

Reproduction in the yellow mongoose revisited

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Previous reports on female reproduction in yellow mongooses, based on anatomical examination of specimens, concluded that this species is monoestral but with an extended breeding period. Our long-term studies on known females provide clear evidence of the production of two litters annually within a period of 2–4 months, females initiating a new oestrus cycle while still lactating. We present a biological explanation for the adaptive significance of polyoestry in this species based on a unique mode of infant nutrition for viverrids.

Anatomiese ondersoek van volwasse vroulike geelmuishonde het aangetoon dat dit 'n mono-estruisspesie is met 'n verlengde teelperiode. Ons langtermynstudie van bekende wyfies toon dat daar jaarliks twee werpsels binne 'n periode van 2–4 maande geproduseer word waar die wyfies 'n tweede estrussiklus tydens laktasie ondervind. 'n Biologiese verklaring vir hierdie verskynsel is gebaseer op die wyse waarop die kleintjies in die spesie gevoed word. Dié manier van voeding is uniek aan die Viverridae.

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Female reproductive patterns in the yellow mongoose *Cynictis penicillata* have been the subject of several investigations (Lynch 1980; Smithers 1971; Snyman 1940; Zumpt 1969; Zumpt 1976), which yielded conflicting results. Snyman reported that females produce two litters per year while the other authors refuted this statement, finding evidence for production of only a single litter. These authors based their findings on the reproductive state of female specimens sampled from populations at Bloemhof (Lynch), West Transvaal (Zumpt) and Botswana (Smithers) at different times of the year. On the basis of the presence of gravid or lactating females in their samples, all authors postulated an extended annual breeding cycle from June to January. In Botswana, Smithers (1971) found gravid females in October and November and again in February and March and also suggested that the species had a wide breeding season but did not attribute this to polyoestry. Lynch (1980) found evidence that only 9% of females in the Bloemfontein sample were polyoestrous and Zumpt (1969) found no evidence for polyoestry at all.

We present data from known individual females from human habituated groups under long-term observation in four widely separated southern African biotopes which indicate that females of this species are at least dioestrous throughout most of their range.

Materials and Methods

The studies were undertaken in the following areas: southern Transvaal (Vaal Dam island — B.W.), Karoo (Hutchinson — P.H.), Kalahari (Twee Rivieren — A.R.) and Namibia (Etosha — A.M. & J.P.) from 1986–1990 with at least one year of consecutive observation of known individuals at each site. The duration of observations in each

location is given in Table 1. Individuals were identified either by the presence of natural marks (scars, coat patterns etc.) or, where the absence of such indicators made identification difficult, by a coded pattern of ear notches.

Oestrus in the yellow mongoose is clearly recognizable by the behaviour of the males. Males vocalize with a variety of purring, 'cawing' and screaming calls while following females continually and attempting to copulate. During the pre- and post-oestrus phases they are loudly rebuffed by the female with bites to the head and neck and a variety of growling and screaming vocalizations. Peak oestrus was considered as the approximately two-day period during which females allowed the male to copulate.

Pregnancy duration was calculated from peak oestrus to birth of the young. Birth of the young was considered as having taken place when the female no longer showed abdominal enlargement and suckling marks were present around the nipples. The female showing these characteristics was considered the mother of the litter. Since more than one female in the group can give birth, these births occurring within 4–10 days of one another, subsequent females showing the abovementioned characteristics were considered the mothers of subsequent litters. These assumptions were confirmed through direct observation of suckling behaviour when the young were 3–4 weeks old. Yellow mongooses frequently suckled their young outside the burrow at this time and size discrepancy between offspring indicated their relative ages. Although allosuckling was observed (Rasa, pers. obs.), young of one age group preferentially suckled from a single female. Since the estimated age of these young correlated closely with the estimated date of parturition of the female in question, she was confirmed as their mother.

Table 1 Breeding data for five yellow mongoose groups under long-term observation in four southern African regions. Exact dates of observed matings and births are given where known. Other dates are estimated from the age of the young when first seen

| Group size (adults) | No. reprod. females | Time of 1st oestrus | Birth | No. young produced | Time of 2nd oestrus | Birth | No. young produced |
|----------------------------|---------------------|---------------------|-----------|--------------------|---------------------|----------|--------------------|
| Transvaal 1986–1988 | | | | | | | |
| 13 | 3 | Aug 6–11 | Early Oct | 2 | Oct 10–14 | Mid Dec | 3 |
| | | Aug 9–15 | Mid Oct | 2 | Oct 13–20 | Late Dec | 1 |
| | | Aug 14–18 | Mid Oct | 2 | Oct 18–26 | ** | |
| Kalahari 1990–1991 | | | | | | | |
| 4 | 1 | Mid Aug | Mid Oct | 2 | Mid Dec | Mid Feb | 2 |
| 5 | 2 | Mid Aug | Mid Oct | 2 | Dec 8–10 | x | x |
| | | Mid Aug | Mid Oct | 1 | Dec 13–15 | x | x |
| Karoo 1986–1988 | | | | | | | |
| 2 | 1 | Mid Aug | Mid Oct | 2 | – | – | – |
| Etosha 1989–1990 | | | | | | | |
| 3 | 1 | Mid Aug | Mid Oct | 2 | Mid Dec | Mid Feb | 2 |

