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Aspects of the social behaviour in a captive colony of the Common mole-rat *Cryptomys hottentotus* from South Africa

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Abstract

Qualitative and quantitative behavioural studies on a captive colony of the social mole-rat *Cryptomys hottentotus* are reported. The colony consisted of two castes: reproductives and non-reproductives. The non-reproductives were divisible into "casual workers" and "workers". The amount of work performed was not related to body mass.

Behavioural acts were subdivided into three major categories: Burrow maintenance, interactive and auto behavioural acts. Social interactions were analysed by age and work category. Many of the behaviours appear to be linked to age and not work grouping. Worker groups did not differ significantly in the amount of digging and soil movement undertaken. Juveniles carried food more frequently than adults.

There was a positive correlation between animals initiating and receiving the following interactions: genital allogrooming, sparring, naso-anal interaction and urino-genital sniffing. Juveniles allogroomed the pelage and genitalia of other colony members more frequently than adults. Juveniles sparred and initiated naso-anal interactions significantly more than adults.

There is a distinct toilet area in which the reproductive animals smear-mark significantly more than the other colony members. Smearing of organically derived chemicals may be the mechanism by which chemo-suppression of reproduction is imposed upon other colony members by the reproductives.

Introduction

Cryptomys hottentotus occurs in mesic and semi-arid regions of South Africa (Smithers 1983). The colonies are familial groups comprised of parents and at least two litters and can vary in size from 4 to 18 individuals (Bennett 1988, 1989; Rosenthal et al. 1992). Non-breeding colony members show co-operative and altruistic behaviour in the foraging, storage and subsequent harvesting of geophytes.

Cryptomys hottentotus has a colony structure which lacks working groups based on the relationship between body mass and the amount of work performed.

Studies on the behaviour of the southern African mole-rats were pioneered by Eloff (1951, 1952) who described the basic general behaviour of *Cryptomys hottentotus*. In particular, reference was made to the orientation of the mole-rats within the burrow system and the utilisation of the kinaesthetic senses of these mole-rats in orientation within the burrow system. Generalised behaviours involving digging, feeding and threat postures have been described for *C. hottentotus* and *C. damarensis* (de Graaff 1964, 1972; Genelly 1965). The general behaviour for incomplete colonies of *C. hottentotus* from the Transvaal have been described by Kinloch (1982), but quantitative analysis of the behaviour were not given.

This paper describes, both qualitatively and quantitatively, the behaviours exhibited by a captive colony of field-captured *C. hottentotus*. The various types of social interaction resulting from each behaviour are analysed where possible with respect to the animals' age and work grouping. Where particular actions were uncommon, qualitative behaviour only is reported.

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Material and methods

A colony of 11 mole-rats was captured in May, 1984 at Darling (33°22′ S, 15°25′ E) S. W. Cape, South Africa. From the colony of 11, three non-reproductive males were accidently killed on capture leaving only eight mole-rats.

The mole-rats were captured with Hickman live traps (Hickman 1979), or by cutting off their retreat with a hoe when they come to seal opened sections of their burrow system (Jarvis and Sale 1971). They were captured over four consecutive days.

The colony was housed in a transparent Perspex burrow system consisting of three 1-m covered runs (65 mm × 60 mm) linking three transparent chambers which served as nests, toilet areas and food stores. Wood shavings were placed in the chambers, paper towelling and dry grass were provided as nesting material. The mole-rats were fed on a variety of root and green vegetables, apples, grapes and a commercially prepared nutritionally balanced breakfast cereal. The mole-rats drank no free water. The room ranged between 26–28 °C in summer and 18–21 °C in winter. These temperatures were comparable to field temperatures recorded in the superficial foraging burrows (Bennett et al. 1988). The nest chamber was warmed with a lamp to approximately 25 °C, a temperature similar to that recorded in the field, in a burrow leading to the nest in a *C. damarensis* burrow system.

The room was illuminated from a window and consequently received a natural photoperiod. Bathyergids have reduced eyes (Cei 1946; Eloff 1958; Rees 1968) and visual centres in the brain (Hill et al. 1957; Pilleri 1960). *Cryptomys hottentotus* have very small eyes which they keep closed except when alarmed. Eloff (1958) claimed *Bathyergus* and *Cryptomys* could not see, but could detect air currents on the cornea. In the *C. hottentotus* colony under observation, no obvious behavioural response was detected to bright flashes of light or to movement by an observer as long as it was not accompanied by sound or by an air current.

The behaviours of the 8 *C. hottentotus* (2 males and 6 females) trapped at Darling in April 1984 were observed for a total of 240 hours between 15th May and 2nd August, 1984. Colony behaviour was observed daily by means of continuous scans for durations of 2 to 6 hours. The roles of the individuals within the colony were determined over the period 15th May to 2nd August.

All statistics were carried out with the aid of Siegel (1956) and Zar (1984).

