Peru showed that the breeding season in the alpaca was from December to March. The females remained in heat until they conceived or, in the case of sterile mating, pseudopregnancy had taken place. Fernández Baca (personal communication) agreed with the preceding author regarding the occurrence of heat and pseudopregnancy in this species, but he did not agree with the restricted breeding season. He found sexually active females even in April, May and June. Moreover, the corpus luteum that formed after sterile mating regressed within 23 days and a new set of growing follicles appeared, as a result of which the females came into heat again and a new service was permitted.

Lama glama, in captivity in England, breeds at all times of the year (Brown, 1936; Zuckerman, 1952–53). Births of *Lama guanicoe* have been recorded in the London Zoological Gardens during May, June and September and of *Lama pacos* from January to August (Zuckerman, 1952–53), the incidence of births varying with the month of the year.

No information is available for the rutting season in *Auchenia*. Some evidence exists that sexual activity in alpacas (Fernández Baca, personal communication) and in vicunas (Koford, 1957) continues throughout the year.

Sexual activity in Camelidae appears to be very variable, though the factors influencing its nature and duration are unknown. Studies on other species, however, show that the nature and duration of the sexual season is related to the extent of domestication, geographical origin and social structure of their group. The varying capacities of domesticated species to adapt their breeding rhythm to changed environment is shown by the way breeding habits are adjusted in captivity. In domesticated breeds of sheep, the incidence of oestrus is inversely related to the day length, which varies more at high, than at low latitudes. The sexual season shows similar variation, being less variable at the equator. In certain countries, sheep were selected and bred in order to obtain autumn lambing and this has slightly obscured the relationship between the sexual season and the day length. At the equator, where day length is constant, any seasonal sexual activity is probably conditioned by environmental temperature, rainfall, pasture condition and nutrition. The onset of the sexual season in sheep has been shown experimentally to be controlled by day length (Yeates, 1949), environmental temperature (Dutt & Bush, 1955) and genetic factors (Hafez, 1952), while sexual activity in the camel has been associated with the longest days (Williamson & Payne, 1959), and pasture condition and

nutrition (Leese, 1927; Bodenheimer, 1954), but there is no experimental evidence to support these ideas. The literature is conflicting and inconsistent even for such a well-studied animal as the mare. In general, mares can be classified into three categories: (1) Those with a well-defined sexual season. Wild breeds of horses manifest several oestrous cycles during a restricted sexual season coinciding with the longest days of the year. The foals are born during a restricted period. (2) Those with a transitory sexual season. Some domesticated breeds and some individual mares exhibit oestrous cycles throughout the year but ovulation accompanies oestrus only during the sexual season. The foals are born during a limited season. (3) Those with year-round breeding. Some domestic breeds and some individual mares exhibit oestrous cycles accompanied by ovulation throughout the year and foals are born throughout the year (Nishikawa & Hafez, 1962). In some areas, mares show oestrous cycles throughout the year, but they do not necessarily conceive at all periods. Where there is a sexual season, the two transitory periods before and after the sexual season are characterized by extreme variability of ovarian activity and sexual behaviour. At this time, the ovarian follicles develop only partially and then undergo atresia. There seems to be a high frequency of prolonged oestrus, oestrus of short duration, and irregular oestrous cycles.

OESTROUS CYCLE AND OVULATION

Leonard (1894) mentioned that the length of the oestrous cycle in the dromedary was variable but appeared to average 2 to 3 weeks and heat was stated to last 3 to 4 days. Bodenheimer (1954) agreed with the preceding author as regards the length of the cycle and heat. He added that females continued cycling during the rutting season until fertilization had taken place. According to Yasin & Wahid (1957), however, heat lasted 21 days and could be recognized by restlessness, swelling and discharge from the vulva. In well-fed females, oestrus could recur as early as 1 month after parturition but generally it was delayed for about a year, although occasionally it occurred much sooner (Williamson & Payne, 1959). According to Mares (1954) and Yasin & Wahid (1957), heat occurred 14 to 25 days after calving.

The length of the oestrous cycle in the Bactrian camel also appears to be variable. Bosaev (1938) found that the intervals between heats varied from 10 to 20 days and sometimes 30 to 40 days. He stated that parous females tended to have longer periods of heat than virgin ones. He also noted that even pregnant females continued to show behavioural heat throughout the year until parturition. Barmincev (1939) stated that the mean cycle length in the Bactrian camel was about 14 days and *post partum* heat was experienced either the day after calving or, more rarely, after 2 to 3 days. The suckling females came into heat regularly but the duration was shorter than in the dry camel.

