Z. Säugetierkunde 54 (1989) 360–376
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ISSN 0044-3468

Reproductive biology (behaviour, breeding, and postnatal development) in subterranean mole-rats, *Cryptomys hottentotus* (Bathyergidae)[1]

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Receipt of Ms. 7. 4. 1988

Abstract

Described for the first time breeding and reproductive biology of *Cryptomys hottentotus* in captivity. Social behaviour (greeting, hierarchy) involves features of mating behaviour. Mating and breeding in established groups were not recorded. In order to stimulate copulation and estrus, the animals were kept in pairs and re-paired daily. Gestation lasted 98 days (SD = 9, range 84–112). Next estrus after parturition was in 78 days (SD = 9). Litter size was 2 (SD = 0.7, range 1–3); male/female ratio of neonates was 1:1. Neonates weighed 7.9 g (SD = 0.5) each. They are altricial (hairless, with closed eyes), with prominent incisors, vibrissae, and partly developed physical coordination (limited active mobility, lifting head, self-scratching). Growth rate was slow: 0.36 g/day from birth to weaning and still slower afterwards. After birth of the next sibling litter, the growth rate of the juveniles of the previous litter: 1. decreased and the animals were undersized still at the age of one year if left with the family, or 2. increased and the animals were grown-up at the age of 210 days if separated from their parents. Many developmental events correlated with the attained body mass (and the age after conception?) but not with the age after birth: hair cover with mass of 10 g (SD = 1) at the postnatal age of 8–10 days; eye opening: 12.9 g (SD = 0.7), 24 (range 13–50) days; weaning: 34 g (SD = 0.3), 82 (72–105) days. Change of coat colour from black to brown to ochre was also mass dependent. Considering the body mass, *C. hottentotus* has the longest development and the lowest reproduction rate among all the rodents. This may be explained by hystricomorph affinities, subterranean life, and sociality. Reduction in activity of pregnant females and development of a caste of helpers may be understood as energy-saving mechanisms which developed in response to long pregnancy.

Introduction

Reproductive biology has been studied in representatives of most of the mammalian families, yet as far as the subterranean mammals are concerned, our knowledge of reproductive characteristics is fragmentary. These animals breed only seldom in captivity and thus the studies could not be pursued on a large scale like in other rodents or insectivores (cf. e. g. the data summarized by Eisenberg 1981 and Nowak and Paradiso 1983). As far as the endemic African family of highly specialized fossorial rodents Bathyergidae is concerned, our knowledge of reproductive biology is particularly limited. Paradoxically, most information on breeding biology has been obtained, thanks to systematic studies by Jarvis (e. g. 1969, 1978, 1979), in the naked mole-rats

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[1] Dedicated to Prof. Dr. Dr. h. c. Dietrich Starck on occasion of his 80th birthday on 29. 9. 1988, and to my academic teacher, Dr. L. Sigmund, on occasion of his 55th birthday. Dr. Sigmund made me acquainted with the monumental work of Prof. Starck. They both taught me that one can hardly understand animal morphology if examining only anatomical specimens and ignoring the animals as living creatures. This paper should also commemorate the great contributions of Prof. Starck to our knowledge of subterranean mammals and his study on biology of African mole-rats published 30 years ago which became the first paper dealing with bathyergids published in Z. Säugetierkunde (1957: **22**, 50–56).

(The results were presented at the 61st Annual Meeting of the German Mammalogical Society at Berlin in 1987.)

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(Heterocephalus glaber), i. e. in the most specialized and one of the least available among the bathyergids.

On the other hand, our knowledge of biology of reproduction in the most common African mole-rat *Cryptomys hottentotus* is actually next to nothing. All the ecological studies missed any convincing evidence on reproduction under natural conditions and the animals were never bred in captivity. The only observations made on captive *Cryptomys* and referring to reproductive processes are those by Bateman (1960) and Hickman (1982). Bateman (1960) described his unsuccessful attempt to rear a litter of three pups of unknown age but gave no clues as to the time of year when the young were found, nor as to their growth. Hickman's (1982) observation of copulations in mole-rats has become the first description of mating behaviour for the whole family.

To my knowledge, the present paper can be considered the first published report on birth and successful rearing of *Cryptomys* in captivity. In addition, the hitherto unknown data on the postnatal development of *C. hottentotus* from birth till the adult-like stage as well as on some other aspects of the reproductive biology and sociobiology in captivity and nature are provided.

Material and methods

A total of 41 live and freshly-dead specimens of the African common mole-rats or blesmols, *Cryptomys hottentotus* subsp. (i. e. *Cryptomys hottentotus* sensu lato, cf. Kingdon 1974), was collected in Chainda (environs of Lusaka), Zambia, between September 1984 and September 1987, sixteen of which were brought alive to Federal Republic of Germany in March 1986 and thirteen in September 1987. The animals are kept at the Institute of Zoology of the J. W. Goethe-University in Frankfurt am Main.

The animals were housed in a room with constant temperature (= 22 °C) and humidity (= 50 %) and an artificial day/night (12 h:12 h) light regime. The animals were kept in standard plastic cages for laboratory rats or glass terraria filled with horticultural peat to a depth of about 3 cm. Cage litter was changed weekly from cages inhabited by two animals. As nest material, toilet and tissue papers were provided. The animals were fed on carrots, potatoes, lettuce, and mixed grain (mostly wheat, oats, and sunflower). Occasionally apples, nuts, beet-root, sweat potatoes, black radish, and other kinds of vegetables were offered. No free water was provided.

The mole-rats from the first shipment were kept in two separate groups (12 and 4 animals) until the end of October 1986 when systematic attempts to breed them started. Four adult females (weighing 63–77 g) and four adult males (92–127 g) (captured in Oct./Nov. 1985) were selected and kept in pairs for most of the next time. Each day each female was conjointed with a different male. When the partners (or just one of them) had been reluctant to mate, or, when a series of copulations had been recorded, the animals were recombined still on the same day. Consequently each female was mated several times each day. The pairing procedure progressed until pregnancy was recognized by palpation, increase in body mass, reduced activity. Since then the pregnant females were left relatively undisturbed in a pair with a male.

