Reproduction of the caracal *Felis caracal* from the Cape Province of South Africa

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Reproduction of the caracal was studied using captive animals, field observations and gross and histological examination of male and female reproductive organs. Mating behaviour was similar to that previously reported for the felids and the mean gestation length was 79 days. The mean litter size was 2,2 for captive animals and wild killed pregnant females carried between one and three foetuses. Age at puberty for males and females was between seven and ten months, and first successful copulations occurred at between 12 and 14 months. Births occurred throughout the year with a pronounced peak in summer. Spermatogenesis was aseasonal with a reduction in reproductive activity in winter.

Navorsing oor voortplanting in die rooikat is gedoen deur die gebruik van gevange diere, veldwaarnemings en growwe en histologiese ondersoek van manlike en vroulike voortplantingsorgane. Paringsgedrag is tipies van die katfamilie, die gemiddelde dragtigheidsduur is 79 dae en die gemiddelde werpselgrootte vir beide gevange en wilde diere is 2,2. Die ouderdom van geslagsrypheid vir mannetjies en wyfies is tussen sewe en tien maande. Rooikatgeboortes het dwarsdeur die jaar plaasgevind met 'n skerp piek in die somer. Spermatogenese was nie seisoensgebonde nie en daar was 'n afname in voortplantingsaktiwiteit gedurende die winter.

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The caracal *Felis caracal* Schreber, occurs throughout the Cape Province (South Africa) with the highest densities in the southern and western parts (Stuart 1981). In such areas, the caracal has become the primary predator of domestic stock (Stuart 1981) and as a result, is regularly culled. In spite of such predator control programmes, the species remains common in the Cape Province (Stuart 1981, in press).

Existing data on the reproduction of the caracal, which are based on a limited number of field observations and observations of captive (zoo) animals, indicate that reproduction can occur throughout the year but that most births occur during an extended summer reproductive season, (Kralik 1967; Kingdon 1977; Pringle & Pringle 1979; Stuart 1981; Lynch 1983; Smithers 1983). Reported gestation length varies from 69 to 78 days (Zuckerman 1953; Gowda 1967; Cade 1968; Smithers 1983; Stuart & Durk Stuart 1985), and the litter size varies from one to five (Smithers 1983).

In this paper we present further data on the seasonality of reproduction, reproductive behaviour, gestation length and litter size, and discuss some of the factors which may be controlling seasonality of reproduction.

Materials and methods

Specimens of the caracal were collected over a five-year period (1976 to 1981) from the Cape Province of South Africa (Table 1). The animals, which were either trapped or shot, were sexed and measured (head and body length, tail length, hind foot length, ear length, skull length, and mass). Reproductive condition of the females was noted and the animals classed as either subadult or adult based on body parameters. Adult males had a head–body length greater than 90 cm and mass greater than 11 kg, and adult females, a head–body length greater than 80 cm and mass greater than 8 kg.

Reproductive organs were removed (testes and penis, and entire female reproductive tract), and the testes and ovaries weighed. Reproductive organs were fixed in 10% buffered neutral formalin and processed for light microscopy. Sections (5 μm thick) were cut from the middle and each end of the testes, from the middle of the cauda

Table 1 List of the monthly samples of adult caracal specimens that were used in this study; the figures in brackets are the numbers of animals from which reproductive organs were prepared for light microscopy

	Male		Female	
January	5	(5)	5	(4)
February	8	(8)	2	(2)
March	5	(5)	11	(11)
April	17	(16)	9	(7)
May	25	(25)	22	(22)
June	26	(22)	10	(10)
July	18	(16)	11	(11)
August	15	(14)	15	(15)
September	10	(8)	10	(6)
October	12	(12)	11	(6)
November	8	(7)	6	(5)
December	3	(3)	3	(2)

epididymidis, from the middle of the vagina and uterine horns (when available), and the ovaries were serially sectioned. All slides were stained with Mallory's trichrome.

Males

Approximately 40 sections through the seminiferous tubules and epididymides of all specimens were examined and the animals placed into one or more of the following four categories: seminiferous tubules inactive; active (spermatogenesis occurring); epididymides without spermatozoa: epididymides containing spermatozoa. A specimen was placed into a specific category if more than 50% of the tubules or sections through the cauda epididymidis were in a particular condition.