Recent studies carried out by Shalash (1965) showed that the corpus luteum in the dromedary was formed only during pregnancy and in a few cases where the cervix was patent. The patency of the cervix in these latter cases suggests that the animals were pseudopregnant. This would indicate that the camel differs from other ruminants in that some type of afferent stimulus, such as

copulation, is necessary if ovulation is to occur. If this is so, and Barmintsev (1951) reported that ovulation in the female Bactrian camel normally occurred during copulation, female camels should not have oestrous cycles comparable to those of spontaneous ovulators. Induced ovulators are theoretically sexually receptive at all times before copulation.

Lama pacos is the only member of the Auchenidae whose oestrous cycle has

TABLE 1
DURATION OF OESTRUS AND ANOESTRUS IN PAROUS FEMALES OF *Lama pacos* (FROM SAN MARTIN, 1961)

<i>Alpaca No.</i>	<i>Oestrus</i>	<i>Anoestrus</i>	<i>Oestrus</i>	<i>Anoestrus</i>	<i>Oestrus</i>	<i>Anoestrus</i>
1	8 days	2 days	26 days	—	—	—
2	18 days	1 day	17 days	—	—	—
3	12 days	1 day	22 days	—	—	—
4	28 days	1 day	2 days	1 day	4 days	—
5	36 days	—	—	—	—	—
6	17 days	1 day	16 days	—	—	—
7	35 days	—	—	—	—	—
8	25 days	2 days	8 days	—	—	—
9	30 days	—	—	—	—	—
10	7 days	1 day	2 days	1 day	8 days	2 days
11	7 days	1 day	15 days	—	—	—

Oestrus was determined by sexual receptivity without allowing copulation.

TABLE 2
DURATION OF OESTRUS AND ANOESTRUS IN VIRGIN FEMALES OF *Lama pacos* (FROM SAN MARTIN, 1961)

<i>Alpaca No.</i>	<i>Oestrus</i>	<i>Anoestrus</i>	<i>Oestrus</i>	<i>Anoestrus</i>	<i>Oestrus</i>	<i>Anoestrus</i>
12	4 days	1 day	22 days	—	—	—
13	29 days	—	—	—	—	—
14	8 days	1 day	22 days	—	—	—
15	5 days	1 day	30 days	—	—	—
16	29 days	—	—	—	—	—
17	35 days	—	—	—	—	—
18	6 days	2 days	4 days	2 days	2 days	2 days

been studied in any detail. It is reported that the females do not exhibit a cyclic sexual activity, but manifest prolonged periods of oestrus interrupted by short intervals of anoestrus (Tables 1 and 2). Ovulation depends upon coital stimulus and takes place 26 hr *post coitum*. Ovulation can also be induced by exogenous chorionic gonadotrophin and occurs 24 hr after the injection. Heat may occur 24 to 48 hr after parturition (San Martin, 1961; Fernández Baca, personal communication).

COPULATION AND MATING BEHAVIOUR

The male camel behaves in an aggressive manner during the mating season, and grinding of the teeth and evagination of the soft palate are observed.

Although this latter 'organ' is present in both sexes, it is never extruded in the female (Leese, 1927). Studies carried out by Charnot (1963b) demonstrated that in the male it increased in length during the rutting season and was capable of evagination. Some individual castrated males might exhibit variation in the length of the soft palate during the rutting season but it was never evaginated.

Both males and females have well-developed glands in the neck just below the occiput. During the rutting season, the glands of the male secrete an evil-smelling reddish fluid which trickles down the long hair of that region (Leese, 1927; Pocock, 1910). Before copulation, the male tries to make the female sit down by biting her shoulders and by applying pressure on her neck with his own. During copulation, both sexes adopt a squatting posture and the male grips the female with his forelegs. Copulation lasts for 7 to 20 min (Leese, 1927; Yasin & Wahid, 1957; Singh & Prakash, 1964).

In contrast to male camels, male alpacas do not undergo changes in appearance and behaviour during the breeding season, except that they pursue females in order to copulate. Lamoids are polygynous like camels. In alpacas, as in ranch vicunas, the customary ratio is 10:1.