Each animal was weighed each day to each third day. Except for one female and one male, the animals became fully hand-tame in the course of study. One female gave birth to one litter but was later killed by another female. Each of the remaining females bred at least twice. Altogether 18 young born in 9 litters were studies. Mean values are given with the standard deviation (SD = s_{n-1}) and/or the range (minimum to maximum found values) and the number of observations (N).

Results

Encounter, aggression

A short greeting and introducing of two unknown animals involved vocalizing; head, rump and ano-genital sniffing; pressing and rubbing chins and cheeks on one another. Usually (but not always) a fight followed between two unknown grown-up animals: 1. a larger male attacked a smaller male; 2. a smaller male (in his own cage) attacked a larger male intruder; 3. a larger female attacked a smaller female or a subadult male; 4. a female in estrus attacked other females. Fight had a character of mouth (teeth) wrestling: the animals locked their incisors together and swayed from side to side. The males did not bite each other but tried to break (and actually broke) the incisors of the rival. Eventually the stronger male (with stronger incisors) won, the defeated male fled, showing an appeasement posture: lordosis, tail arched high, presenting posterior towards the winner, excited shaking the body, „barking“. Females and subordinate males took appeasement posture even if the dominant male did not show any apparent signs of aggression. The described subordinate behaviour towards an unfamiliar male was observed as early as in a ninety-day-old male pup (and this despite the fact that the young are immune from aggression by all adults).

The fight between a male and a female lasted very long (up to one hour with short breaks) or, on the contrary, did not take place at all. Such a fight was not serious, there were no attempts to break incisors, the animals were not highly aroused, and wrestling became progressively a character of playful behaviour in which the role of the attacker frequently changed.

If a female was the attacker of another female (or a subadult male), she did not respect the appeasement postures (if any), did not try to fight mouth-to-mouth but bit the retreating animal. All the killed females were wounded in genital regions and on teats.

A male born in captivity and separated from adult animals at the age of 25 weeks (see chapter on postnatal development) attacked (when grown-up) even females, did not respect appeasement postures of defeated animals, and did not show appeasement posture when defeated himself.

Mating

The mole-rats in established groups (i. e. among the animals familiar to each other and getting along well) and in a known environment did not copulate or copulated very rarely.

Mating took place, when a male encountered: 1. a new female (in his own as well as in the female's cage), 2. a female which had been separated from the particular male for some time, 3. a female which had been soaked by a foreign smell during a contact with other animals and/or their smell (e. g. during a stay in a foreign cage).

Unfamiliar environments especially provoked mating. Thus when a pair of mole-rats had been set in a new cage, the animals copulated readily. In two cases, mating was observed even shortly after capturing the mole-rats in the field (from the same burrow system) and housing them in a cage. In another case the mole-rats copulated in a small pail into which they were put off just for few minutes while their cage was cleaned. A pair of mole-rats attempted to copulate while being transported in a small box. Mating could be repeatedly elicited in two younger animals by removal of the elder individuals from a common cage in which the group had been housed.

In general, the course of courthsip and copulation corresponded to the detailed description by Hickman (1982), so only some complementary observations will be noted here.

Although most animals vocalized intensively during courtship and copulation, some were completely silent. Many females kept on soliciting until they were eventually mated. When a male had not responed to soliciting practised by a female, he was eventually mounted by the female. Soliciting of females from males was more frequent than molesting and raping of reluctant females by males. Sometimes the female crawled during copulation carrying the male on her back. Some males attempted to grasp with teeth at the fur of the nape and shoulders of a restless female. The mounts were short (about 5 to 15 seconds). A bluish (bruised?) genital region, evident opening of the vagina, and even bleeding from the vagina were signs of estrus and/or that intromission took place.

In established and breeding pairs, even pregnant and lactating females were spontaneously (i. e. without any apparent courthsip) mounted.

Although mating was most common between appropriate sexual partners, it was observed that a larger (dominant) animal (particularly male) mounted a smaller (subordinate) one of the same sex. Soliciting of a subordinate male from a dominant male had a typical female character but was usually only short and if the larger male did not react, soliciting ceased.

Reproductive characteristics of males

There is no scrotum in *C. hottentotus* and the testes are held abdominally. There was no behavioural evidence that the males would be seasonal breeders. I did not study morphology of the reproductive tract nor periodic changes (if any) in the size of gonads.

Estrus

Even after more than a year of living relatively undisturbed in large terraria, the animals in groups did not breed. Three weeks elapsed since the beginning of pairing experiments before the first female conceived.

Only behavioural and externally apparent symptoms of estrus were followed. The estrus in females was characterized by enhanced agility, activity, and aggressiveness against other females, intensified soliciting from adult males, a reddish and swollen genital region, drop in body mass (Fig. 1), and (as a consequence of mating?) evident opening of the vagina and bleeding from the vagina. The symptoms of estrus persisted for three to seven days.

Next conception after parturition occurred at 78.4 days (SD = 9.1; range 70–91; N = 6) and was roughly correlated with time of weaning. In two cases, when lactation (litters V and VI) was longer than the "norm", the females conceived still before weaning. If pregnancy was spontaneously interrupted (resorption of embryos, abortion), or if the litter was lost, and – in one case – after normal parturition and rearing of a single pup (litter VII), the next estrus and conception occurred within 2–3 weeks.

Gestation

Gestation lasted 98 days (SD = 9.2; range 84–112; N = 9). Pregnant females calmed down and spent most of their time in the nest. The partner males and the adolescent young supplied the pregnant females in the nest with food. The females left the nest usually only to excrete. Pregnant females put on weight regularly (Fig. 1) and increased their body mass by 20 to 35 %. The embryos could be palpated as early as about ten weeks before birth, i. e. some four weeks after conception. When held in an upright position, females in the early stages of pregnancy urinated or even defecated immediately, unable to hold back their excreta. (In animals, particularly females, not accustomed to regular handling, such an involuntary excretion occurred, however, as an apparent expression of fright.) Urine (at least initial and last drops) became progressively thick and whittish (indicating higher contents of proteins?). The whole gestation was characterized by a somewhat swollen genital region. From about the fifth week of pregnancy the inguinal teats became progressively prominent. One to two weeks before parturition, the pectoral teats (particularly the upper pair) increased in size and became more apparent, too.