The results obtained for many of the behavioural acts were tested statistically to determine if there were significant differences for the age and role of the mole-rats in the colony Darling 1. Sexual differences are not recorded here because there were only two males.

Results

Burrow maintenance behaviours

Four behaviours fall under this heading a) digging and gnawing, b) sweeping and transport of wood shavings in the burrow excluding near the toilet, c) nestbuilding and the carrying of nesting material and d) food carrying. These behaviours are readily quantifiable and are believed to approximate behaviours that occur in the wild (Bennett 1988). In the wild, nest building and the carrying of nesting material involve transporting stripped husks and root epidermis from harvested bulbs, tubers and rootstocks etc. to the nest chamber. These were the only materials found in the nests of wild colonies. In captivity wood-wool was provided for this purpose. In the wild, bulbs, corms and other small food items are carried to the food store and in captivity small items of food were also transported to one clearly identifiable section of the system. The food items were carried between the incisors, the head being held high and the mole-rat moved backwards or forwards with its load.

Based on the type and amount of work performed by individuals and on their reproductive role, the mole-rates in the colony of eight animals were placed into three categories. A reproductive caste and a non-reproductive caste composed of two work-related groups, "workers" and "casual workers" (see Table) (Bennett 1989).

The three workers (w) were the younger, smaller sized mole-rats. They were involved in 12.3 to 22.3 % of the total work done by the colony.

The three casual workers (cw) were usually the larger mole-rats, although a juvenile was ranked within this group. They were involved in 5.5 to 6.8 % of the total work undertaken by the colony.

The two reproductive mole-rats (RF, RM) could not be distinguished from workers or

Analysis of the amount of work performed by members of the Darling 1 colony

Data were collected over four months May to August, 1984. (After BENNETT 1989)

Animal I.D.	Group	Sex	Weight capture April	Weight August	Frequency of digging and soil transport	Total work (N)	% of total work
No. 1001	W	F	28.1	76.1	17	47	12.3
No. 1002	W	F	27.4	87.0	29	51	13.3
No. 1004	W	M	36.0	102.0	51	85	22.3
No. 1007	R.F.	F	55.5	95.0	92	116	30.4
No. 1040	R.M.	M	75.0	131.0	4	13	3.4
No. 1070	C.W.	F	45.0	82.5	19	26	6.8
No. 1008	C.W.	F	59.0	90.0	16	21	5.5
No. 1003	C.W.	F	31.0	66.0	5	22	5.7

W = worker; C.W. = casual worker; R.F. = reproductive female; R.M. = reproductive male; F = female; M = male.

casual workers on the basis of the amount of work undertaken (U = 3, p = 1.20 and p = 1.20, Mann Whitney U-test p = 0.05 level of rejection) but clearly differed from the others in being the only reproductive animals in the colony. The male did little work (3.4 %), but the reproductive female undertook 30.4 %, especially that associated with nestbuilding and sweeping.

There was a significant tendency for workers to maintain the burrows and work more frequently than casual workers (U = 0, p = 0.05 Mann Whitney U-test, 1 tailed test).

Using the Kruskal-Wallis test it was found that the three groups did not differ significantly in the amount of digging and soil movement undertaken ($p = > 0.05$).

There was a significant difference in the frequency of food carrying by the mole-rats ($\chi^2_7 = 22.45$, N = 89; $p = < 0.01$). This was linked to the age of the mole-rat; juveniles carried food significantly more frequently than adults (U = 1.5, p = 0.028, Mann Whitney U-test).

Interactive behaviours

Naso-anal interaction

Naso-anal interactions involve contact between the nasal region and anal region of two animals, lying side by side, head to tail. The behaviour does not lead to sexual activity and is undertaken by all colony members. The animals appear very excited during the activity and vocalisation may occur.

There was a positive correlation (rs = +0.55) between the number of naso-anal interactions initiated by particular animals and those in turn received (Fig. 1). Juveniles initiated significantly more naso-anal interactions than did adults (Mann Whitney U = 0; p = 0.028). Reproductives were rarely involved in naso-anal interactions.

Urino-genital sniffing

One mole-rat sniffs the anal region of another individual which raises its tail and simultaneously emits a series of high pitched squeals whilst jumping with its hind legs with each squeal.

There was a positive correlation (rs = +0.55) between the number of urino-genital sniffing sequences undertaken by particular individuals and the frequency with which they inturn received these interactions (Fig. 1).