In February 1966, while working at la Raya (Cranja Experimental de Auquenidos—Peru), the author was able to make observations on sexual behaviour in alpacas under natural conditions. The method of study was to watch an undisturbed group of alpacas from distant points with binoculars, which enabled the observer to reach or leave his post without disturbing the animals. Events occurring within a large range could easily be seen. Observations were made from the day on which the males were placed with the females until signs of sexual activity disappeared.

As soon as the males were allowed to enter the females' field, they ran off to chase females. Coitus took place rapidly, all the males copulating almost simultaneously. Nearby females, necks and heads outstretched, slowly approached copulating males and then lay down in a squatting posture round the copulating pair. In one instance, up to eight females were seen in this position around a copulating couple. At another time, while a female was lying down, another female mounted her and they stayed in this posture for 5 min.

At first, sexual activity is particularly intense. Males could be seen copulating with two or three females in succession and served up to ten or more in a day. In the afternoon, the most active males could be observed lying down in the streams, possibly in an attempt to relieve the effect of the excessive rubbing. Fighting was common among the males. One extremely pugnacious male drove away nearby males that were either copulating or chasing females. Another male was apparently impotent, making several attempts to copulate without achieving intromission.

Sexual activity gradually diminished until no copulation was observed during the day. Instead they grazed quietly, reserving the mating time for the evenings when they were herded into the corral, and less effort was required to reach the females.

During coitus (Plate 1), the female lies recumbent—as when resting—with the male straddling her. In this position the head of the male is above and

PLATE 1

Alpacas during coitus.

slightly behind that of the female, his elbows grip close behind her scapulae and his forefeet are clear of the ground. The strongly flexed hindlegs of the male are placed laterally to those of the female, his metatarsi resting flat on the ground, the thighs of the two being nearly parallel. The male holds his sacral region vertically, close behind the rump of the female, the base of his tail being about 4 in. above the ground.

As copulation proceeded, the female lay quietly, her ears back. From time to time, she turned her head and neck with normal alertness or lifted her head to nuzzle the chest or chin of the male, or spit at his head. During one observation, after several minutes of intercourse, the female rolled on to her side, causing the male to rise, but copulation was soon resumed. This interruption was repeated twice more in the same manner, at intervals of several minutes.

In contrast to the calmness of the female, the male was excited during coition. His ears trembled constantly, his nostrils dilated and flattened at short irregular intervals, and the tail flipped up and down. At intervals, he squirmed and wriggled as if to get as far forward as possible on the back of the female. One male pushed his closed mouth against one ear of the female, and for several seconds held it pressed flat against her head. He did this several times. Pelvic thrusts were usually given at an irregular rate, from one to three per second, but occasionally the pelvis of the copulating male remained motionless for an interval of a minute or longer. After completing an uninterrupted coition with a cooperative female, the male paid no further attention to his sexual partner or to other females, but if copulation, which usually lasted about half an hour, was broken off the male took action to resume it.

Although it has been reported that oestrus in camels could be easily recognized by restlessness, swelling and discharge from the vulva, no such indications existed in alpacas, except that the female lay down when she was 'requested' by a male. Studies on other species showed that manifestation of sexual behaviour was influenced by the specific cues and sensory modalities of the two sexes as well as by physical and social environments. The organization of sexual behaviour corresponded with the sensory specialization of the species concerned.

The time of onset and cessation of oestrus may be controlled by diurnal changes. By contrast, in cattle, oestrus ceases more often in the early morning and afternoon than during the night. Oestrus is shorter in the tropics and subtropics than in the temperate zone. The manifestation of oestrus is also influenced by the presence of the male, an effect which has been used to improve sheep fertility. Australian scientists introduced the ram to ewes during the transition from anoestrus to the sexual season. The intermittent association with the ram increased the number of ewes exhibiting oestrus and the lambing percentage. The effect of continuous association with rams throughout the year on the onset of sexual season in ewes is not entirely clear. Schinckel (1954) showed that continuous association stimulated silent heat (ovulation unaccompanied by oestrus), in the ewes that had not already begun cyclic oestrous activity. The stimulation provided by the ram's presence is more marked in certain breeds and in certain localities than in others.

The substances responsible for olfactory stimulation of sexual behaviour

are not identified in any species. The preputial glands of the boar secrete a lipophilic substance, probably muscone (Dutt, Simpson, Christian & Barhart, 1959), that has an extremely penetrating odour. Sows could distinguish males from females without first smelling the genitalia, and it is surmised that the olfactory cue might arise from salivary gland secretions. In this respect, no studies exist about the glandular secretions of the male camel.

