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## Observations on Parturition and Related Phenomena in the Hyrax (*Procaviidae*).

By J. B. SALE.

### Introduction.

The long gestation period (about seven months) and advanced development of the new born in hyrax has produced repeated comment (VAN DER HORST, 1941; MURRAY, 1942; WEBB, 1946). The absence of any account of parturition in the wild may be accounted for by the fact that birth normally takes place in the deep recesses of the hole. Although hyrax breed in captivity (WEBB, 1946; JARVIS & MORRIS, 1963), the females rigorously avoid attention during parturition. Few observers have seen new-born hyrax (HAUSER, 1951) and few, if any, have witnessed parturition. Seven litters of Mount Kenya Hyrax (*Procavia johnstoni mackinderi*, Thomas) have recently been born in captivity here and in one case the entire process was observed and photographed.

### Gestation period, breeding season and litter size.

Table 1 presents information relevant to the seven births under consideration. The gestation period of D (SALE, 1965) was 214 days and that of B<sub>1</sub> 222 days. This confirms the only previous direct observation (MURRAY, 1942) that the gestation period of *Procavia* sp. is seven to seven-and-a-half months. It will be seen that the three newly-captured animals (A, B and C) all produced young in January, suggesting that COE's (1962) estimate of the breeding season for this species as August to November needs modifying to include January. His conclusion was partly based on an estimate of the age of two juveniles seen in December as four months, but it is very likely that he overestimated the age, for the development of the young at birth is surprising (see below). COE's (1962) statement that "no animal apparently ever produces more than one young at a time" also requires modification judging by the cases under consideration, five of which produced two young and one three. COE informs me that the observations on which his statement is based were made in the Teleki and Gorges Valleys of Mount Kenya where the population density of hyrax is particularly high. A, B and C were all females recently captured from the Mackinder Valley where the population density is relatively low. D was a Teleki Valley animal but underwent the entire pregnancy in a captive colony where there was no lack of food. Her second

TABLE 1.  
*Summary of data on the seven births under consideration.*  
(B<sub>1</sub>, C<sub>1</sub> and D<sub>1</sub> are later births of animals B, C and D respectively.)

CASE	A	B	C	D	B <sub>1</sub>	D <sub>1</sub>	C <sub>1</sub>
Age group	Old adult	Young adult	Adult	Adult	Adult	Adult	Adult
Time in captivity	7 days	18 days	18 days	17 months	19 months	26 months	20 months
Circumstances at time of parturition	In cage with 2 other pregnant females	In cage with 1 other pregnant female	In cage with 1 other female and 2 young	Member of a free-ranging col. (see text)	Member of colony	Member of colony	Member of colony
Site of birth	Dark section	Dark section	Dark section	Darkest corner of "home"	"home"	"home"	"home"
Observation	Intermittent	Nil	1st birth nil 2nd throughout	Intermittent	Nil	Nil	Nil
Date of birth	10 Jan. 1963	21 Jan. 1963	21 Jan. 1963	3 Nov. 1963	24 July 1964	30 Aug. 1964	3 Sept. 1964
Time of day	1.00 p.m.	9.00 a.m.– 12.00 noon	9.00 p.m.	4.30 p.m.	8.00 a.m.	10.0 a.m.– 12.0 noon	1.0–2.0 p.m.
Sex of young	♂	♂	♀	♀	♂	♂	♀
Interval between births	10 mins.	?	1 hr. 45 mins.	10 mins.	?	—	?
Wt. of young	310 g	295 g	380 g	350 g	275 g	300 g	335 g
Body length	17 cm	16.5 cm	19.5 cm	19 cm	18 cm	21 cm	20 cm
						19 cm	22 cm
						19 cm	19 cm
						19 cm	19 cm

pregnancy ( $D_1$ ) commenced very soon (2 months) after the twin birth (D), which may account for the fact that only a single young was produced from this pregnancy, whereas  $B_1$  and  $C_1$  were multiple births following a longer resting period (19 months and 20 months respectively). CALHOUN (1949) has shown that in rats overpopulation can result in pregnant females getting insufficient food leading to a reduction in the size and viability of the litter. It is thus possible that litter size in the hyrax depends on the population density and food supply of the area in which the pregnant female is found. The discrepancy between the present observations and those of COE may be explicable along these lines but more data is required before definite conclusions can be reached on the litter size of the Mount Kenya Hyrax.