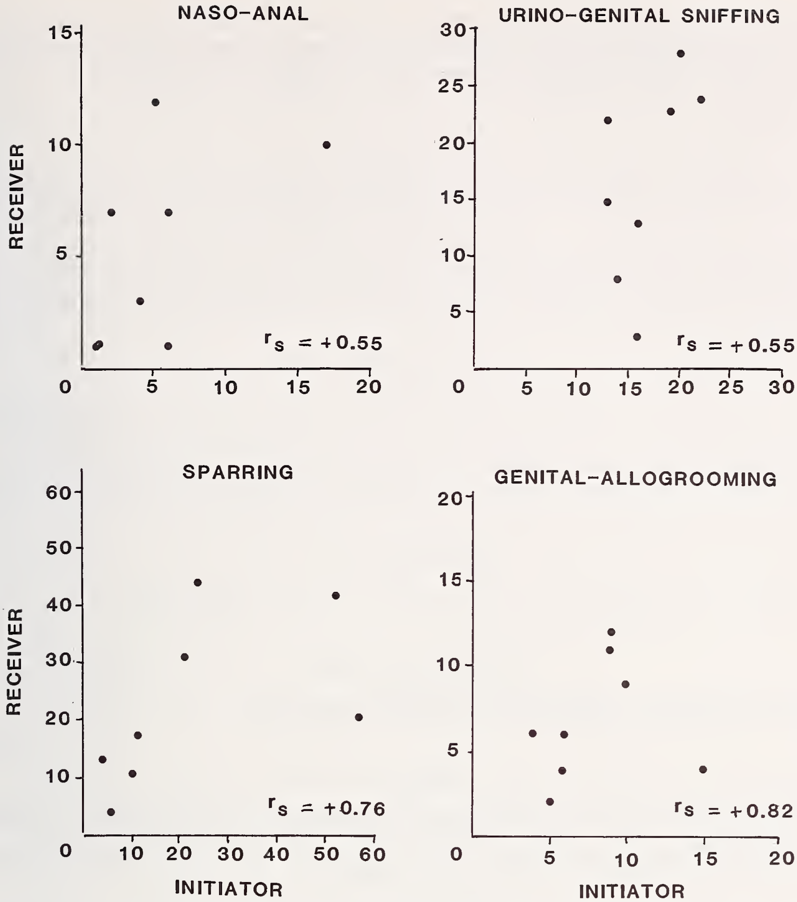

Fig. 1. The Spearman Rank correlations between the frequency of initiating and receiving naso-anal, urino-genital sniffing, sparring and genital-allogrooming behavioural interactions

There was no correlation with the age of the mole-rat (Mann Whitney U = 5; p = 0.486).

Sparring

Sparring consists of 3 types of interactions: Adult-adult, adult-sibling, sibling-sibling interactions. In sparring, two animals gently lock their incisors and then have a tug-of-war. During the tugs-of-war the individuals brace themselves in the burrow with their forefeet and try to pull one another. This may be interspersed with nose-butting and pushing at each others faces with their forefeet. The skin is never bitten and interactions are terminated either by one animal rolling over onto its back and exposing its belly and genitalia or by one animal reversing at high speed along the tunnel system. Adult-sibling and sibling-sibling interactions are common. Whereas adult-adult interactions are infrequent.

A significant positive correlation (rs = +0.76) was found between the number of sparring episodes initiated by particular animals and the frequency with which these animals inturn received sparring interactions (Fig. 1). Juveniles sparred significantly more frequently than did adults (Mann Whitney U = 0; p = 0.028).

Juvenile-juvenile sparring constituted 64 %, adult-adult 7 % and adult-juvenile 29 % of all observed sparring interactions (n = 183). These data suggest that sparring is important in pup development and the subsequent incorporation of pups into the colony.

Tail-pulling

When two animals are moving in the same direction within the burrow, and the anterior male-rat then stops to feed or rest, the posterior male-rat may pull the obstructing individual back along the burrow by its tail. The towed animal usually turns on its back and attempts to brace itself against the sides of the burrow. Once released the mole-rat will often return to the place from which it was initially towed from and tail-pulling may be initiated again.

Passing over

Mole-rats usually passed each other by flattening their bodies and pulling against the mole-rat that they were passing. The mole-rat on top was usually the faster moving individual (unquantified). Before passing, mole-rats would often chirp, especially when passing animals dominant to themselves. Small mole-rats passed side-by-side in the tunnel system.

Passing under

This occurred when one mole-rat passed another by moving underneath it.

Passing side-by-side

This behaviour occurred in the tunnels and is self explanatory.

Biting

Biting occurred when one mole-rat encountered another in the nest, when one animal blocked the path of another, or during a tussle over food. It involved the biting of the tail, leg or rump. The bites varied in intensity from nibbling to a severe bite.

Rump chewing

This behavioural act involves one mole-rat mouthing the fur on a conspecific's rump and then taking the rear between the incisors. The incisors were moved in a gentle chewing action.

Mouthing

When mouthing, one animal would take another's head between its incisors, sometimes moving the mouth in a chewing motion. The aggressor would then often drag the victim along by its head.

Pushing

This behaviour involved a mole-rat pushing its hindlegs against a conspecific whilst bracing itself with the fore legs and raising the head. In this position the mole-rat would move backwards while pushing the other down the tunnel.