Ending of several pregnancies (within first five weeks) can be explained by resorption of embryos or apparent miscarriage incidents (with bleeding from the vagina persisting for two days in one case).

One female (C3) developed a false pregnancy with all signs of a real gestation. The animal had increased its body mass and retained it since then (Fig. 1). The upper incisors became fragile. The female became aggressive and was isolated. After 15 weeks the female was joined with a male again, conceived within two weeks, and normal pregnancy followed.

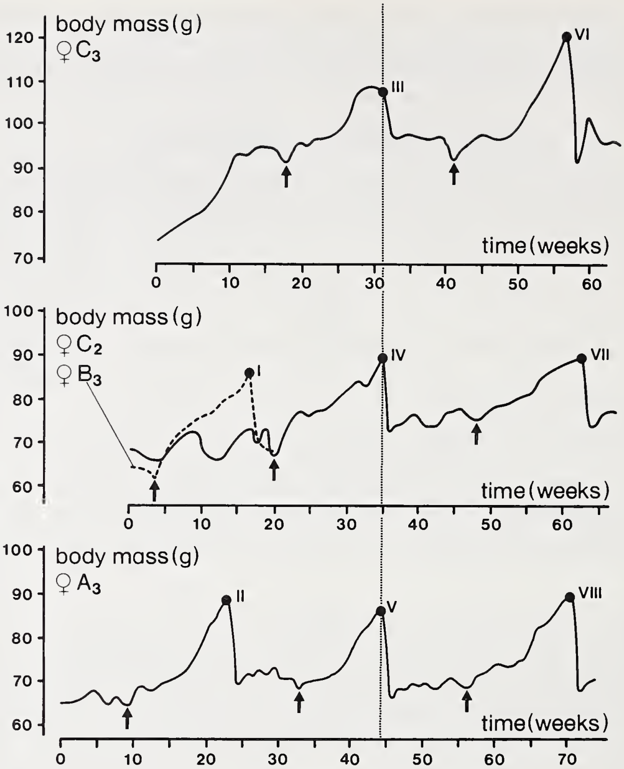

Fig. 1. Changes of body mass in four females across the time of study. 0 – start of pairing (= 27th Oct. 1986). Female B3 was killed in the 20th week by the female C2. Arrows = time of conception, Roman numerals = particular litters. The individual curves are synchronised according to one litter (intersecting vertical line)

Birth, and litter characteristics

The male and the offspring from a previous litter stay in the nest with a bearing female. The actual course of the parturition has not yet been observed. The first observations were done some 15–30 minutes after a single pup was born. The female was engaged in cleaning the neonate and herself for about one hour before falling asleep. The male "froze" in the nest and did not move at all for two hours of observation. He provided a "thermal screen" while the female put the pup between him and herself. It was noted in a litter of three that the pups must have been born in intervals of about one hour between each two pups.

The average size of a litter was 2.0 (SD = 0.75; range 1–3, N = 9). The ratio between male and female neonates was 1:1 (N = 18).

Newborn pups

Newborn pups weighed 7.9 g (SD = 0.5) (Table 1). The nose-tail tip length of the neonates was 59.9 mm (SD = 2.4) out of which 15.4 mm (SD = 1.5) was head and 5.9 mm (SD = 0.6) tail.

The neonates (Fig. 2) were practically naked, the vibrissae, however, well developed. Additionally, short tactile hairs on the body were present but still unconspicuous. Black guard hairs did not penetrate the skin yet but made it to appear rather dark in some pups.

The head spot (blaze) was apparent at birth already. The skin appeared loose, folded, and wrinkled, particularly at the neck and shoulders. The fingers, toes, and claws were normally developed. The tail appeared to be relatively longer than in grown-up animals. The incisors were prominent but not in mutual contact and were partly reddish due to the pulp showing through. The head was comparatively big and round, the snout blunt and the nose convex. A bulged skin-fold represented the auricle; the external opening of the acoustical meatus seemed to be closed. It was found out that the middle and inner ears were mature in a five-day-old pup which (apparently) did not develop after birth.

The newly born pups were able to crawl unsteadily and to hold their head lifted for few seconds.

Except for one litter (VIII) there was always an apparent dimorphic difference between the litter mates, one pup being always larger (up to 0.5 g heavier), darker, and more active.

Postnatal development

Growth

Three periods characterized by a different growth rate could be distinguished: 1. from birth to weaning, 2. weaning to birth of the next sibling litter by the mother, 3. afterwards (see Table 1 and Figs. 4, 5 for details). The growth rate was constant within the defined periods and became progressively slower in each subsequent period. In one male pup which grew slowly after birth, the growth rate increased to the norm after weaning. If left with the family in the third period, the juveniles slowed down their growth substantially and were still undersized at the age of 300 days. On the other hand, the growth rate increased in two pups which were separated from their parents (and from other adult animals) when their mother gave birth to the next litter. These animals reached the range of

Fig. 2. A three-day-old pup of *Cryptomys hottentotus*

Fig. 3. Nursing of twin 15-day-old pups

Table 1. **Body mass in neonates and growth rate in surviving pups of *Cryptomys hottentotus***

0 DAB (birth)	Pups which survived (N = 13): 8.2 (± 0.4) (range 7.9–8.8) g	
	Pups which died (N = 5): 7.4 (± 0.2) (range 7.2–7.5) g	
	Pups altogether (N = 18): 7.9 (± 0.5) (range 7.2–8.8) g	
0–5 DAB	Growth is constant or drops by 10 to 20 %	
5 DAB – weaning	0.36 (0.04) (range 0.26–0.42) g/day	
Weaning-birth of the next sibling litter	Females: 0.21 (0.04) (0.17–0.27)	Males: 0.31 (0.01) (0.307–0.319) g/day
Afterwards	Separated from parents Female: 0.33 g/day Male: 0.63 g/day	Left with parents Female: 0–0.08 g/day Male: 0–0.16 g/day
Age at which grown-up	210 DAB	???