### **Behaviour associated with parturition.**

In cases A, B and C the parturient females were confined in a cage 120 cm. by 90 cm. by 60 cm., including a dark section 45 cm. by 90 cm. by 60 cm. There were either two (in the case of A) or one (in the cases of B and C) other females in the same cage. D was a socially integrated member of a small *colony* comprising three adult females, one old male, one sub-adult male and four juveniles of around nine months old. This group had the run of a flat concrete roof 250 m<sup>2</sup> in area. Their "home" consisted of a completely dark box structure 106 cm. by 90 cm. by 60 cm., divided into two tiers and raised on legs 120 cm. above the ground. Three "door-eye" one-way lenses permitted unobtrusive inspection by an observer. Access for the animals was by a sloping board. Most of the day was spent inside except for half-hour periods in the morning and evening when the animals emerged to feed. In cases  $B_1$ ,  $C_1$  and  $D_1$  the females were members of the same colony as D except that the old male had died. In early June 1964 the group had been moved with their "home" to a wire enclosure on the ground, 3.7 m. long, by 2.1 m. wide, by 2.4 m. high.

A few days prior to parturition the aggressiveness of the pregnant females increased. A, in particular, became restless and anxious to escape. This aggressiveness was far less marked in D,  $B_1$ ,  $C_1$  and  $D_1$  who were in more natural surroundings and had been in captivity for a very much longer period than the other three. We can therefore regard their (D,  $B_1$ ,  $C_1$  and  $D_1$ ) behaviour as the most normal of the seven. In case D, the old male left the proximity of the group about four hours before the births took place and found shelter in a dark corner some thirty metres away. He did

not return until the early hours of the following morning. The rest of the group vacated the quarters immediately prior to the event and remained outside making excited twittering noises. An inquisitive youngster occasionally poked his head inside to see what was happening and later sniffed and lightly licked the newborn. The group did not settle down again in the company of the nursing mother and her offspring until more than four hours after the birth. D showed no aggressiveness towards the others during this period. Case C<sub>1</sub> also showed some separation of mother and newborn from the colony. About an hour after the birth, two of her three young accidentally fell from the "home" to the ground and the mother immediately joined them in response to their twittering, leaving her third offspring in the "home" with the rest of the colony. She appeared contented at being separated from the colony and immediately lead her two young to shelter beneath some large stones on the ground. There was no question of the inability of the young to climb back up to the "home" as two of them had already done so earlier. The third young was now placed with them by the observer. The group settled down in this temporary shelter for the next nine hours at least but had rejoined the colony by the following morning.

During their births B<sub>1</sub> and D<sub>1</sub> were both in the colony and made no attempt to leave it or to separate their young from the others. B<sub>1</sub>, however, was removed from the colony with her young about half an hour after their birth and kept under close observation. She showed no uneasiness or aggressiveness when placed back in the colony more than twelve hours later. In contrast, the animals in confined conditions did show considerable aggressiveness. A was clearly harassed by the presence of the other females (B and C) and attacked one of them who was accidentally sheltering one of her newborn. She was much more contented when separated from B and C. Similarly, in between the births of her first and second offspring C, a dominant highly aggressive female, viciously attacked her cage-mate B who had two newborn young already. B and her young were removed immediately.

The above evidence might indicate that females prefer to be entirely alone during parturition but must be considered in the light of the following important field observation. When captured in an advanced state of pregnancy (see Table 1), A, B and C were found together as the sole occupants of an isolated hole a short distance (about 15 metres) from other members of the colony. This suggests that pregnant females approaching parturition isolate themselves from the rest of the colony and form a temporary nursery group. The fact that A, B and C gave birth within eleven

days of each other (B and C on the same day) strengthens this possibility. Also, it has often been observed in the field that several nursing mothers with young of the same age are found together. In the case of D she was the only pregnant female in the colony and hence there was no possibility of a nursery group being formed. This, together with the lack of alternative shelter for the colony, could explain the very short duration (four hours) of this female's isolation. In case C<sub>1</sub> it would appear that the mother immediately took advantage of the accidental separation of two of her young from the colony to get temporary isolation. Had more suitable shelter than a small draughty crevice on the ground been available, the isolation may have been longer but this is a matter that needs more investigation. The possibility that a nursery group is formed is strengthened by the fact that the young are indiscriminate in their suckling and providing a female is lactating will suckle from her whether she is their mother or not.