Allogrooming

Allogrooming consists of nibbling and ano-genital licking. In "nibbling", the groomer bites gently at the groomee's head, neck, shoulders, flanks or back. In "ano-genital licking" one animal licks the ano-genital region of another, this may also involve some nibbling of the fur in the ano-genital area. Allogrooming occurs in the nest and usually occurs when a mole-rat has just entered the nest. Grooming is initiated when the groomee is lying in a relaxed position. The groomer moves to the head and thoracic region of the groomee and nibbles at its fur, occasionally another region of the body will be groomed. The groomee responds by moving the part of its body being nibbled towards the groomer it rarely responds by immediately reciprocating the groom. The groomee may however reciprocate-groom the groomer after a short time lapse.

In ano-genital grooming, the groomer usually approaches the groomee from the rear and pushes its nose between the hind legs of the groomee. During ano-genital grooming the groomee gives out a high pitched sibilant twitter and may on occasion thrust its hind legs into the face of the groomer. The fur around the ano-genital area may also be nibbled, but licking occurs 90 % of the time. Ano-genital licking is a short-lived behaviour lasting only a few seconds. Allogrooming around the groomee's mouth and nasal area also occurs frequently.

The two reproductive animals and a casual worker (Nos. 1040, 1007, 1008) autogroomed significantly more frequently than they allogroomed ($p < 0.05$, $N = 299$; S.E. = 0.026, binomial test rejecting at $p = < 0.05$ level). Two workers and a casual worker (Nos. 1001, 1002, 1003) allogroomed more frequently than they autogroomed, whereas one worker and one casual worker (Nos. 1004, 1070) autogroomed and allogroomed with equal frequency. Juveniles allogroom significantly more frequently than adults (Mann Whitney $U = 0$; $p = 0.028$).

There was no significant difference in autogrooming between adults and juveniles (Mann Whitney $U = 6.5$; $p = 0.486$).

With genital allogrooming, however, there was a strong direct correlation ($rs = +0.82$) between those mole-rats initiating and those in turn receiving grooming to the genitalia (Fig. 1).

There was a significant trend for juveniles to genital allogroom more frequently than adults ($p = 0.0170$, $N = 64$; S.E. = 0.058; Binomial test $p = < 0.05$ level of rejection).

Allocoprophagy

Allocoprophagy is rarely undertaken except by young or juvenile mole-rats. These animals beg faeces from an adult engaged in autocoprophagy. The begging individual approaches the rear or side of the donor, while giving a high pitched mewing noise resembling Sue-Sue-Sue. The mole-rat then pushes its nose between the hind legs of the donor, probes the anus of the donor with its teeth and pulls out faecal material. While this is taking place, the donor produces a high-pitched sibilant cry, similar to that produced by an individual who is being allogroomed in the ano-genital area. Adult mole-rats have been seen eating faeces previously voided by another colony member in the toilet area.

Autobehaviours

Autogrooming

There are three methods of cleaning the coat, namely, scratching with the hind leg, licking and nibbling with the incisors.

Scratching is usually applied to the head, neck, shoulders and flank region, the hind leg moving in a rapid series of arcs and combing the fur on the downbeat. When the head or neck is being groomed the head is tilted to the side of the body with the hind foot being used to scratch. The forefeet brace the mole-rat as it grooms itself.

Licking is used to clean the paws, lower belly and ano-genital area. The animal either first licks and moistens its paws which are then combed through the fur, or it directly licks its fur using small sweeping movements. In the case of ano-genital licking, slight lapping movements are utilised. When cleaning the belly, the ano-genital region or the toes of the hind feet, the animal rolls backwards and supports its body on the sacral region, its hind legs are splayed out and its forelegs may be used to balance the body. Incisors are groomed by the mole-rat initially licking its paws and subsequently grooming its incisors and nose with the paws. The digits of the hind feet are nibbled and groomed with the incisors.

Tooth-sharpening

The incisors of the bathyergids grow continuously and in the natural environment are worn down as they chisel-tooth-dig through the soil. In captive animals the incisors are worn down and sharpened by tooth-sharpening. Tooth-sharpening usually occurs (96 % of the time) in the nest area. The mole-rat initially braces itself with its forepaws while adopting the normal tooth-sharpening posture. Forward and backward and side to side actions of the lower jaw are then used to file the upper and lower incisors against one another. Squeaky filing noises are produced during these movements. Short forward thrusts of the lower incisors against the upper ones sharpen the lower incisors, whereas longer slower backward movements of the lower incisors across the upper incisors sharpen the upper. Loose flakes and dust of chipped incisor are periodically flicked out ot the mouth by the tongue.

There was a highly significant difference in the frequency of tooth-sharpening episodes between colony members ($\chi^2{}_7 = 24.56$, $N = 367$; $p = <0.001$ Chi-square, one tailed test).