Sows show a characteristic 'mating stance' (rigidity in the hind legs) when pressure is applied to their backs by a herdsman. Signoret, du Bouisson & Busnel (1960) have experimentally partitioned the stimuli which elicit this mating stance. They showed clearly that the rhythm of the boar's courting song, 'chant de cœur', was an important cue. Similarly, the 'cri de cœur' of the copulating alpaca male was recorded on tape and played back to the herd. Intense curiosity was shown by all females, one of which lay down close in front of the tape recorder, a normal indication of readiness to accept a male (Guilbride & Moro, 1965).

GESTATION

In estimating gestation length in Camelidae, the difficulty lies in determining the time of fertilization because of the number of copulations which occur during the mating season. In this respect, the observations carried out by San Martin (1961) and Fernández Baca (personal communication) on the alpaca should be taken into account in order to determine the length of pregnancy in this species. San Martin and his collaborators recovered embryos from alpaca females mated under natural conditions and found that, in spite of the number of services, the stage of development of all the embryos dated from the first mating. Similar observations were made by Fernández Baca. He noticed that the number of matings did not increase the fertility rate, i.e. females which failed to conceive on the first service developed pseudopregnancy. It would also appear that, in the Bactrian camel, the first mating is the most important. Barmincev (1939) found that the mean duration of pregnancy in 850 cases was 406 days, calculated from the last mating. From a single mating, the mean was 410 days.

Mehta, Prakash & Singh (1962) mated female dromedaries so as to allow only a single service. The mean length of pregnancy calculated from the day of service to the day of calving, both days inclusive, was 389.89 ± 2.1 days.

A list of gestation lengths is given in Table 3. The authors of these reports do not cite the basis of their data.

FEMALE REPRODUCTIVE TRACT

Anatomy

Study of the reproductive organs in Camelidae has remained incomplete. No literature is available on the species of the Genus *Lama*; only very little information exists on the female camel.

Ovaries. Lesbre (1903) described the ovary in the camel as having the gross shape of a pear or nut with many ovisacs on its surface. Leese (1927) described

the ovary as a flattened organ measuring about 2.5 cm in length. Asdell (1946) noted the length of the Graafian follicle as 1 to 1.5 cm which, when fully mature, attained a size of 2.5 to 3 cm. The best account of camel ovaries was given by Tayeb (1950), who described a reddish, flattened, lobulated organ with a circular outline. The presence of numerous follicles on the surface gave it the appearance of a bunch of grapes. The lateral and medial surfaces

TABLE 3
GESTATION LENGTHS OF CAMELIDAE AND AUCHENIDAE

Species	Length of gestation (days)	Authors
<i>C. dromedarius</i>	308 to 364	Leonard (1894)
	336	Bodenheimer (1954)
	336 to 364	Yasin & Wahid (1957)
	370	Williamson & Payne (1959)
	364	Heape (1901)
<i>C. bactrianus</i>	364 to 392	Podberezkin (1951)
<i>L. pacos</i>	240	Kenneth (1947)
<i>L. glama</i>	308	Brown (1936)
<i>L. guanicoe</i>	308	Cabrera & Yepes (1940)
	308	Brown (1936)
<i>V. vicugna</i>	280	Cabrera & Yepes (1940)
	280	Romero (1927)

TABLE 4
MEAN VALUES $\pm$ S.E. FOR THE DIAMETER AND WEIGHT OF CAMEL'S CORPUS LUTEUM DURING PREGNANCY (SHALASH, 1965)

Type	Diameter (cm)		Weight (g)	
	Right	Left	Right	Left
Active corpus luteum of pregnancy	1.85 $\pm$ 0.3	1.88 $\pm$ 0.36	4.15 $\pm$ 1.69	4.68 $\pm$ 2.07

were slightly convex, and the hilus somewhat straight. The ovary was enclosed in a long, conical, pocket-like fold of mesosalpinx, the bursa ovarii. The apex of this bursa formed a large circular orifice within which lay the fimbriae of the oviduct.

The circular shape of the ovary is subjected to many variations during pregnancy depending on the size, position and form of the corpus luteum. During pregnancy, the corpus luteum was a soft, flabby, laterally-compressed sphere, protruding wholly from the ovary's surface and it retained its size, weight (see Table 4), shape and position but changed its colour (Shalash, 1965).