In cases A and C, although the other females present were either pregnant or nursing and had been hole-mates in the wild, the conditions were extremely unnatural. The animals had only recently been brought into captivity and because of their preference for the smaller dark portion of the cage it was impossible for the parturient animal to get more than a short distance (60 cm.) away from its cage-mate(s). In the hole where they were captured it would have been possible for one animal to hide away in a secluded crevice temporarily out of contact with the others. Hence the attacks in cases A and C were, in all probability, the result of stresses due to the unnatural circumstances and not an indication that a parturient female normally undergoes complete isolation. Further, the fact that D allowed inquisitive youngsters to sniff and lick her newborn shows that strong aggressiveness towards other members of the colony is not a constant feature of the behaviour of parturient female hyrax.

### **Labour and birth.**

Nothing in the nature of a nest was ever produced but parturition always took place in the darkest region of the quarters. It was accompanied by a hoarse squeaking noise, the frequency of which coincided with contractions. During an actual contraction the female would stand still with the hind quarters raised and her head held slightly up, the eyes staring straight ahead. There was some muted sighing between contractions and during this period the female moved uneasily round and round. Female B made some unusual squeaking noises during the evening prior to parturition.



Fig. 1. C giving birth to her second young which can be seen half way out of the vulva.

This noise was similar to the noises made during labour but it seems unlikely that true uterine contractions could precede birth by such a long period. This could have been a case of false labour due to the intensifying of Braxton Hicks contractions. True labour in fact began approximately twelve hours later. The birth of C's second offspring was carefully observed and photographed. The long delay (one hour and forty-five minutes) in this birth was probably due to the shyness of the animal exposed in artificial light before two human observers. In cases A and D both young were born within ten minutes and in the other cases there were indications that the interval was also brief.

The ease with which C gave birth was remarkable. Throughout the long interval she showed no sign of acute discomfort but merely made the sighing noise periodically as she strained mildly. Towards the end of the period restlessness increased and the animal only stopped moving round and round during an actual contraction. She did not lick her genital area or attempt to rupture the membranes, omissions resembling ungulate behaviour (COLLIAS, 1956) and contrasting with that of many of the smaller mammals (ROWEY, 1961). Suddenly, whilst C was still on the move, the head of the young appeared from the vulva and was rapidly followed by the rest of the body, there being a brief delay in the "mid-trunk" region (see Fig. 1). The whole birth from the appearance of the head took less than one minute. The female provided



*Fig. 2.* C and her newborn immediately after birth. The membrane is covering the head and entire body except for one foreleg which is protruding.

little or no “push” during the process, and made no attempt to lick the emerging infant which was almost completely enveloped in the amniotic membrane (see Fig. 2). The afterbirth (placenta and membranes) followed immediately and, as in all the other cases, was not eaten by the female who also left the cord to break without her aid. In four cases this happened at birth or shortly afterwards, the cord breaking off at the navel. Other offspring had the cord and placenta attached for about two hours after birth without any attempt by the mother to remove it. The cord eventually parted as the youngsters moved around. Cord length varied between 13 and 20 cm.

#### **Establishment of the mother-young bond.**

Immediately C’s offspring was born its eyes were open and it began to wriggle and attempt to crawl around on its belly. This resulted in the enveloping membrane being broken in the head region and working back to behind the shoulders (see Fig. 3). The mother stared at the moving youngster, sniffed it and then began to lick it in a rather casual manner. As a result of this licking the



*Fig. 3.* C sniffing the moving infant. The membrane has now worked back to the thoracic region, exposing the head and neck. The older infant can be seen crouching below the neck of the mother.

rest of the membrane was eventually removed but the mother did not eat any of it. The sniffing suggests that the mother was attracted by the smell of the membrane and birth fluids as well as by movement. Hunger and particularly thirst are unlikely to be great at this time as hyrax normally eat only twice a day and rarely drink, hence the casualness of the licking and failure to ingest the membrane or placenta. The attraction of the smell and movement served to introduce the mother to her newborn offspring.