DAB = days after birth

adult-like values of body mass at about 220 days after birth (DAB) and continued to grow slowly afterwards.

Hair cover and colouration

The development of the hair coat and its colouration were primarily dependent on the attained body mass (Table 2, Fig. 4). In normally growing pups (0.32–0.42 g/day), short and thin hairs penetrated the skin 3–5 DAB. The bristle fringe on the tail and the feet was more apparent. Pups could be considered furred (with thin, still sparse but relatively long, grey hairs) after 8–10 DAB. Within few days the pelage became thick and dark slate grey to (metallic) black. Simultaneously the white hair on the blaze appeared. Later on the coat became progressively greyish brown, brown, and eventually ochre. The animals which had been relieved of subordinance appeared to change their colour earlier. The relative size and shape of the white head spot did not change throughout the life. There was no general resemblance in the size and shape of the spot between parents and their offspring in the first filial generation.

Eyes, nose, ears, and teeth

Eye opening correlated with attaining the body mass of about 13 g at 13–50 (mostly about 23) DAB (Table 2, Figs. 4, 5).

In the course of the postnatal development, the nose flattened to become eventually adult-like, i. e. flat and somewhat concave (pig-like and slightly funnel-like) at 40 DAB.

The auricular skin-fold did not develop further. The actual opening of the external ear canal could not be recognized.

The incisors lost their reddish colouration within 1–2 DAB (5 DAB in two pups). The upper incisors grew a little quicker than the lower ones. At 3 DAB the incisors were in contact. The development of the molariform dentition was not studied.

Development of coordination

After the 5th day the (normally growing) pups tended to leave the nest spontaneously and were able to return. Frequency of leaving the nest increased each day. Self-scratching and cleaning was observed in two-day-old pups. Mutual play was recorded in the six-day-old siblings. The young tried to bite into my finger at 23 DAB. Burrowing activity and transporting of nest materials and food were observed in youngs of about 50 DAB. The pups vocalized since birth but mostly only when protesting to being retrieved or cleaned by their parents.

Feeding and parental care

The pups were suckled till attaining the body mass of about 34 g at 72 to 105 DAB (Table 2, Figs. 4, 5), when also drops of milk still could be extracted easily from the upper pair of the maternal pectoral teats. During suckling the mother was supine, and infants prone on her belly. Very rarely also huddling and sitting postures of nursing were observed. Female *C. hottentotus* have one pair of inguinal and two pairs of pectoral (the more caudal pair can be denoted axillar) teats. Only suckling from the (cranial pair of the) pectoral teats was noted (Fig. 3). In addition to being suckled, the pups began to feed on oat flakes and lettuce in 19 DAB. Attempts to feed on roots and potatoes were not successful till the age of 25 to 30 DAB. Begging for feces from an adult male (accompanied by intense vocalization) as well as autocoprophagy was observed as early as in one-month-old pups.

Both parents and even older siblings from the previous litter took care of the pups. They retrieved them into the nest whenever finding them outside. When retrieving, they grasped the body or the head of the (usually “protesting”) pup between the widely opened incisors. Pups could be effectively retrieved till 25 DAB (weighing about 15 DAB). Later on the retrieval became more and more symbolical: the parents attempted to grasp the pup but apparently were not able to retrieve it because of its resistance. Eventually the retrieving attempts ceased (30 DAB, 17 g). Cleaning of pups was performed particularly by the mother. The pups preferred to sleep on bodies of their parents or between them. In families with a single pup, the parents (mostly mother) or older siblings played with the young. Play behaviour in *C. hottentotus* will be the subject of a separate report.

Table 2. **Age and body mass at which certain developmental events start to take place**

	Age (DAB)	Coeff. var. (%)	Body mass (g)	Coeff. var. (%)
Eye opening	23.6 (8.9) (13–50)	37.7	12.9 (0.7) (12.1–13.9)	5.3
Weaning	82.5 (15.4) (72–105)	18.7	34.1 (0.3) (33.8–34.5)	0.9
Apparent fur Black colour	9.3 (1.1) (8–10)	11.8	9.9 (0.9) (9.3–11.0)	9.1
Brown colour	67.0 (21.2) (51–91)	31.6	26.6 (3.8) (22.3–32.8)	14.3
Ochre colour	102.5 (14.4) (92–113)	14.4	36.4 (1.9) (35–38)	5.2

DAB = days after birth; coefficient of variation = standard deviation: mean·100. The given values are means (standard deviations and range of extreme values).

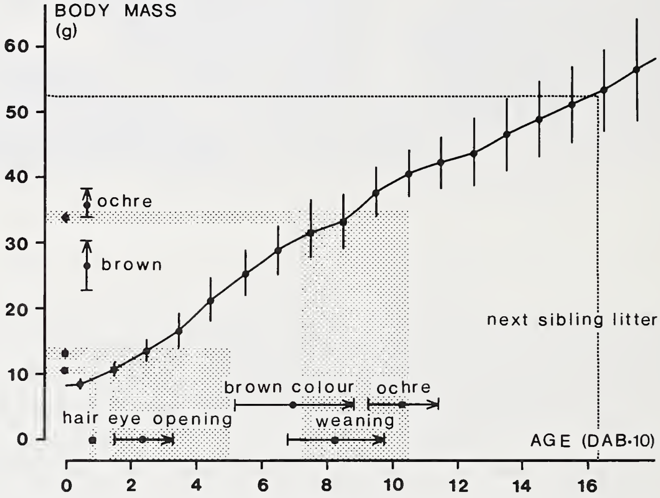

Fig. 4. Increase in body mass (mean and standard deviations) across the age (in decades of days after birth) in surviving pups. Indicated are also mean values and standard deviations of time and body mass at which certain developmental events start to appear. The horizontal and vertical strips indicate the range of extreme values for development of hair cover, eye opening, and weaning

Sexual maturity

A female born in captivity (litter II), separated from parents 160 DAB, grown-up 200 DAB und re-paired with different males each three to seven days, conceived when 340 days old but apparently resorbed the embryos a month later. Females which were not separated from the family and still remained undersized at the age of 300 days were not sexually attractive for males and were not attacked by alien females. Similarly, the undersized males did not attempt to copulate.