Females

Females were classed as pregnant or non-pregnant, lactating or non-lactating, based on gross morphology of the reproductive tract. Specimens that were prepared for light microscopy were examined and placed into one or more of the following five categories: ovaries without Graafian follicles; with Graafian follicles, all with a diameter less than 4,0 mm; with Graafian follicles with a diameter greater than 4,0 mm: with active corpora lutea; with regressing corpora lutea or corpora albicantia. Assessment of luteal activity was based on vascularization and size of the corpus luteum, as well as the size of the luteal cells and their nuclei, and the degree of vacuolation of the luteal cell cytoplasm.

Seasonality of reproduction

Analysis of the seasonal nature of reproduction was based on field observations of pregnant females and new-born kittens made during the study period; on the reproductive condition of adult female specimens (pregnant or lactating); and on a histological examination of the male and female reproductive organs of adult animals.

Reproductive behaviour

Data on reproductive behaviour, litter size, and gestation length were obtained from observations on captive animals at the Vrolijkeid Nature Conservation Station.

The length of the oestrous cycle was calculated using adult, solitary females, and was defined as the time from the onset of one period of oestrous behaviour, as indicated by an increase in the frequency of urine squirting (Stuart unpublished observations), to the onset of the next period. Observations on copulatory behaviour were made when individual males were introduced into enclosures containing single females in the oestrous condition. The gestation length was calculated from the cessation of copulation, to within 12 h of parturition.

The age of puberty, defined here as the age of onset of follicular development and spermatogenesis, and the age of sexual maturity, defined as the age of first successful copulation, were estimated from a histological examination of the gonads of a small number of known-age animals that had died in captivity; from the age of first successful copulation in known-age captive animals; and from an analysis of gonad growth rate in wild killed animals. Mean monthly testis mass was compared using analysis of variance and Student's t test.

Results

Oestrous cycle, mating behaviour, gestation and parturition

The mean length of the oestrous cycle of the caracal was 14 days (n = 15). The oestrous condition, in the absence of fertile copulations, lasted between three and six days ($\bar{x}$ = 4,5; n = 20) and occurred every two weeks (n = 15).

When individual males were introduced into cages containing single females in oestrous condition, the males initially examined the urine spray sites and then approached the female. Copulations occurred over a period of from one to three days ($\bar{x}$ = 1,8; n = 7) after introduction of the male, and a single copulation lasted from 90 s to 8 min ($\bar{x}$ = 3,8; n = 12). The copulation sequence was always initiated by the female assuming lordotic position, the male would then approach, mount quickly and disengage rapidly after (presumed) ejaculation. This sequence was followed by self-grooming (by both male and female) in all 12 observed copulations, and on two occasions, aggressive behaviour towards the male.

Males introduced into enclosures containing single females in a non-receptive condition (di-oestrus or pregnant) examined the spray sites, did not approach the female, but backed off when approached by the females (n = 3).

Gestation length varied from 78 to 81 days ($\bar{x}$ = 79; n = 5). One parturition was observed in a captive animal. The first stage, which lasted 35 min, was associated with restlessness, genital and mammary cleaning and scratching at the earth floor. The second stage was characterized by rhythmic, slow contraction of the abdominal muscles. The neonate emerged head first and was followed shortly after by the placenta. The female licked the neonate before eating the placenta. The second stage from onset of contractions to suckling lasted 110 min. Lactation lasted approximately four months with young being weaned between 15 and 20 weeks old.

Litter size, based on captive births, ranged from one to four kittens ($\bar{x}$ = 2,2; n = 15), while pregnant females sampled in the veld carried between one and three foetuses ($\bar{x}$ = 2,2; n = 22). Of 27 pregnant females for which ovarian material was available, 15 had a corresponding number of corpora lutea and foetuses, seven had a single foetus and two or more corpora lutea, and for the remaining five, the number of foetuses was not recorded. The number of corpora lutea in the two ovaries varied from one to four ($\bar{x}$ = 2,7: n = 27).