As licking proceeded the youngster straightened its legs and as soon as licking ceased, after several attempts to do so, climbed up onto its mother's back and sat there for some twenty minutes, only jumping down when she moved. As soon as she was still again the youngster went to her and regained his position on her back. This



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*Fig. 4.* B<sub>1</sub> with one of her newborn attempting to climb onto her back. The infant is three hours old.

*Fig. 5.* B<sub>1</sub>. The two newborn (three hours old) suckling at the inguinal mammae. Note the retracted upper lip exposing the incisors as she makes the whinnying call.

strong tendency of the newborn to climb onto the mother's back was noted in all other cases and often preceded the initial attempt at suckling. Apart from the first few hours after birth when the mother was alone the young of D did not confine themselves to their mother's back but would jump up onto the back of any member of the colony, especially when huddled inside the "home". Similar observations on climbing were made in cases B<sub>1</sub>, C<sub>1</sub> and D<sub>1</sub>. In the wild I have observed young sitting on the back of a female basking in the midday sun on a hot rock. This behaviour persists, with diminishing frequency, until the young are about five months old, which is well after the period of dependence on the mother (see below).

The instinctive urge to climb up and sit on top of objects is very marked in hyrax, but I have never observed an adult sitting on one of its mates. In wild adults the object is generally a high rock or stout plant such as a giant groundsel (COE, 1962) which affords a wide view of the surrounding terrain and enables predators to be seen more easily. In captivity, young from a few hours old frequently perched themselves on any protrusion or ledge on the wall of the cage. In the newborn the nearest elevated "object" is generally its mother and the basic urge to climb would seem to be an



Fig. 6. D inside the "home" with one of B<sub>1</sub>'s young (three weeks old) sitting on her back.

important component in the climbing of the young onto the back of its mother (and other animals) soon after birth. This component gets progressively transferred to inanimate objects such as rocks as the young grow up, until in the adult it is no longer expressed in climbing onto other hyrax.

Instinctive climbing onto the mother and other animals in the young hyrax serves a number of important functions. Firstly, it constitutes the first clearly defined social-contact action on the part of the newborn in relation to the mother. COLLIAS (1956) has pointed out that in ungulates the rising of the newborn on its legs is an important aspect of imprinting. In hyrax the mere fact of the young straightening its legs, in response to licking, is an ill-defined action as, compared with ungulates, hyrax have very short legs in relation to body size. Of greater stimulus value to the imprinting process will be the climbing of the young onto its mother's back which immediately follows. The mother-young bond is possibly further cemented by this climbing behaviour because it brings

the young into direct contact with the mother's dorsal gland which is the site of scent production in hyrax. Thus in the first few hours of its life the young will bear its mother's scent rather than that of other members of the colony. Once the mother-young bond has been firmly established by the added contact produced by suckling (see below) the young begin to gain acceptance with other adults and both the above functions of the climbing behaviour play a part in this. It is in the context of the whole group that a third function of climbing can be seen. Inside the hole, hyrax tend to huddle close together in the furthest corner from the entrance which is normally the darkest and free from draught. If the young did not climb onto the top of the "huddle" they would be in danger of being smothered and trampled upon. By sitting on the backs of the adults such dangers are avoided whilst contact with the group is maintained together with the advantage of heat insulation. Indeed, thermal comfort may constitute a fourth function of climbing. Certainly if the young do the opposite, i.e. crouch beneath adults, they are liable to be in ventral contact with either cool rock inside the hole or very hot rock when outside, discomforts avoided under both conditions by sitting on the back of the adults. Some idea of the temperatures of the rock may be gained from air temperature measurements. In a typical hole in the Rift Valley the air temperature remained around 15°C day and night, while above exposed rock outside the afternoon maximum air temperature was over 40°C. The rock floor of the hole would be at a lower temperature than the air and the exposed rock considerably higher than the outside air temperature.