** = Litter lost at or around the time of birth. x = Observations discontinued. – = No oestrus or births observed.

Results

The breeding data for five groups under observation in the various areas are shown in Table 1. Mean litter size was $1,9 \pm 0,52$ ($n = 12$) young, slightly higher than Lynch's value of 1,8 but lower than 3,2 recorded by Smithers (1971) and 2,3 by Rowe-Rowe (1978). Our data, however, refer to the number of young emerging from the burrow (approximately three weeks after birth) rather than the number of foetuses present, on which the other data are based. The mean number of litters produced/female/year was $1,8 \pm 0,45$. The only area where a single litter was produced annually was the Karoo. This case, however, is rather atypical in that mean group size was small and the area was under severe drought conditions at the time of observation (1986–1988).

Discussion

In contrast to Zumpt's (1969) findings that pregnant females are present from June onwards, we found a remarkable similarity in the time of onset of first oestrus as indicated by mating activity (early to mid-August), irrespective of location. In all areas, gestation period was 60–62 days, in contrast to Zumpt's (1976) estimate of 42 days. This gestation period for *Cynictis* agrees well with those reported for other viverrid species with altricial young where exact gestation periods are known e.g. dwarf mongoose *Helogale* 56–58 days, (Rasa 1977), banded mongoose *Mungos* 60 days (Thurnheer 1990) *Herpestes ichneumon* 60 days (Michaelis 1972). Gestation period appears to be independent of body mass, *Helogale* representing the smallest of the mongooses with a mean body mass of 400 g (Rasa 1977), *Herpestes ichneumon* being amongst the largest of the herpestids with a mean body mass of 2,9 kg (Michaelis 1972). First litters were born in October, thus coinciding in general with Lynch's findings but in contrast to those of Zumpt. With the exception of the Karoo case, all females came into oestrus again after birth of the young. The second oestrus period is

not subsequent to weaning, lactation continuing for at least 2–3 weeks after remating has taken place even in the latest onset of oestrus. This relatively short time between birth of a litter and onset of the next oestrus could account for the double peak in the proportion of gravid females found in the population by both Lynch and Smithers but interpreted by them as indicative of an extended breeding period rather than polyoestry.

Lynch (1980) found corpora lutea to be absent in *Cynictis* in advanced pregnancy, suggesting that progesterone is produced by some other tissue, possibly the placenta. This could help to explain the unusually rapid post-partum onset of oestrus in *Cynictis* in comparison to, for example, *Suricata*. In the latter, corpora lutea are conspicuous throughout pregnancy and second oestrus occurs post-weaning with a definite pause of at least a month after the suckling stimulus has stopped before pregnant females are present in the population again (Lynch 1980). Since both species normally suckle young for approximately the same period of 6–8 weeks, although 4–5-month-old *Cynictis* young may still suckle occasionally (Rasa, pers. obs.), the suckling stimulus does not appear to result in a long-term inhibition of post-partum oestrus in *Cynictis*, as it does in *Suricata*.

On the basis of our findings, we conclude that the confusion existing in the literature is probably due to the sampling methods used by previous authors and the erroneous estimation of the gestation period. *Cynictis* appears to be polyoestrous and is thus similar to the majority of the Herpestinae (Ewer 1973) but is atypical in that the onset of second oestrus occurs during the lactation period and not post-weaning as in most of the other species investigated to date. Our finding that the second litter is born within 2–4 months of the first would be difficult to identify as two separate breeding instances from random samples taken from a population. To determine whether polyoestry occurs,

long-term studies on known individuals are necessary, as in this case.

Whether the second oestrus falls within the definition of a post-partum oestrus or not is speculative, owing to the time-span involved. Post-partum oestrus has been recorded for *Mungos* (Rood 1975; Thurnheer 1990) where it occurs 7–10 days after parturition. Several viverrids have been reported to initiate a new oestrus cycle rapidly after loss of a litter and concomitant cessation of lactation. Here, time-spans varied from 5–20 days, depending on the age of the young at death (Ewer 1973; Rasa 1977). Only the data for the Transvaal group fall within this range. The occurrence of oestrus 5–8 weeks after birth when young are still present and lactation is continuing (Kalahari, Etosha), has never previously been recorded for any other viverrid. Oestrus onset in these cases could be due to a decrease in suckling activity by the young, which start eating solid food at approximately 4–5 weeks old. The finding that the second oestrus occurs rapidly post-partum in the Transvaal but up to two months after birth in Etosha and the Kalahari, resulting in a six-week discrepancy in breeding season length, in the different areas, may be dependent on climatic factors influencing food type and food availability. Further research is, however, necessary to clarify this point.