Oviduct. The oviduct in the camel is 25 to 28 cm long. The isthmus is less coiled than the ampulla and the ovarian part of the Fallopian tube. The fimbriae lie

in the bursa at a short distance from the ovary. The lumen of the ampulla is 4 to 5 cm in diameter at its ovarian opening in the depths of the fimbriae. The lumen of the isthmus is 1 to 2 mm in diameter. Each oviduct opens into the uterine horns by a narrow orifice at the summit of a papilla 3 to 4 mm in height (Tayeb, 1953).

Uterus. The uterus of the camel is of bicornuate type and is large enough to occupy a position which is mostly abdominal but partly pelvic. Its upper surface is convex while its lower surface is flat. The body of the uterus is relatively short. The cornua are intimately united in their caudal portions. The divergence of the anterior portions is characterized by forming a T-shape with the uterine body rather than a Y-shape. The right cornu is shorter than the left one. The mucous membrane of the uterine body and both cornua are smooth and present no cotyledons (Lesbre, 1903; Leese, 1927; Tayeb, 1953; Barmintsev, 1951; Shalash, 1965).

Cervix. The cervix bears ridges arranged in three or four rows. The cervical canal protrudes about one centimetre posteriorly into the vagina forming two blind cavities, one situated dorsally and the other ventrally. The size of the ridges varies with the stage of the ovarian activity. The average length and diameter of the cervical canal during follicular activity was 5.32 ± 0.98 and 5.96 ± 0.92 cm, respectively, while during ovarian inactivity, the length and diameter were found to be 4.96 ± 1.25 and 5.79 ± 0.99 cm, respectively (Shalash, 1965).

Placentae. Savi (1843) was the first to note that the foetal placenta in the dromedary was diffuse in nature, as in the mare, and not cotyledonous as in other ruminants. He described the thick chorionic membrane in the dromedary as being covered with short, shrub-like tendrils, or villi, in which arterio-venous connections sometimes occurred. He considered, on these and other taxonomic points, that camels were more closely related to pachyderms than to ruminants. Owen (1866-68) also noted the diffuse nature of the placentae in Camelidae.

Meschia, Prystowsky, Hellegers, Huckabee, Metcalfe & Barron (1960) examined llama placentae *in situ* and found that they were epithelio-chorial in type. Morton (1961) found the microscopic appearance of llama, Bactrian camel and dromedary placentae and the arrangement of the amniotic and allantoic membranes were essentially similar in the three species. The presence of the diffusely scattered, plicated, villous tufts arranged in areas of varying density was also similar, except that, in the llama, a more definite bare area was present along the lesser curve of the chorion. Microscopical examinations revealed that the three Camelidae placentae are analogous in appearance to those of the pig and horse at full term. Bustinza (1961) described the *L. pacos* placentae as diffuse epitheliochorial.

Histology

Sections through the camel ovary reveal the same structures as in other domestic animals. Tayeb (1950) noted a close resemblance to that of the sow, except in lobulation which is flattened in the camel and globular in the sow. Shalash (1965) found numerous Graafian follicles at various stages of develop-

ment, even in the presence of active corpora lutea of pregnancy. It seems that the presence of a corpus luteum in the ovary does not necessarily prevent a Graafian follicle from increasing in size as developing follicles were observed in 4.82% of pregnancies.

Microscopic examination of the corpus luteum during pregnancy revealed a gradual decrease of lipids and fats in the lutein cells and an increase of connective tissue elements as pregnancy advances. A week after birth or abortion, the corpus luteum changed into a hard, laterally compressed sphere and gradually decreased in dimensions (Shalash, 1965).

Before ovulation, the vaginal histology of the alpaca (*L. pacos*) in oestrus showed a similarity to that found in other domestic animals. However, the vaginal epithelium in the alpaca reflected persistence of the oestrogenic phase, even for 13 days after ovulation (Silva Santisteban, 1961). Studies on the uterine endometrium correlated with the preceding observation. Fuertes Quispe (1961) studied the histology of the uterine endometrium of the alpaca in oestrus and found an analogous picture to that of other animals during the follicular phase. This oestrogen-stimulated uterine endometrium persisted for 7 to 10 days after ovulation. Fuertes also found that the corpus luteum of pregnancy reached a size of about 1.5 cm 5 days after ovulation and remained so for an unknown period (not less than 10 days). Signs of secretory activity were seen between 7 and 10 days after ovulation; this was also the time when the reproductive tract showed progestational changes. As in the camel, follicles at varying stages of development were seen in the presence of active corpora lutea.