However, this was not related to age (Mann Whitney $U = 7$; $p = 0.886$). The score of each individual weighted the statistic, thus animal No. 1004 tooth-sharpened 44 % more frequently than the mean frequency obtained for tooth-sharpening, whereas animal No. 1070 tooth-sharpened 40 % less than average.

Coprophagy

Autocoprophagy commonly follows ano-genital grooming. The animal rolls backwards and supports its weight on its sacral region. Its hind legs are splayed laterally and the animal doubles up. The forelegs of the animal are used to balance and brace the animal. The incisors are used to probe and pull faecal material from a slightly everted anus. The faeces are then eaten. The duration of coprophagy may last a few seconds to many minutes.

Some animals practiced autocoprophagy more often than other individuals ($\chi^2{}_7 = 35.59$, $N = 195$; $p = <0.001$ one tailed test), but this was not related to the age of the mole-rat or its role (Mann Whitney $U = 2$; $p = 0.114$). However, the reproductive male engaged in the least amount of autocoprophagy. In this study animals No. 1004 and No. 1040 weight the χ^2 statistic.

Alarm and threat posture

There are essentially two alarm and threat behaviours used in response to disturbances from outside the colony: head-back threat posture and pumping.

In the head-back threat posture, the animal stands with its head thrown back, its eyes open and its mouth fully agape. The forefeet are placed firmly in front of the mole-rat and the hind limbs are widely splayed laterally but braced for a rapid advance or retreat. Periodically the mole-rat snorts and chatters its teeth. The posture is firm and rigid with the animal making short jerks or jumps towards the agonistic source.

Pumping

In pumping, the mole-rat cautiously approaches the source of alarm to threat repeatedly sniffing the air and holding its tail out straight. While still 10–20 cm or more from the source of alarm, the animal stands with its fore and hind legs splayed laterally, its head is stretched out forward and its body flattened dorso-ventrally. The mole-rat then pumps its hind region (legs and sacral area) up and down. This action is quite forcible, especially on the downstroke. In a very high-level threat situation the whole body posterior to the shoulders is lifted off the ground with the upstroke.

A pumping sequence may consists of between six and twenty downstrokes, each sequence is followed by a refractory period, in which the mole-rat first remains very still and then advances a few centimeters closer to the source of aggravation. The pumping display is then repeated. The mole-rat is extremely cautious and may rapidly retreat backwards along the burrow.

General movement in the burrow

Cryptomys hottentotus move backwards and forwards in the burrow system with equal ease. They walk and run along the burrow with their hind legs held far apart with most of the sole of the foot held off the ground. The limbs are short giving them a low body carriage. The head is usually held straight out, but is occasionally slightly lowered. The eyes are kept closed except when investigating a new disturbed or damaged area in the burrow system. The mole-rat then opens its eyes, holds its head held high, sniffs the air and cautiously approaches the area. During this cautious approach the fore and hind feet are braced against the perimeter of the burrow to facilitate rapid retreat.

The mole-rat turns within the burrow system by curving its body and rotating sideways, using its forefeet to do much of the pushing, however, a final thrust is provided by the hind feet.

The mole-rats are generally very agile, the actual speeds with which the animals move in the natural underground system have not been recorded, but mole-rats kept in the laboratory are capable of moving both forwards and backwards, at speeds of up to 15 cm/second.

Cryptomys hottentotus are exceptionally aggressive animals and will bite on capture, this being most noticeable in freshly captured specimens. They are extremely sensitive to air currents which Eloff (1958) suggests are detected by the cornea of their eyes. A series of short sharp rapid jumping movements with the mouth agape accompanied by grunting sounds are evoked if one blows air into the face of an individual (de Graaff 1964; Bennett, pers. obs.).

Toilet behaviour

There is a well defined toilet area within the burrow system, usually a blind ending tube that is utilised by all the colony. There are essentially three types of toilet behaviour: Grooming and smearing, urination and defaecation.

Grooming and smearing

In grooming and smearing, the mole-rats may enter the toilet area and not urinate or defecate. This is common in *C. hottentotus*. On entering the toilet area the mole-rat spends time smelling the area and then vigorously grooms its head region, flanks and belly, sometimes the genitalia are also groomed. Before leaving the toilet, the animal kicks back with its hind legs for a few times, and leaves the toilet while dragging its ano-genital region along the burrow. A small amount of fluid (urine?) is left in a trail along the tunnel. This wet trail is smelt by other colony members as they pass along the marked section of the burrow.

Some animals groomed and smeared within the toilet area significantly more often than other colony members ($\chi^2_7 = 17.41$, N = 138; $p = < 0.01$). This was not linked to the age of the mole-rats (Mann Whitney U = 4; p = 0.342). There appears to be a tendency for the reproductive pair to groom and smear more frequently than the rest of the colony (Mann Whitney U = 0, p = 0.072), although not significant at $p = < 0.05$ level (Fig. 2).