A possible biological explanation for the two anomalies in *Cynictis* breeding biology, namely, the small and constant litter size and the rapid production of a subsequent litter, is that these evolved as a reproductive strategy to maximize juvenile survival. Our observations have shown that *Cynictis* is unique amongst viverrids in that it is the only species ever recorded as bringing large prey items (rodents, bats, reptiles and large arachnoids) to young while they are still in the burrow, behaviour more typical of the social canids and felids (Macdonald 1983). In all our observation areas we found that the food item is secured and eaten by one of the offspring only and, as is typical of other viverrids (Rasa 1987), there is no food sharing between young. This necessitates frequent provisioning by adult group members. Observations on other social mongooses, *Helogale* (Rasa 1989) and *Mungos* (Rood 1975), have shown that young are not fed at the den and must accompany the adults foraging at 3.5 to 4 weeks of age. Young *Helogale* suffer heavy predation losses during this period, mainly as a result of raptor attacks (Rasa 1989). In contrast, *Cynictis* young are provisioned at the den during this vulnerable phase and first accompany the adults foraging at approximately eight weeks old, when they are large enough to fall outside the prey spectra of a large number of raptor species and are also more agile in avoiding aerial attacks. To date, no *Cynictis* young have been observed killed by raptors, compared with 47% losses owing to raptors observed in *Helogale* (Rasa 1989). During the time they are in the den, however, they are exposed to the same terrestrial predator spectrum as recorded for *Helogale* young during their den phase (Rasa 1989). For *Helogale*, however, attacks by terrestrial predators were far less frequent than those by raptors (13 vs. 102), therefore extension of the den phase in *Cynictis* young is unlikely to result in predation levels equivalent to those observed in species where young leave the den early in life. In this study, young have only been lost to snakes (Transvaal, Kalahari) and monitor lizards (Karoo). By extending

the period the young can remain in the den by feeding them there, the predator spectrum as well as the predation rate on the juveniles is therefore reduced.

If the main threat to the young is from terrestrial predators, they would be particularly vulnerable if only the mother was involved in their protection during this sedentary phase since she must leave them to feed. Although a single case of a female successfully raising young alone was recorded (Etosha, present study), all group members usually aid in offspring care. They not only bring food to the den but also remain there with the young while the mother(s) forages. Present data (Kalahari) indicate that females, both mothers and non-mothers, play a predominant role in guarding the young at the den, alternating with one another, while males are primarily involved in provisioning the offspring; a sex-biased role differentiation in infant care similar to that recorded for *Helogale* (Rasa 1989). The number of offspring a group can raise successfully should therefore not only be dependent on the number of females of reproductive age present but also on group size i.e. the number of 'helpers' available. This correlation has been shown clearly for *Helogale* (Rasa 1987, 1989) but present data on *Cynictis* are insufficient to show a statistically significant trend.

Young are nutritionally independent at 16–18 weeks old. Since several reproductive females may be present in a group and oestrous cycles are relatively synchronized (Wenhold 1991 and present study), several dependent young can be present at any one time. Although, as previously mentioned, all group members are involved in provisioning the offspring, food supply and the number of helpers would limit the number of young which could be provisioned successfully. Producing two small litters rapidly one after the other could ensure that all young born into a colony received adequate food during their dependent phase (from 4–16 weeks of age) and minimize the number of 'helpers' necessary. Since there is no breeding suppression in subordinate females, production of larger litters such as has been recorded for other social viverrids — *Helogale* 4–5, *Suricata* 2–5, *Mungos* 3–5 (Ewer 1973) — would result in the simultaneous presence of large numbers of young. It is unlikely that 'helpers' could adequately provide for these, and, as a result, juvenile mortality owing to poor nutrition could be expected to be high. Alternatively, group size would need to be so large to ensure adequate help for all offspring that, in territorial species, available food resources would be inadequate to support the necessary increase in individuals. In the other social mongoose species, either breeding suppression of subordinate females is present (Rasa 1973) and/or litters are widely spaced (Ewer 1973), with the sole exception of *Mungos* where very large group sizes (40+ individuals) and semi-nomadism have been reported (Rood 1975). For species with reduced reproductive capacity, the actual number of dependent young present at any one time would thus be similar to that for *Cynictis*.

The yellow mongoose therefore appears to have evolved a unique breeding strategy for viverrids, the production of small, relatively sedentary, litters following each other rapidly in time. This can be considered a means of coping with environmental constraints such as fluctuating food supply — no second litter being produced when food is scarce (Karoo) — and protection against predators. By these

means, the necessary high level of nutritional investment in the young is spread over a longer time-span and predator pressure is reduced, resulting in enhanced survival rates for offspring.

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