The two youngest males to successfully fertilize females were 12,5 and 14 months old and the two youngest females to be successfully fertilized were 14 and 15 months old. However, a histological examination of the ovaries of three known-age females (seven and ten

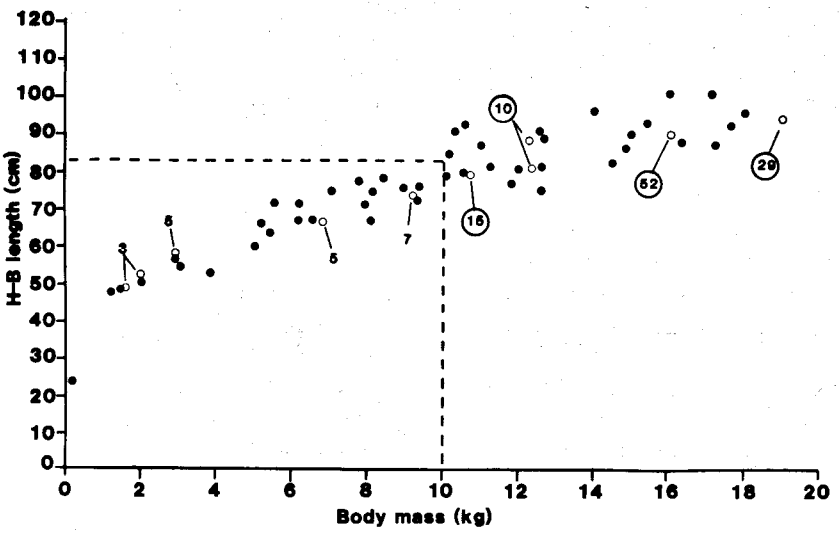

Figure 4 The relationship between body mass and H–B length for male caracal. The age (in months) of known-age specimens (open circles) is given and known-age specimens that were reproductively active have been indicated by ringing the age. The dashed line indicates the chosen body parameters that separate pubertal specimens from immature animals.

and 90 cm, then the growth curve for males (Figure 4) indicates that puberty is probably reached at between seven and ten months of age.

Seasonal nature of reproduction

Reproduction in the caracal occurred throughout the year with a pronounced peak of births between October and February (Figure 5).

Backdated wild births (calculated by comparing body parameters and dentition of wild killed animals, which were less than six months old, with known-age animals in captivity) occurred during every month except August, and a captive birth was recorded for this month (Figure 5). However, 74% (46 out of 62) of these births occurred in the five months between October and February. Furthermore, pregnant females were collected in every month except February, and the percentage of pregnant females in the monthly female sample was highest between August and December (Figure 5). Large Graafian follicles (diameter greater than 4,0 mm) occurred in the ovaries of at least one member of each month's sample (with the exception of April) (Figure 6), indicating that follicular development was probably aseasonal. However, the percentage occurrence of ovaries with large Graafian follicles showed a seasonal fluctuation, with a peak in late winter and a trough in late summer (Figure 6). The occurrence of corpora lutea followed the pattern

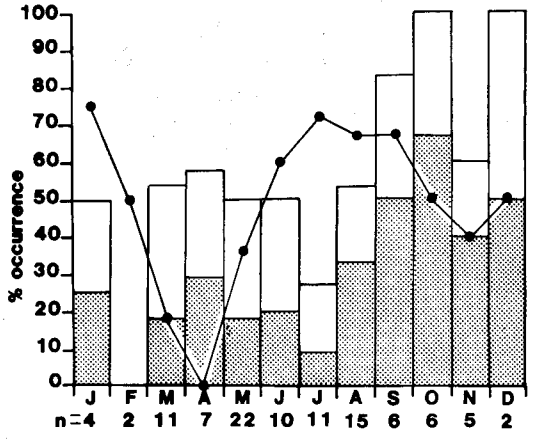

Figure 6 Summary of ovarian activity of adult specimens showing changes in percentage occurrence of ovaries with large Graafian follicles (●–●); corpora lutea (shaded component of histogram) and corpora albicantia (non-shaded component of histogram).

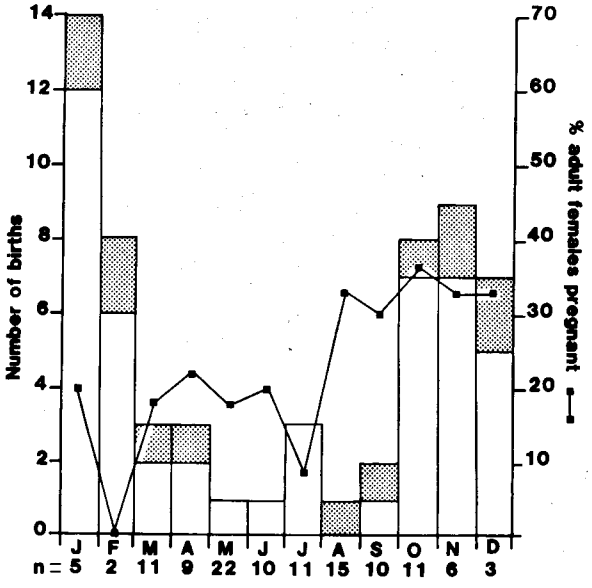

Figure 5 Summary of female reproduction in adult caracal showing the monthly occurrence of births (histogram) and pregnancies. The shaded component of the histogram represents captive births, and the non-shaded component backdated births. The points on the graph represent the percentage of each month's sample of females that were pregnant.

months old) and three known-age males (10 and 15 months) indicate that gametogenesis was occurring at a younger age than the first successful copulations.