Mortality, infanticide

Of eighteen young born in captivity so far, five pups died within 5 to 40 DAB (killed or abandoned by their parents and/or euthanasiated because too weak to survive). They all

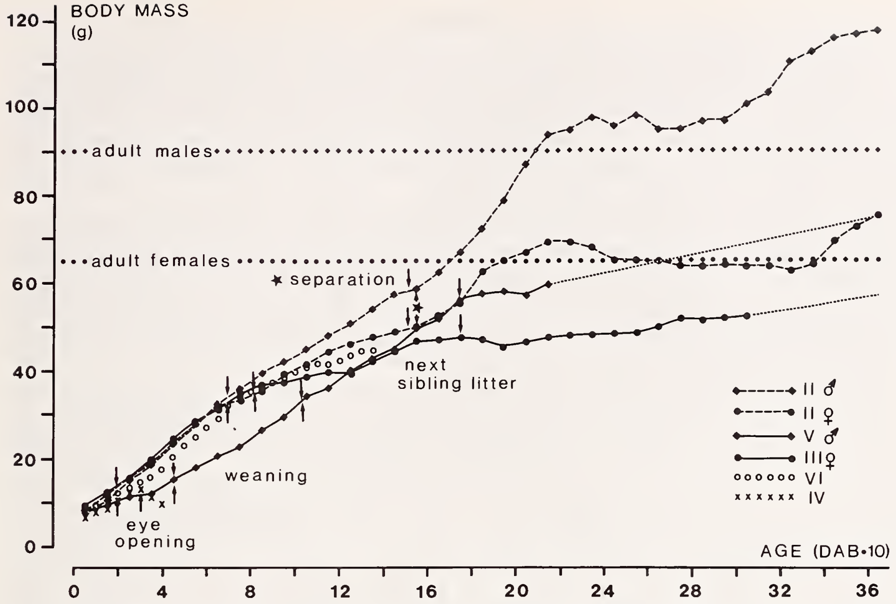

Fig. 5. Individual increase in body mass in pups of several different litters (Roman numerals). Pups of the litter II were separated, pups of the litters III and V were left with their respective families when the next sibling litter was born. Dotted lines indicate the expected trend of the further growth. Pups of the litter VI were female triplets (mean growth rate is given). Pups of the litter IV did not survive the 40th day. Adult-like values refer to lower limits of the respective ranges

were characterized by a neonate weigh less than 7.5 g. In one case, the female was found to bite off and eat the hind legs of her (still alive) five-day-old pup.

Discussion

Materials and methods

When the pairing procedure started the animals were accustomed to captivity but not to regular handling. When the females conceived for the first time, they were still aggressive. Two animals remained aggressive and yet were breeding. The pairs were living in relatively small cages with just a little soil to burrow. Some animals were kept for some time even on sand or saw dust. I kept a breeding pair at home, too. Consequently it is concluded that the defined conditions of housing, "natural housing", lack of disturbances and tameness of animals are not prerequisites for breeding *C. hottentotus* in captivity.

Encounter, aggression

The present findings indicate that appeasement posture, soliciting (and copulation) have also social function and express subordinance of an individual and thus supress aggression of a dominant male. Aggression of females (which are, in general, more aggressive than males) cannot be suppressed in this way. All recorded fatal incidents were actually caused by interacting females.

Mating

Since Hickman (1982) observed mating in *C. hottentotus* in an artificial burrow system into which mole-rats of two different (until then isolated) groups were introduced and since he wrote: "Copulations were effected in all regions of the tunnelways where initial encounters took place . . .", it is apparent that in Hickman's study the copulation was actually triggered by an encounter of two animals unknown to each other in an unknown environment as concluded in the present study.

The present findings indicate that pairings among partners from different systems may occur (as suggested also by Hickman 1982) and that this mating strategy may have great biological importance in reducing inbreeding. On the other hand, once a pair had been established, separated from other animals, and once it started to breed, the animals copulated repeatedly and continued to breed. Mating in (younger) animals was apparently suppressed by presence of other (older) animals.

Hickman (1982) compared copulatory behaviour in *C. hottentotus* to that described for subterranean myomorph rodents: *Spalax* (Nevo 1969) and geomyids (Andersen 1978; Schramm 1961). The differences (spontaneous nature of copulation and short intromissions in *C. hottentotus* vs. long courtship and long duration of intromissions in *Spalax* and geomyids) were explained by differences in social biology and burrow systems (social vs. solitary; copulations not restricted to particular areas vs. mating in specially constructed widened areas) (Hickman 1982). It is suggested here that the basic character of copulatory behaviour in *C. hottentotus* may relate to the common mating pattern exhibited by most hystricomorphs, too (cf. Kleiman 1974) and hence the difference may be also phylogenetic. Further comparative studies are needed to assess reflection of phylogenetic affinities and adaptive significance of copulatory behaviour.

Reproductive characteristics of males

There is no true scrotum and the testes do not descend extra-abdominally in any hystricomorph (Weir 1974). Hence the statement by De Graaf (1972) that "the testes of the male *(C. hottentotus)* usually descend during the breeding season as in rats" is obscure. No hystricomorph male has been reported to be a seasonal breeder (Weir 1974) and *C. hottentotus* is most probably not exceptional in this respect.

Estrus

The estrus (breeding) cycle in *C. hottentotus* in captivity cannot be related to the year's seasons. Nevertheless, there was periodic recurrence of estrus, once the female started to breed (cf. Fig. 1). Certain stimuli (pairing, loss of embryos or litter) elicited occurrence of estrus within three weeks. There was no postpartum estrus. Occurrence of the next estrus after parturition in *C. hottentotus* (about 78 days) is the longest cycle reported for any hystricomorph rodent (cf. Weir 1974). The estrus can be denoted as postlactation.

Suppression of estrus and the enhanced aggressiveness of females (vs. females) was reported for *Heterocephalus*, too (Jarvis 1969).