### **Suckling behaviour.**

Suckling has been observed both in the present animals and in the field, where it takes place either in the seclusion of the hole (indicated by suckling noises) or outside on the rocks. When the newborn are not sitting on the back of their mother they crouch on the ground beneath her belly and in the case of the Mount Kenya Hyrax, are practically hidden by the long hair of the mother. From this position the suckling posture is very easily assumed and for this reason it is difficult to establish the exact sequence of events leading to the initial suckling. Nuzzling of the belly fur by newborn crouching below the mother is frequently the first sign of appetitive suckling behaviour and may be met by passivity or even withdrawal by the mother. In hyrax both inguinal and pectoral mammae are used, hence the chances of the

newborn young discovering a teat initially are good whichever way it happens to be facing while crouching below the mother. Several attempts to suckle have been observed immediately after licking has ceased but, as stated above, initial suckling often comes later, after the young have spent some time on the mother's back. The first indisputable successful suckling observed was one and a quarter hours after birth. The newborn young make a high-pitched two-syllable twittering noise, generally commencing shortly after birth. FLOWER (1932) described it as "a loud chirping noise like the voices of little birds". Among the mammals it compares most closely with the call of young guinea pigs. The twitter functions as a distress call, as evidenced by the fact that its frequency and intensity are increased when the young are separated from the parent and until they are again in physical contact with her. On such occasions the parent responds to the distress signal by producing the adult contact call (a deep guttural twitter) and running in an agitated manner towards her offspring. The separation of the young alone, i.e. without twittering, does not evoke such a reaction on the part of the mother. For example B's female offspring remained silent in a corner away from her for about seven hours on the first day and she made no attempt to get it back to her. She accepted it readily, however, when placed near her at the end of this period, showing that this was not a case of rejection. Hyrax do not retrieve their young in the manner of many rodents (ROWELL, 1960) and carnivores (EWER, 1963) but merely try to place themselves in physical contact with them and then, if necessary, lead them to shelter.

Intense twittering on the part of the young sometimes precedes a suckling attempt (including the initial one) and here constitutes a begging call, the function of which is to cause the mother to remain still. Apart from the first few meals, when the young are still learning to find the teats, if the mother is already stationary the twitter is rarely given but the young proceed directly to nuzzling. The mother responds to this by slightly raising herself on her legs, enabling the young to get at the mammae. The inguinal mammae, of which there are two pairs, are approached from the front of the hind legs in the usual ungulate manner. There is a single pair of pectoral mammae and while these may be approached from behind the foreleg, the young often reach them from the front. The mother responds to suckling by drawing her upper lip tightly back over the gums, exposing the upper incisors. She then continuously emits a whinnying type of noise. Its production involves the abdominal muscles which contract powerfully during each intensive burst of the noise. During this process the

female looks straight ahead, only occasionally turning her head in the direction of the young. While suckling the young occasionally emit a more guttural form of the twittering noise which seems to be an expression of excitement and satisfaction. The guttural twitter is also the contact call, given on all occasions of renewed contact with the parent and persists in adult life as the contact call (greeting) between members of a colony.

Often both members of a pair of young will approach the female together. Sometimes one member of a pair will induce the mother to nurse and is then usually joined immediately by his mate. The young seldom suckle for more than three minutes, apart from the first week when longer periods of up to seven minutes (first day) have been observed. They frequently change teats during a suckling period. Termination may be voluntary on the part of the young or may be brought about by the mother crouching down or moving away.

Suckling occurs at about one-and-a-half-hourly intervals in the first few days. As early as two days old young hyrax begin to nibble adult food and run around outside among the adults basking in the sun. Suckling does not appear to be the main food source for long and soon shows a marked decrease in frequency, brought about by the mother's refusal to nurse. During this period when suckling is being reduced the twittering young frequently chase the parent who refuses to remain still. Suckling has been observed at three months but does not occur at significant intervals, from the point of view of nutrition, after ten weeks.