Assuming that the onset of reproductive activity is marked by a rapid increase in gonad mass, then puberty in females may be attained at a body mass of between 7 and 9 kg (Figure 1B), and a head–body length of between 70 and 80 cm (Figure 1A). Such body parameters correspond to a combined ovarian mass greater than 0,3 g (Figures 1A,B), and no ovaries with a combined mass of less than 0,3 g contained large Graafian follicles or corpora lutea. The growth curve for female caracal, including the known-age animals (Figure 2), shows that puberty, as indicated by a body mass of 8 kg and head–body length of 75 cm, is probably reached at between seven and ten months of age. Furthermore, these body parameters correspond closely to those of the smallest wild killed females that were pregnant or lactating ($\bar{x}$ mass = 7,9 kg; $\bar{x}$ head–body length = 76 cm; n = 3) and indicate that sexual maturity is attained shortly after puberty.

For the males, the period of rapid testis mass increase occurred at a head–body length of between 60 and 90 cm (Figure 3C), and a body mass of between 9 and 12 kg (Figure 3B). The percentage of testes, in each mass class, that was spermatogenically active increased sharply over a similar mass range (Figure 3A). Assuming that spermatogenesis begins at or prior to the attainment of a mass of 10 kg and a head–body length of between 80

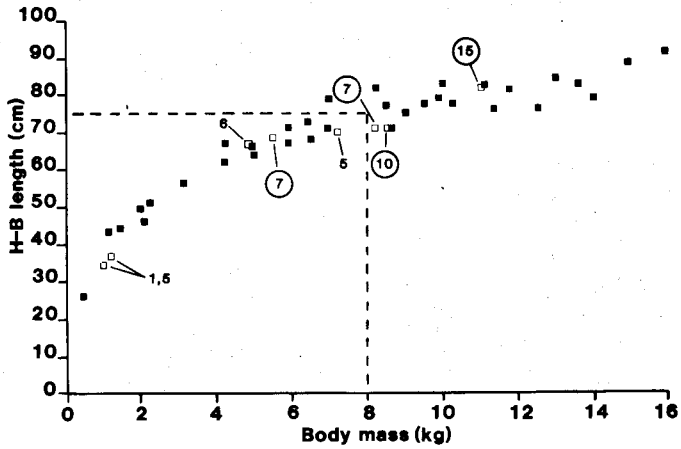

Figure 2 The relationship between H–B length and body mass for the female caracal. The age (in months) of each known-age specimen (open squares) is given, and known-age specimens that were reproductively active have been indicated by ringing the age. The dashed line indicates the chosen body parameters that separate the pubertal specimens from the immature animals.

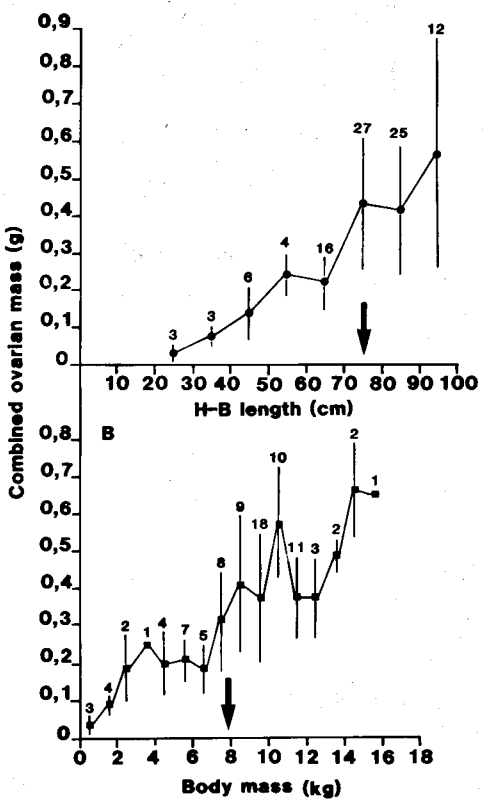

Figure 1 The relationships between combined ovarian mass and head–body (H–B) length (Figure 1A), and combined ovarian mass and body mass (Figure 1B). The two arrows indicate the $\bar{x}$ H–B length and $\bar{x}$ body mass of the three smallest wild killed pregnant or lactating females. The mean ± 1*SD* is indicated and the numbers above the *SD* s are the sample sizes.