Gestation

Occurrence of the described diagnostical symptoms of pregnancy since the estrus in which the female supposedly conceived, indicate that delayed implantation and/or embryonal diapause were not responsible for the extraordinarily long pregnancy.

A long gestation period was found in the other bathyergids too: 70 days in

Heterocephalus, at least 87 days in *Heliophobius,* and about 2–2.5 months in *Bathyergus suillus* (Jarvis 1969, 1984; the date for *Heliophobius* and *Bathyergus* are estimations).

Comparison of relative developmental times among different families of Rodentia is provided in Figure 6. In this graph, the time elapsed from conception to rearing the young of a comparable developmental level (specifically: gestation + age at which the eyes are opened and the pups are furred) was plotted against the mean adult body mass. Based on literary date (see the figure legend), mean generic values were counted and, in turn, averaged to get the "family values". The general correlation between the body mass and the length of development was described for different mammalian orders by Eisenberg (1981) and analysed in more details in Rodentia by Burda (in press). Following conclusions may be derived from the comparison provided in Figure 6: 1. Bathyergidae and some other families of Hystricomorpha have relatively long (slow) development. 2. The available data indicate that subterranean Myomorpha have an average or even shorter relative developmental length. Consequently one may speculate that the length of prenatal development is primarily determined by phylogenetic factors and the body size and that there is no general effect of the (subterranean) ecotope upon the length of gestation.

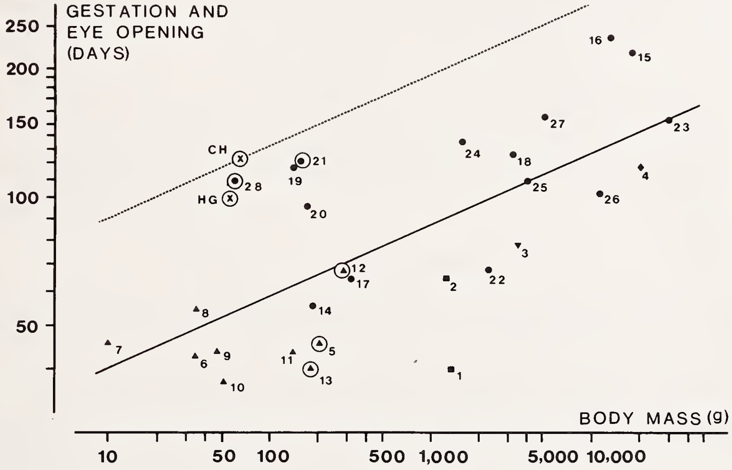

Fig. 6. Correlation between development time and mean body mass of adult females in different families of rodents. Encircled are subterranean forms. Sciuromorpha: 1 = Aplodontidae, 2 = Sciuridae; Theridomyomorpha: 3 = Pedetidae; Castorimorpha: 4 = Castoridae; Myomorpha: 5 = Geomyidae, 6 = Heteromyidae, 7 = Zapodidae, 8 = Dipodidae, 9 = Gliridae, 10 = Muridae, 11 = Cricetidae, 12 = Rhizomyidae, 13 = Spalacidae; Hystricomorpha: 14 = Ctenodactylidae, 15 = Erethizontidae, 16 = Dinomyidae, 17 = Echimyidae, 18 = Capromyidae, 19 = Abrocomidae, 20 = Octodontidae, 21 = Ctenomyidae, 22 = Caviidae, 23 = Hydrochoeridae, 24 = Chinchillidae, 25 = Dasyproctidae, 26 = Hystricidae, 27 = Thryonomidae, 28 = Bathyergidae; HG = *Heterocephalus glaber;* CH = *Cryptomys hottentotus.* Regression line (log body mass/log time): slope = 37.6, intercept = −11.8, corr. coeff. = 0.68. Based on literature data: Eisenberg (1981), Görner and Hackethal (1988), Kingdon (1974), MacDonald (1984), Walker (1975), Weir (1974), and present study

Litter size and sex ratio

Bateman (1960) reported finding of a litter of three pups, De Graaf (1972) found two females with five foetuses each; according to Smithers (1983) the number of foetuses found in *C. hottentotus* ranged from one to five. Mc Connell and Hickman (in prep., pers. comm.) found, that out of 11 *Cryptomys* females, 7 had two, 2 one, 1 three, and 1 four foetuses, which makes the mean number of foetuses to be 2.1 (SD = 0.8). No litters were noted by Mc Connell and Hickman. My findings (mean litter size = 2.0; SD = 0.7) are thus fully consistent with the results of Mc Connell and Hickman.

A small litter size seems to be a general characteristic of bathyergids (Jarvis 1969) and hystricomorphs in general (Weir 1974). Fossorial myomorph rodents (as well as insectivores and marsupials) produce small litters, too (Nevo 1979). In particular, living in a subterranean ecotope is not strictly correlated with production of small litters. The mean litter size is twelve in *Heterocephalus* (Jarvis 1984) and five in *Ctenomys talarum* (Weir 1974), which in both cases is a relatively high offspring number for a hystricomorph rodent (cf. Weir 1974).

The sex ratio of neonates of *C. hottentotus* born in captivity was balanced between both sexes (1:1). In Zambia, we caught, however, more (subadult to adult) males than females (23:18 = 1.28, N = 41) (Burda, Kawalika, Westenberger, unpubl.). This ratio corresponds exactly to that found by Genelly (1965) (49:38 = 1.29, N = 87) in South Rhodesia (now Zimbabwe). The lower percentage of females among trapped animals in contrast to newborn pups (subjected that my sample of births in captivity is representative for wild populations of *C. hottentotus*) can be explained in two ways: 1. Higher aggressiveness in females causes sexually different mortality. 2. Females (having a long gestation and being long involved in maternal care) are less active and therefore less frequently captured than males. However, it will be postulated later on that only a small percentage of females breed.

In *Ctenomys,* the male/female ratio of alive young at birth was 1.07 (Weir 1974). The adult sex ratios (= about 0.4) in ctenomyids as well as in spalacids, rhizomyids, and geomyids are, however, unbalanced in favour of females (Nevo 1979). Since it is known that at least in *Ctenomys* and *Spalax,* the territorial aggression is higher in males than in females, it was proposed by Nevo (1979) that this factor could account for sexually differential mortality.