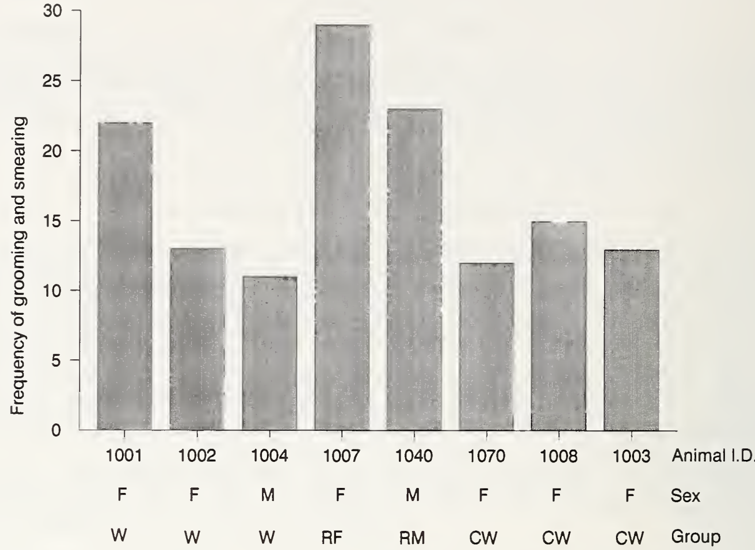

Fig. 2. The relative frequencies of grooming/smearing sequences in the toilet area of a *Cryptomys hottentotus* colony. RM = Reproductive Male; FR = Reproductive Female; CW = Casual Worker; W = Worker; F = Female; M = Male

Urination

Urination usually occurs after an animal has roused from rest or after feeding. The animal moves its hind legs apart, lowers its rear and raises its tail. Short jets of urine are voided. At the end of urination the animal briefly drags its rear along the burrow. A conspecific passing over the drag-marked region sniffs the marked zone and then moves on. Urination is not restricted to a particular site in the system (vs defaecation) and the site appear to be randomly selected.

There was no significant difference between colony members in the frequency of urination ($\chi^2_7 = 7.48$, N = 170; $p < 0.3 > 0.2$).

Defaecation

Defaecation occurs after awakening from sleep or after feeding. The mole-rat approaches the toilet area head first and smells it briefly, before reversing out of the toilet area and turning around. The animal then backs into the toilet tube. During defaecation, the mole-rat stands with its hind feet well apart and its tail raised. Its body is held rigid until the pellets are voided. The faeces then are kicked with the hind legs towards the blind end of the toilet area. After defaecating, the mole-rat grooms itself thoroughly starting with its head and finishing at the ano-genital area. In *C. hottentotus* defaecation follows or precedes urination but the two occur in different parts of the burrow system.

Feeding

When feeding the mole-rat squats on its hind feet and holds the food with its forefeet. When feeding on bulbs such as *Oxalis* sp., *Homeria* sp. and *Romulea* sp. the mole-rat grips the bulb between its forepaws and dehusks it, slowly rotating the bulb as it bites off the scaley outer layer. Once the bulb has been dehusked, the mole-rat cuts off and eats small portions of it. Food shaking and brushing precede eating and occur at irregular intervals during feeding. The bulb is occasionally shaken with the fore paws or held in the incisors and brushed with the forefeet. This action dislodges any attached soil.

Discussion

These first in-depth behavioural studies on a captive colony of *C. hottentotus* have provided an opportunity to describe basic colony behaviour in this social bathyergid. This study on *C. hottentotus* provides a comparison with the other social bathyergids which may help elucidate which features in the behavioural repertoire of the social bathyergids evolved first.

Maintenance behaviours

Digging and burrowing

Digging behaviour of all the genera of the bathyergids is very similar, although there are differences in the actual mode of excavation. Digging in all genera is initiated by alternate movements of the forepaws. However when extending the burrow through well packed substrata, the mole-rats of four genera excavate the soil with both the upper and lower incisors, whereas the genus *Bathyergus* utilises its claws and only occasionally its teeth for digging (Genelly 1965; Jarvis 1969; Jarvis, pers. comm.; Bennett, pers. obs.). In *C. hottentotus*, the two major maintenance behaviours (digging and soil movement) are not restricted to particular groups. In contrast, these behaviours are performed mainly by the frequent worker caste in *C. damarensis* (Bennett 1988) and by small-sized workers in *H. glaber* (Jarvis 1981; Lacey and Sherman 1991). Thus, in these behaviours there appears to be a difference between *C. hottentotus* and the two more highly social bathyergids.