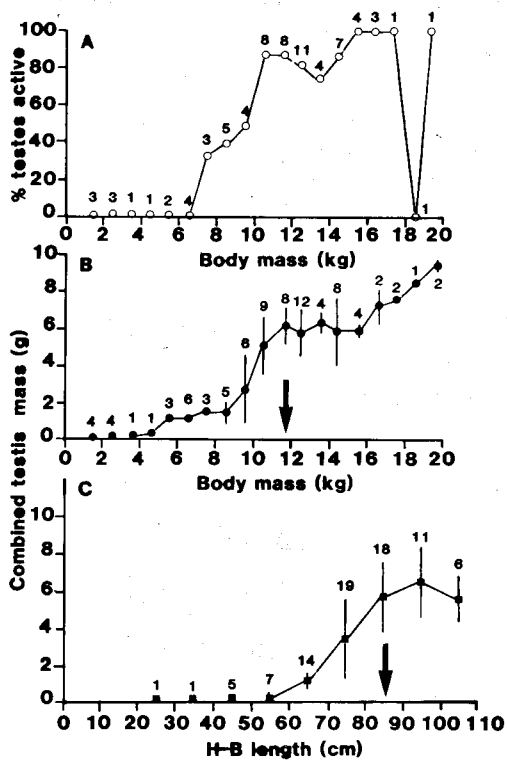

Figure 3 Relationships between combined testis mass and H–B length (Figure 3C), and combined testis mass and body mass (Figure 3B). The two arrows indicate the mean mass and H–B length of the three youngest known-age animals in which spermatogenesis was occurring. The percentage occurrence of active testes for each mass class (Figure 3A) shows the rapid increase from 0% to 80% active between body masses of 7 and 11 kg.

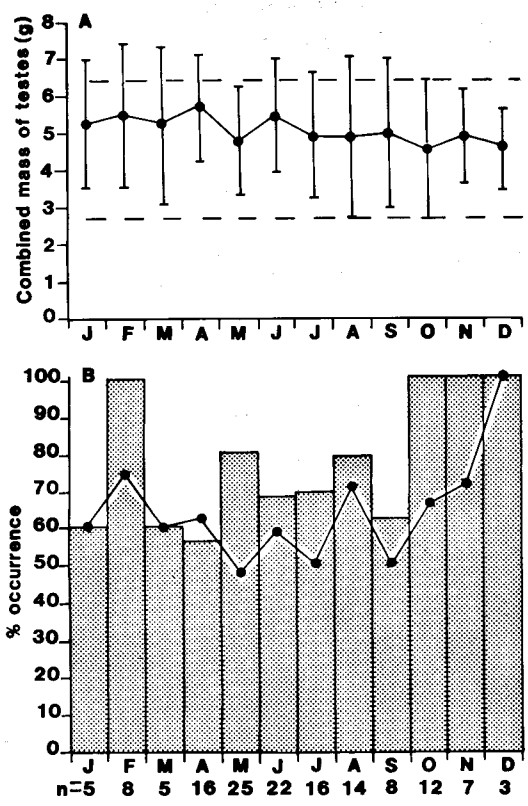

Figure 7 Summary of male reproductive activity of adult animals showing the percentage occurrence of active testes (histogram), and cauda epididymides containing spermatozoa (●–●) (Figure 7B), and monthly changes in mean combined testis mass (Figure 7A). Mean is given ± 1*SD*, the sample size is the same for both figures.

of occurrence of pregnancies (Figure 6).

Lactating females were caught in October (1), November (1), and March (2).

Spermatogenesis was aseasonal and each month more than half of all the testes examined were active, and in all months except May, the epididymides of at least half of the specimens contained spermatozoa (Figure 7B). Specimens with inactive testes, where the seminiferous tubules were lined by spermatogonia and Sertoli cells, were collected during January, and from March to September, suggesting a period of reduced reproductive activity in winter (Figure 7B). Mean monthly testis mass (Figure 7A) was compared using an analysis of variance and there were no significant differences ($P > 0{,}05$).