Newborn pups

The size of neonates was independent of sex. It was correlated with the length of gestation (which was variable!) partly combined with the litter size. The litter size as a sole factor was not however, informative of the body size. Body mass of neonates amounted to about 11 % of the maternal weight. In general, relatively large neonates are typical for most hystricomorphs (Weir 1974). In contrast to most other hystricomorphs, the *Cryptomys* neonates should not be called precocious at all. There is some resemblance to the neonates of ctenomyids and octodontids (cf. description provided by Weir 1974) but the altricial state of *Cryptomys* neonates is still more pronounced and persists for a longer time. Similarly, *Heterocephalus* and *Heliophobius* are born at an altricial level (Jarvis 1969). It is reasoned elsewhere (Burda in press) that altriciality in *Octodon – Ctenomys – Cryptomys – Heterocephalus* is a consequence of reducing the body size in these genera of hystricomorph rodents. Yet compared to e. g. the house mouse or to laboratory rats, the *Cryptomys* neonates are psychophysically more developed.

Postnatal development

The long postnatal development seems to be a general characteristic for the family Bathyergidae. According to Jarvis (1978) it may take a juvenile *Heterocephalus* at least a year to reach adult size.

It is highly probable that the growth rate (at least after the age of about six months) is under a pheromone control of adult animals. Pheromonal effect upon the acceleration or retardation of growth and/or puberty is known or suspected in *Heterocephalus* (Jarvis 1984), some other hystricomorph rodents (Rowlands and Weir 1974), and in rodents in general (Brown 1985).

The rate of postnatal growth did not correlate with sex, nor with the number of litter mates. However, the pups which were relatively undersized at birth continued to grow slowly or did not grow at all and eventually died. Due to individual differences in the rate of postnatal growth, it may be concluded that certain aspects of physical and psychical development (particularly eye opening, development of hair cover and its colouration, leaving the nest) and weaning depended primarily on the attained body size and not on the actual age.

The statement in Nowak and Paradiso (1983) that "even the newborn (bathyergids) can inflict severe bites" seems to be exaggarated – at least if presented as it is, i. e. as a family characteristic. The statement by De Graaf (1972) that "the females often start breeding before reaching maturity" seems to be unwarranted as well.

Coat colour

The colour change of the pelage is another interesting phenomenon and will be subject of a more detailed report (in prep.). Coat colour in *Cryptomys* was treated as a taxonomical or ecological feature related to geographic distribution and/or to soil colour (cf. Ansell 1960; De Graaf 1972; Rosevear 1969). While in *Spalax*, the coat colour was found to vary with the substrate and thus to be adaptive (Nevo 1979; Heth et al. 1988), a lack of a selective factor for coat colour in *Cryptomys* was suggested (Genelly 1965). Poduschka and Nopp (1978) found their *C. hottentotus* to change their individual colour after coming to captivity. The authors attributed the phenomenon to the change of soil conditions. De Graaf (1972) and Genelly (1965) concluded that the coat colour was independent of age. Smithers (1983) writes correctly that the juveniles tend to be darker than adults but does not give any further details.

As found in the present study, each animal in the course of its individual life changed its colour markedly several times. This change was independent of substrate and of sex. The change followed the same trend in all the studied animals. Timing of changes was correlated with the attained body mass and thus with age and social status.

Parental care, interactions between parents and offspring

The position adopted by the young during suckling and the mother's nursing posture in *Cryptomys,* i. e. mother supine and infants prone, was not reported for any other (hystricomorph) rodent (cf. Kleiman 1974).

So far, there have not been any indications that the adolescent and grown-up mole-rats would be repulsed by their parents. On the contrary, they were fully integrated into the group life. I can confirm the observation by Roberts (cited by Kingdon 1974) that the younger animals were usually the first to be trapped. Robert's explanation that "this suggests that the older animals drive out the younger ones to forage and bring back food to the storage chamber" is, however, speculative. A more plausible explanation was presented by Hickman (1980): the young animals are inexperienced, more explorative and less cautious. In addition, I observed young animals to be more active and spending more time outside the nest than older animals. Yet when isolated, there was no difference in activity patterns between different age (weight) groups (Hickman 1980).

Breeding cycle in captivity and in nature

The period between two subsequent births given by a particular female was 25.2 (±2.2) (range 22–27) weeks. It can be concluded that (at least in captivity) the female *C. hottentotus* may (successfully) breed twice a year.

Most of the hystricomorph rodents (Weir 1974) and most of the fossorial mammals

(Nevo 1979) are known to have long breeding cycles. *Heterocephalus glaber* is an exception since a female may produce a large litter every 80 days. Offspring production is, however, efficiently minimized in other ways (Jarvis 1984).

Practically nothing is known on the breeding cycle of *C. hottentotus* in nature. The available samples are too small and not comparable. *C. hottentotus* is considered to be a seasonal breeder probably breeding once a year (Genelly 1965; Kingdon 1974; Jarvis 1984), or it is supposed to breed throughout the year (Ansell 1960; Smithers 1983).

Subjected that growth rate in nature is comparable to that found in captivity, date of birth can be estimated in juveniles weighing less than 45 g (and younger than 6 months). Of 41 mole-rats captured in Zambia from July to December during two subsequent years (Burda, Kawalika, Westenberger) only six animals could be divided into three distinct age groups: animals born in February/March (N = 4), May (N = 1), August/September (N = 1). (The youngest pup must have been only 40 days old.) These findings indicate that there is no clear relation between the timing of breeding seasons and climatic regime for *C. hottentotus* in Zambia.

Many observations (referring to pairing behaviour, interactions between adult animals, between parents and offspring, between offspring from different sibling litters) made in captive animals and described in this study, allow speculations that the natural groups inhabiting particular burrow systems are families consisting of a single breeding parental pair and its offsprings from different litters. In other words: it is suggested that there may be many adult females and males which do not breed. An analogous (but probably still more pronounced) situation is known in *Heterocephalus glaber* (Jarvis 1972, 1984). The "helpers" in *Cryptomys* families are smaller and darker (more brown, less ochre) than the breeding pair.