In the ovaries of 1-year-old alpacas, some indications showing the possibility of oocyte formation during adult life have been found. The ovaries of year-old alpacas treated with gonadotrophins showed higher mitotic activity and larger numbers of primary follicles than normal. The ovaries of the animals treated with the highest doses of gonadotrophins contained polyovular follicles (San Martin, De La Vega & Consales, 1960).

Physiology

Shalash (1965) found ovulation rate in the camel to be much higher in the left ovary than in the right; the difference being 12.92%. Similar results were obtained by Tayeb (1953) and Barmintsev (1951). Shalash also found that 99.24% of pregnancies were in the left horn. The foetus and the corpus luteum occupied opposite sides in 37.73% of cases, probably indicating ovum migration.

As in the camel, the left ovary in the alpaca is the more active in the production of ova. This difference in activity is greater after natural service than after hormonal treatment. San Martin (1961) found 63% of ruptured follicles in the left ovary after natural service but only 59% after treatment with chorionic gonadotrophin.

Immature alpacas treated with gonadotrophins show follicular growth as well as ovulation. Acosta Rodriguez (1961) found that 160 i.u. of Prolan A were enough to produce optimum follicular growth and subsequent treatment

with Prolan B (360 i.u.) produced ovulation and superovulation in immature alpacas, though not all the mature follicles ovulated.

MALE REPRODUCTIVE TRACT

Anatomy

There is no published account of the anatomy of the reproductive organs of the male llama. Information on the male camel is scarce and only one good account (Tayeb, 1951–52) is available.

The testes of camels are ovoid in shape and are found in the scrotum in a perineal position as in the dog (Lesbre, 1903). The length of the long axis and weight of the camel testes vary in animals older than 3 years, from 2.8 to 4 in. and from 80 to 110 g, respectively (Tayeb, 1951–52). Each testis is located in its pouch, lying obliquely to the vertical axis. The anterior edge is nearly straight and is linked with the epididymis. The posterior edge is free and convex, and the inferior and superior extremities are rounded.

The epididymis is formed on the anterior edge of the testis, extending from the inferior extremity to just above the upper edge. The head of the epididymis is joined to the testis. The spermatic cord is 18 to 20 in. long, and is enlarged at its point of issue at the inferior extremity in association with the venous pampiniform plexus. The deferent duct is flexed except at the end where it enters the urethra.

According to Lesbre (1903) and Leese (1927), the camel penis showed a close resemblance to that of the bull. Tayeb (1951–52) agreed with the preceding authors as regards shape and structure, but stated that the camel penis differed from that of the bull in the shape of the glans. In the former, it was like a crochet-needle and in the latter, like a sharp needle. Moreover, in the camel penis, the sigmoid flexure was pre-scrotal whereas, in the bull, it was post-scrotal.

The prepuce was pendulous and was formed by two layers, parietal and visceral. Between these two layers, three groups of muscles were found: the anterior muscles, or protractors of Lesbre; the posterior muscles, or retractors of Lesbre; and the lateral muscles. The fibres of these muscles joined to form a conical mass around the preputial orifice. Due to the action of these muscles, the prepuce could be moved onwards or backwards during erection or urination respectively. These muscles also controlled dilatation and constriction of the preputial orifice (Tayeb, 1951–52).

Lesbre (1903) noted the accessory sex organs in the camel and mentioned the presence of Cowper's glands and a prostate gland, but did not find seminal vesicles. Leese (1927) confirmed the absence of seminal vesicles. Tayeb (1951–52) described the prostate gland in the camel as a simple discoidal mass, dark yellow in colour. It was located on the superior edge of the first portion of the pelvic urethra, at the level of the neck of the bladder. It measured 3.7×5 cm in its longitudinal and transverse axes respectively. The bulbo-urethral glands, according to Tayeb, were formed by two lobules situated on either side of the terminal portion of the pelvic urethra. They were whitish in colour, almond shaped, and measured 2.5×1.2 cm.