### Discussion.

For its size *Procavia* has a very long gestation period and bears large offspring. Many of the smaller artiodactyls have a gestation period of seven months (that of *Procavia*) or less. For example, the Impala antelope (*Aepyceros melampus*) weighs 30 Kgm. (MABERLY, 1960) and has a gestation period of six-and-a-half to seven months (ASDELL, 1946); the domestic sheep (*Ovis aries*), weighing 50 to 80 Kgm. according to breed, is generally around five months. There appear to be no records for the very small antelopes, such as the Suni (*Nesotragus* sp.) and Dik-Dik (*Rhynchotragus* sp.), but in view of the fact that the much larger Steenbok (*Raphicerus campestris*) is recorded as six months (BIGALKE, 1963), they are unlikely to be much longer than this. Comparing with non-ungulate mammals of the same size as *Procavia*, Nutria (*Myocastor coypus*) bears large young for its size (3,500 gm.) and

has a gestation period of five months, whilst the domestic cat is only two months. It seems highly probable from present records, that *Procavia* has by far the longest gestation period for a mammal of its size, excluding cases of delayed implantation.

LEITCH *et al.* (1959) compared the pre-mating weights of the young adult female with the total weight of a newborn litter in 114 species of mammals. From their data the authors deduced that "relatively the larger mammals carry a smaller weight of young" and gave the following equation to predict the weight of young carried from the weight of a mother:  $N = 0.5408 M^{0.8323}$  where N is the weight of the young and M the weight of the mother. They admit that the prediction value may not be very high but it is interesting to note that animals giving values of N significantly above the one predicted are either domesticated species, where nutrition and selective breeding may have interfered, or wild rodents with unusually long gestation periods for their size such as the Viscacha (145 days, ASDELL, 1946). Since hyrax is in neither of these two categories, it is interesting to compare the predicted values of N with those actually found in the present cases. Table 2 presents the relevant data, giving litter weight (N) as a percentage of maternal weight in order to facilitate comparison with other species.

The actual litter weight (as percentage of maternal weight) is higher than that predicted in all cases. The average difference (7.2) is considerably higher than that of any other wild mammal recorded by LEITCH *et al.*, apart from several rodents. The only ungulates nearing this value are domesticated species, including heavier breeds of sheep that have undergone artificial selection for high birth weights. Since B was the only young adult of the four, more importance could be given to this case than the other three when comparing with the data of LEITCH *et al.* It would, however, be unwise to draw conclusions from a single example but it is interesting to note that the difference value for B (14.2) is only exceeded by a vole (*Microtus arvalis*) and laboratory guinea pigs (*Cavia porcellus*).

It must be borne in mind that the present observations were on an isolated high altitude species of hyrax. From records and unpublished personal observations on lowland species, however, there is no reason to believe that these conclusions cannot be applied to all living hyraxes. The Cape Dassie (*P. capensis*) has the same gestation period (MURRAY, 1942) as the Mount Kenya form but information on the litter weight is lacking in the literature. Litter size (ASDELL, 1946) is also small. *Dendrohyrax* sp. appear to have similar weights and litter size to *Procavia* sp. (WEBB, 1946). The

TABLE 2.  
Maternal and neonatal weights compared.

Case	Wt. of mother (non pregnant average)	Wt. of litter	Litter wt. Maternal wt. × 100		
			Actual	Predicted	Difference
A	3627 g	605 g	16.7	13.6	3.1
B	2544 g	730 g	28.7	14.5	14.2
C	3590 g	575 g	16.0	13.7	2.3
D	2630 g	680 g	25.9	14.8	11.5
B <sub>1</sub>	2544 g	640 g	25.2	14.5	10.7
D <sub>1</sub>	2630 g	405 g	15.4	14.4	1.0
C <sub>1</sub>	3590 g	857 g	23.9	13.7	10.2
Average	3022 g	642 g	21.3	14.1	7.2

above comparisons of gestation periods and neonatal weights suggest that the modern hyrax may have descended from a larger animal, these two factors having been reduced at a slower rate than adult size during the evolution. The small litter size supports this evidence, although inconclusive when considered alone.