Since *C. hottentotus* and *Heterocephalus glaber* are the smallest forms among all hystricognath rodents and thus are characterized by relatively and absolutely long developmental times, respectively (see also Burda in press), strategies to reduce energy budget had to be developed. The overall reduced activity of the female during pregnancy as well as development of (eu)sociality and establishment of the caste of helpers may be understood as such strategies. These reasonings may explain why only so few findings of pregnant females were recorded in the literature.

Conclusions

K-strategy was adopted (as a phylogenetic trait) by most of the hystricomorphs (Weir 1974), and (as an adaptive convergent trait) by most of the subterranean mammals (Nevo 1979) and by many mammals forming complex social groups (Eisenberg 1981). *C. hottentotus* being a socially living subterranean hystricomorph combines all the three prerequisites for K-strategy. Actually all the factors reducing reproduction rate are present in *C. hottentotus*: long prenatal and postnatal development, small litter size, no postpartum estrus (?) and thus at a maximum two breeding periods possible across the year (?), a long time spent by pups in learning situation, and selection for a temporary non-reproductive caste. Combination of all these factors make the K-strategy in *C. hottentotus* most effective (and the reproduction rate relatively slowest) among all the rodents. In many aspects of its reproductive and social biology, *C. hottentotus* seems to resemble *Heterocephalus* (cf. papers by Jarvis). It is suggested that this similarity is primarily due to hystricomorph (hystricognath) affinities and small body size. The abiotic and biotic factors characterizing their respective habitats are, however, different in both species.

Acknowledgements

The animals were collected during my senior lecturership at the University of Zambia (1984–1986), and this would not have been done if it were not for my student, Mr. Mathias Kawalika, whose great and devoted assistance in the field is highly appreciated. The study on captive animals would not be conducted if it were not for Prof. Dr. V. Bruns (Frankfurt/M) who provided generously refuge for me and my animals in his laboratory. Stimulating discussions were held with Dr. D. Kock (Frankfurt) and Doz. Dr. W. Poduschka (Wien) who supplied me with literature. Most valuable comments and advice to the first draft of the manuscript were provided by Prof. Dr. G. C. Hickman (Pietermaritzburg), Prof. Dr. E. Nevo (Haifa), Doz. Dr. W. Poduschka, and Prof. Dr. P. Vogel (Lausanne). Prof. Dr. G. C. Hickman and Doz. Dr. W. Poduschka helped to improve the manuscript through their linguistic corrections and suggestions. Last but not least my great thanks are due to Mrs. Gabriele Elter, my wife Jana, and Dr. J. Novotny (Lusaka) for their devoted and enthusiastic assistance.

The study was supported by the Alexander von Humboldt-Foundation and Deutsche Forschungsgemeinschaft (SFB 45/B 21).

Zusammenfassung

Fortpflanzungsbiologie (Verhalten, Zucht und postnatale Entwicklung) subterraner Graumulle, Cryptomys hottentotus (Bathyergidae)

Es wird erstmalig über die regelmäßige Aufzucht von *Cryptomys hottentotus* in Gefangenschaft berichtet, und die wichtigsten Aspekte der Fortpflanzungsbiologie werden beschrieben. In einer geordneten Gruppe und in bekannter Umwelt wurden keine Kopulationen beobachtet. Um die Tiere zur Paarung zu stimulieren, wurden sie in Paaren gehalten, und die Paare wurden täglich neu kombiniert. Die Tragzeit betrug 98 Tage (Standardabweichung 9, Min. 84, Max. 112 Tage). Der nächste Östrus mit Konzeption war nach 78 (S. A. 9) Tagen. Die Wurfgröße betrug 2.0 (0.75, 1–3). Das Verhältnis zwischen weiblichen und männlichen Neugeborenen lag bei 1:1. Das Geburtsgewicht betrug 7.9 g (S. A. 0.5). Die Neugeborenen sind nackt, haben geschlossene Augen, besitzen jedoch entwickelte Schneidezähne und Tasthaare. Selbstkratzen, unbeholfene Lokomotion und Kopfheben wurden bereits ein bis zwei Tage nach der Geburt beobachtet. Das Wachstum war langsam: 0.36 g/Tag bis zum Absetzen und danach noch langsamer. Nach der Geburt des nächsten Geschwisterwurfes wurde das Wachstum der Jungen aus dem ersten Wurf: 1. stark vermindert, und die Jungtiere waren im Alter von einem Jahr noch nicht erwachsen, wenn sie bei der Familie blieben; oder 2. stark beschleunigt, und die Tiere waren im Alter von 210 Tagen erwachsen, wenn sie von den Eltern getrennt waren. Wichtige Entwicklungsereignisse und die Fellfarbenänderung (von schwarz zu braun zu ocker) waren mehr vom erreichten Körpergewicht bzw. vom Alter nach der Konzeption, jedoch nicht vom Alter nach der Geburt abhängig: So war die Behaarung beim Gewicht von 10 (S. A. 1) g im Alter von 8–10 Tagen vollständig; Öffnen der Augen: 12,9 (S. A. 0.7) g, 24 (13–50) Tage; Absetzen: 34 (S. A. 0.3) g, 82 (72–105) Tage. Unter Berücksichtigung der Körpergröße hat *C. hottentotus* unter allen Nagetieren die relativ langsamste Entwicklungsgeschwindigkeit und die relativ geringste Fortpflanzungsrate. Dieses kann auf die hystricomorphe Verwandtschaft, subterrane Lebensweise und die komplexe Sozialstruktur dieser Art zurückgeführt werden.

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Zeitschrift/Journal: Mammalian Biology (früher Zeitschrift für Säugetierkunde)

Jahr/Year: 1989

Band/Volume: 54

Autor(en)/Author(s): Burda Hynek

Artikel/Article: Reproductivebiology (behaviour, breeding, and postnatal development) in subterranean mole-rats, Cryptomys hottentotus (Bathyergidae) 360-376