Histology

Sections through camel testis showed marked histological changes with months and seasons of the year. During December to March, the diameter of the seminiferous tubules was 183 μ m with five to six layers of germ cells in various stages of differentiation and abundant mitoses. Many spermatozoa were seen between the Sertoli cells. From March onwards, degeneration set in, more and more of the tubules were devoid of spermatozoa and vacuolization became conspicuous. In May, this degeneration was well advanced, the germ cell layers of the seminiferous tubules were greatly reduced, spermatozoa and mitoses were almost absent and the diameter of the tubule was reduced to 131 μ m. In October, regeneration of the cells began simultaneously with the disappearance of the degenerated cells. From November to January, development progressed, reaching its annual peak in February. Observations on the epididymis and thyroid showed changes correlated with the seasonal trend of the testes (Bodenheimer, 1954). Similar results were obtained by Charnot (1964).

Histological studies on the epididymis, deferent duct and accessory glands of the alpaca (*L. pacos*) showed some differences between this species and others such as horse and cow. Osorio & San Martin (1966) found the deferent duct in the alpaca had a muscular layer divided into two strata, whilst other domestic mammals have three strata in their muscular layer. In both gross and microscopic studies, they did not find seminal vesicles. Acidophilic concretions, not seen in other species, were found in the prostate and the ampulla of the vas deferens. The prostate gave a negative, or weak-positive, reaction to the Mayer's mucicarmine stain, while the Cowper's glands gave a strong positive response to the same stain.

Physiology

Analysis of 17-keto steroids in male camel urine over a 24-hr period showed that the level was higher in spring than in summer (Charnot, 1958). The neurosecretory cells of the anterior pituitary gland were more active when sexual activity began than during sexual rest (Santini, 1964). The alpha LH-secreting cells and beta FSH-secreting cells of the anterior hypophysis of the male camel were hyperactive in the rutting male and hypo-active during sexual rest (Charnot & Racadot, 1963).

INFERTILITY

The fertilization rate in camel is extremely low as compared with that of other domestic mammals, and observations in Peru show that on most alpaca farms fertility is only 50%. In 1964, in Russia, 100 female camels yielded only thirty-seven to forty-three young (Yuzlikaev & Akhmediev, 1965). Similar results are found in other countries, but little is known about this problem. Barmintsev (1951) found that though female camels came into heat and were repeatedly mated, no follicles could be palpated. Infertility was attributed to the failure of follicle development. Yuzlikaev & Akhmediev (1965) carried out trials to stimulate full follicular maturation and ovulation. Seven females, not fertilized in January to February after two or more mounts, were given PMSG

in a dose of 5500 to 8000 i.u. and then 48 to 72 hr later, all the females were mated. The results showed 100% calving rate.

PMSG has also been tested successfully in increasing sheep fertility (Nalbandov, 1964). The purpose of using PMSG in sheep was to find out if raising the ovulation rate, and increasing the number of eggs fertilized, would increase the number that implant. The results indicated that it was indeed possible to increase the fertility of sheep significantly by the injection of PMSG.

Embryonic mortality appears to be another cause of low fertility in the camel. In recording numbers of corpora lutea, Shalash (1965) found 12.45% of animals had two or three corpora lutea and yet the incidence of twins or triplets was only 0.13%. Tayeb (1953) believed that the presence of two corpora lutea with a single foetus indicated the death of one of the ova. Anatomical abnormalities in the females are also important; in the camel, these were noted as the main cause of total infertility (Shalash & Nawito, 1963).

Superovulation has been recorded in alpacas (*L. pacos*). The percentage varied among the groups under observation, from 5.5 to 22.2%, and yet no case of twins or triplets has so far been recorded (Fernández Baca, 1967). In this respect, San Martín (1961) reported a 10% level of double ovulation.

Pseudopregnancy is a common occurrence in alpacas, and according to San Martín (1961) was due to the high percentage (21%) of azoospermic males. Moreover, Fernández Baca (1967) found that mating by intact males as well as by vasectomized males did not induce ovulation in all the females. He recorded 80 to 85% ovulation after copulation by intact males and 75% after service by vasectomized males. Some individual variations were noted in the ability of the males to induce ovulation, but the injection of chorionic gonadotrophin induced 100% ovulation. Embryonic mortality in alpacas occurs throughout pregnancy. On the 3rd day after mating, one or more fertilized eggs were recovered in 70% of all the females under observation. On Days 20, 45 and 90, the percentages of viable pregnancies fell to 69, 65 and 60, respectively (Fernández Baca, personal communication).

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