MAYR (1958) has pointed out the value of behaviour studies in elucidating phylogeny and states that "the more behaviour elements are consistent with a postulated phylogeny, the greater the probability that the phylogeny has validity". Fossil evidence points to the development of the hyracoids from a primitive subungulate stock (ROMER, 1945) from which the proboscideans and sirenians also developed. *Moeritherium*, the most primitive ancestor of the proboscidean group, was about the size of a large hog and possessed a number of features in common with the hyrax, especially the skull and teeth. A relationship with the elephants and *Sirenia* is borne out by the placentation in all three groups (WISLOCKI and VAN DER WESTHUYSEN, 1940). The serology (WEITZ, 1953) and a study of the plasma proteins and haemoglobins in hyrax and the elephant (BUETTNER-JANUSCH, BUETTNER-JANUSCH and SALE, 1964) support a relationship between them. Some workers emphasize the affinities of the hyracoids with the *Perissodactyla* (WHITWORTH, 1954), pointing to the mesaxonic limb arrangement and "distinctly ungulate type" of brain. The present consideration of some aspects of hyrax behaviour provides evidence of a basic ungulate type of ancestry and also supports the relationship with the early proboscidean stock.

Nesting behaviour often provides a reliable guide to taxonomy, as shown amongst the birds, and the lack of a nest in hyrax strongly contrasts the group with burrowing rodents and insec-

tivores (WIESNER and SHEARD, 1933; BARNETT, 1963; GODFREY and CROWCROFT, 1960) and indicates ungulate affinities. The formation of a nursery group of females and young has frequently been described among ungulates and modern elephants (SHORT-RIDGE, 1934) and if it occurs in hyrax would be consistent with a relationship with these orders.

The absence of maternal activity directed towards the young during birth has already been noted as an ungulate feature. Amongst ungulates some species eat the placenta while others fail to do so as in hyrax and hence no real importance can be attached to this point, except perhaps to note, by way of contrast, that rodents and carnivores do eat the placenta and foetal membranes.

The early activity of the newborn, manifested in climbing, is also a feature shown in most ungulates, where the young soon have to keep up with the movements of the herd. This early development, often associated with small litters, is a frequent feature of non-burrowing herbivores and is found in such plains-dwelling forms as the hare as well as in typical ungulate species. The response of the mother to the distress call of the young is also typically ungulate but the suckling behaviour is less markedly so, showing features more specifically like the elephant. The tendency to keep the head still during nursing is noticeably similar in elephant (personal observation) and hyrax and contrasts with many ungulates who lick their young while suckling. It is interesting that both groups also have pectoral mammae, although hyrax possesses the more common inguinal ones as well.

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#### Zusammenfassung.

Die lange Tragzeit, das hohe Geburtsgewicht und die zahlenmäßig kleinen Würfe lassen vermuten, daß die Körpergröße des Hyrax im Laufe seiner Evolution reduziert worden ist. Das Verhalten während und nach der Geburt weist auf Erbverwandtschaften mit Ungulaten und Probosciden hin und nicht auf Tiere, deren Junge im Schutze tiefer Höhlen geboren werden. Das Verhalten ist demjenigen der rezenten Ungulaten sehr ähnlich, die ebenfalls nur

eine kleine Anzahl von Jungen in einem fortgeschrittenen Stadium der Entwicklung werfen. Solche Junge benötigen kein Nest und werden sehr früh von ihren Müttern unabhängig. All diese Beobachtungen erhärten das fossile Beweismaterial, wonach sich der jetzige Hyrax aus recht großen Subungulaten, die Savannen und offene Buschgebiete Afrikas bewohnten, entwickelt hat und nicht von Vorfahren abstammt, die wie der heutige Klipp- und Baumschliefer ökologisch spezialisierte Höhlen besaßen.

*Résumé.*

La longue période de gestation, le poids élevé des nouveau-nés et leur petit nombre à la mise-bas suggèrent que la grandeur de daman a été réduite au cours de son évolution. Les traits du comportement, la parturition et la post-parturition dénoncent les affinités ancestrales du daman avec les ongulés et les proboscidiens. Ces affinités n'existent pas avec des animaux dont les petits naissent sous la protection d'un gîte bien abrité. Le comportement est similaire à celui des ongulés modernes qui ont des jeunes en petit nombre et dont le développement à la naissance est avancé. Ces jeunes n'ont pas besoin d'un nid et deviennent rapidement indépendants de leurs mères. Les découvertes fossiles, affirmant que les damans modernes dérivent d'assez grands ancêtres ongulés vivant dans les savanes et les forêts claires d'Afrique, plutôt que d'animaux occupant des niches écologiques aussi spécialisées que celles habitées par les damans des rochers et des damans des arbres d'aujourd'hui, sont corroborées par nos propres observations.