Carrying food

In the burrow system much of the food encountered by the mole-rats while digging is carried to the food chamber. The mode of transportation varies with the size and nature of the food. The social species store food in a common food store the animals actively involved in foraging will probably also collect, transport and store the food. In *C. hottentotus*, juveniles (workers) carry food significantly more frequently than adults. In the colony of *C. damarensis* the frequent workers (which are often the juveniles) carry significantly more frequently than infrequent workers (Bennett 1990), while in *Heterocephalus glaber* there is a significant negative correlation between body mass and carrying food (Jarvis 1991; Lacey and Sherman 1991).

Interactive behaviours

Naso-anal interaction

Naso-anal associations, or mutual smelling of the partner's anal region, has not been recorded in *C. damarensis* and together with urino-genital sniffing illustrates that *Cryptomys damarensis* and *C. hottentotus* are behaviourally distinct.

In *C. hottentotus* there was a highly significant tendency for juveniles to initiate naso-anal interactions. The reproductive pair were involved in only 4 % of the interactions, whilst the juveniles were involved in 80 % of the interactions. Juvenile-juvenile interactions constituted 59.5 % of the observed naso-anal associations.

By contrast in *H. glaber*, the majority of naso-anal interactions occur between the reproductive animals. High ranking non-reproductive colony members are less frequently involved and juveniles rarely or never (Jarvis 1981, 1991; Lacey et al. 1991). In *H. glaber*, the behaviour is primarily important in the pair-bonding between the reproductives and they rest in this position in the nest (Jarvis 1991). In *C. hottentotus* the function of the behaviour is not apparent, but it may be important in maintaining colony cohesion.

Urino-genital sniffing

Urino-genital sniffing was observed in *C. hottentotus*, and occurred away from the nest. Although the behaviour was unrelated to gender or age, the reproductive pair tended to receive few of these behaviours in comparison to the more subordinate individuals. The function of urino-genital sniffing is unknown. It may possibly serve to identify individuals as belonging to the colony or to determine which of the two interacting animals is dominant.

Sparring

In all species of the Bathyergidae sparring appears to play an important but yet undefined role in the development of the pups. In both solitary and social genera it begins early in the life of the pup. In *Cryptomys*, sparring begins about 10 days after birth (Bennett and Jarvis 1988a; Bennett 1990), while *H. glaber* pups begin to spar when 14–20 days old (Jarvis pers. comm.). The solitary *Bathyergus suillus* and *Bathyergus janetta* begin to spar 13 and 16 days after birth (Jarvis, pers. comm.), while *Georychus capensis* begins later (35 days) (Bennett and Jarvis 1988b).

In all the solitary genera, sparring is between litter mates and the intensity increases until injury is inflicted or the pups disperse. It is also possible that in the young mole-rats the increased frequency of sparring is a consequence of play, but as the solitary pups develop sparring becomes more intense with escalation into fighting, this does not take place in the social mole-rats. In the social bathyergids, sparring is initially almost entirely between litter mates, though, the older juveniles also spar with adults. The adults appear tolerant to the young mole-rats and allow the juveniles to spar with them very vigorously. The reproductive animals in the genus *Cryptomys* spar throughout their lives. Thus the reproductive male and female *C. hottentotus* spar predominantly among themselves and rarely with the other adults. The reproductive male *C. damarensis* rarely sparred. The reproductive female was involved in many interactions but these were mostly with young animals (Bennett 1990). Injuries were not inflicted during any of the encounters observed. The frequent worker caste in *C. damarensis* contains many of the "younger" animals within the colony which could explain the tendency for frequent workers to spar more readily than infrequent workers. Sparring interactions in *H. glaber* (called tooth fencing and incisor tussels) continue until the animals are about 2 years old then become infrequent.

The significance of sparring in the social bathyergids is at present open to conjecture. Two possible roles are, firstly, a training for defence of the colony and secondly establishing a position within the colony hierarchy.

In both *C. hottentotus* (this study) and *C. damarensis* (Bennett 1990) there is a strong positive correlation between the frequency with which an animal initiates sparring and allogrooming (r_s = +0.7 and r_s = +0.5 respectively). This perhaps suggests that both behaviours play a role in establishing a young animal within the colony hierarchy. In sparring the juveniles interact most with the reproductive pair and with other juveniles, while in allogrooming the juveniles interact with the reproductive male.

Within the Geomyidae, Spalacidae and Ctenomyidae, sparring interactions are not reported to occur amongst either the young or adults, but adult spalacids placed together do fight (ANDERSEN 1978; PEARSON 1959; NEVO 1961, 1969).