The number of pregnancies experienced by each adult female per year could not be calculated. Four wild caught females (two lactating and two reported to have had young) had no large Graafian follicles in the ovaries, suggesting that a period of lactational anoestrus may separate successive pregnancies. Of the 27 pairs of ovaries from pregnant females, 12 had both corpora albicantia and corpora lutea, 10 had corpora lutea and large Graafian follicles (diameter greater than 4,0 mm), and five had corpora lutea and no Graafian follicles. No females that were both lactating and pregnant were found, suggesting that there is probably no post-partum oestrus.

Discussion

The mating behaviour, gestation length and litter size reported here are in agreement with and supplement existing data for this species (Roberts 1951; Kralik 1967; Cade 1968; Ewer 1973; Rowe Rowe 1978; Pringle & Pringle 1979).

The ages of puberty and sexual maturity of the caracal are similar to those reported for the domestic cat (*Felis catus*), where they are reached at between seven and twelve months for the females and nine and fourteen months for the males (Scott 1970; Jones & Coman 1982).

The timing of reproductive events reported here for the caracal is similar to that reported for other parts of its geographic range (Shortridge 1934; Kingdon 1977; Smithers 1983). It seems likely that the seasonal peak of pregnancies and births was a result of seasonal oestrus rather than any seasonality of male reproduction. Although there was a period of reduced reproductive activity in winter, a high percentage of males from all months had spermatogenically active testes.

Three general strategies associated with the timing of seasonal reproduction are photoperiod prediction, prediction by plant cues, and opportunism (Bronson 1985). The first two strategies can be expected to result in clearly defined periods of reproductive activity and quiescence in both males and females. Opportunism, in which female reproduction depends on female nutritional status, may result in seasonal or continuous reproduction depending on energetic and nutritional considerations (Bronson 1985). An opportunistic strategy would necessitate continuous male reproduction as occurs in the caracal (present study).

An opportunistic strategy, controlled by female nutritional status, can explain the timing of reproductive events seen in the caracal in the Cape Province. Female nutritional status can be expected to vary at the end of winter (August) so that females will reach the required condition for reproduction over several months, and as a result births will occur over a similar period. Specimens feeding predominantly on domestic stock may be expected to retain a higher nutritional status than others and therefore may be able to reproduce during winter. However, it is difficult to separate the effects of one strategy from those of another. In the caracal, the increasing occurrence of pregnant females between July and October (Figure 5) coincides with increasing day length suggesting that changes in photoperiod may be important in controlling the seasonality of reproduction. Increasing day length may not, however, be the proximate factor, but may be influencing nutritional condition of the female caracal via an effect on the reproduction of one or more prey species. Opportunistic reproductive strategies are found in global colonizers such as the house mouse (*Mus musculus*) and the Norway rat (*Rattus norvegicus*) (Bronson 1985) and it may be that this reproductive strategy is responsible for the resilience that the caracal has shown to the effects of the predator control programmes.

Although the data pertaining to the number of pregnancies experienced by each female per year were incon-

clusive, several deductions can be drawn. Assuming that parturition was followed by a period of lactation anoestrus that lasted for the full length of lactation, then consecutive births should have been separated by a period of about six-and-a-half months (four months lactation anoestrus and two-and-a-half months gestation). It would therefore theoretically not be possible for a female to produce two litters during the five month favoured season. This is different from the Scottish wild cat (*F. silvestris*) (Matthews 1941), and the domestic cat (*F. catus*) (Jones & Coman 1982; Rowlands & Weir 1984) which have two pregnancies during the reproductive season. In the Scottish wild cat, the pregnancies are separated by about three weeks of lactation anoestrus, while in the domestic cat, there may be a post-partum oestrus or an oestrus may occur during lactation. If the period of lactation anoestrus in the caracal is reduced to about two months, then it would be possible for a female to give birth at the beginning of the reproductive season (October) and again at the end of the favoured season (mid-February). This could explain the slight bimodality in percentage occurrence of ovaries with large Graafian follicles, ovaries with corpora lutea, and births, that occurred between August and February (Figures 5 & 6). The occurrence together of corpora lutea and corpora albicantia can not be taken to indicate the occurrence of a post-partum oestrus, or that subsequent pregnancies were not separated by long periods, since the corpora albicantia of the felids are known to be long lived (Mossman & Duke 1973).

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