Tail-Pulling

Tail-pulling occurs in the social mole-rats *Heterocephalus* and *Cryptomys*. The behaviour occurs during cooperative burrowing (JARVIS 1969; BENNETT 1988). The act of tail-pulling in the genus *Cryptomys* appears to be associated with the dominance of particular individuals, the dominant mole-rats pulling the tails of the subordinate mole-rats. In *C. hottentotus*, of the eight occasions on which tail pulling was observed, seven involved the dominant animals pulling the tails of subordinates. In the Damaraland mole-rat, "frequent workers" used tail-pulling significantly more frequently than infrequent workers (BENNETT 1990). Tail-pulling in *C. damarensis* is employed mainly during chain digging sequences. In such a sequence three mole-rats may be burrowing in a particular sector of the burrow. However, after a period of time one of the posteriorly directed mole-rats may pull the tail of an anteriorly positioned animal in an attempt to exchange digging positions. Tail-pulling may also be used to remove an individual resting or blocking a particular entrance or sector of the burrow.

Allogrooming

In *C. hottentotus*, juveniles bodily allogroom significantly more frequently than adults. The juveniles groomed other juveniles and the reproductive male in preference to other colony members.

In a colony of *C. damarensis* containing two litters of known age animals (BENNETT 1990) allogrooming by the reproductive male was directed towards the reproductive female. The reproductive female most frequently allogroomed the reproductive male and her most recent litter (hereafter called juveniles). All age groups also groomed the juveniles, while the juveniles themselves groomed the reproductive pair, the most dominant non-reproductive male and a female yearling. The reproductive male was groomed by all of these age and sex categories of young colony members while the reproductive female was only groomed by her most recent pups and the reproductive male.

Ano-genital allogrooming in *C. hottentotus* differed from more generalised allogrooming in that it almost always involved juvenile animals. All the other colony members (excluding the reproductive male) ano-genital groomed the juveniles.

The juveniles directed much of their ano-genital allogrooming towards the adult female colony members (in particular the reproductive female) as well as between the juveniles themselves. Ano-genital allogrooming between adult animals was uncommon.

Allogrooming in the genus *Cryptomys* could serve two main roles, to remove external parasites or as an appeasement behaviour.

Information concerning external parasites associated with *C. damarensis* and *C. hottentotus* is meagre (SHORTRIDGE 1934; DE GRAAFF 1972). Small mites are found in the pelage of the common mole-rat *C. hottentotus* (BENNETT, unpubl.).

Allogrooming results in close physical contact between individuals and its performance could therefore have an indirect appeasement action. This interpretation is supported by the fact that the colony members in general tend to groom the dominant reproductive mole-rats (BENNETT 1988). This has certainly been suggested for social mongooses (RASA 1977). The dwarf mongoose (*Helogale undulata rufula*) occurs in small colonies with a strict monogamous breeding set up. A high degree of division of labour exists within the group which is not unlike that of *C. damarensis*. In such groups there are definite preferences for subordinate mongooses to groom the dominant animal of the opposite sex (Rasa 1977). Social grooming also occurs in the common marmoset *Callithrix jacchus* in which subordinates groom their peers, the reproductive pair (Rothe 1971; Abbott 1984). Kinloch (1982), observed allogrooming in groups of *C. hottentotus* resting in the nest areas, however, quantitative studies on the frequencies of allogrooming were not reported. In the naked mole-rat, allogrooming is not apparent between colony members, perhaps because they lack a pelage (J. U. M. Jarvis, pers. comm.).

Autobehaviours

Autogrooming

In the *C. hottentotus* colony, no tendency occurred for juveniles to autogroom more frequently than adults. However, in *C. damarensis*, juveniles tended to autogroom more frequently than adult animals (Bennett 1990).

In *Cryptomys*, juvenile animals tend to autogroom significantly less frequently than they allogroom (Binomial Test p = < 0.05 probability rejection level).

The problem of maintaining a clean coat is exacerbated by living a totally subterranean existence. Burrowing and digging movements through the soil result in sand and soil particles being dislodged and caught within the fur. The pelage is kept clean by regular and thorough grooming and also by shaking of the fur and twitching of skin. In *C. hottentotus*, there was no correlation found betweeen the frequency of excavating and autogrooming (rs = +0.23). There was, however, a significant correlation between the frequency of moving soil or sawdust and that of autogrooming (rs = +0.77). Similarly, in *C. damarensis* there was no correlation between the frequency of excavating and that of autogrooming (Bennett 1990). However, in contrast to *C. hottentotus* there was no correlation between the frequency of moving sawdust and that of autogrooming (Bennett 1990). Grooming sequences within the rodent moles are very similar. Grooming begins with the face, the slightly cupped paws are used independently as they are rubbed over the incisors, nasal region and the cranial area. The incisors and forefeet are used synergistically to groom the abdomen, genitalia and the parts of the hind region which are accessible. The digits are cleaned using the incisors. The above description is common to *Tachyoryctes splendens, Heliophobius argenteocinereus, C. damarensis, C. hottentotus, G. capensis* and *H. glaber* (Jarvis 1969; N. C. Bennett, pers. obs.).

Autogrooming in the genera *Cryptomys* and *Georychus* appears to mainly occur after awakening from a period of rest, after a visit to the toilet area or after a period of soil movement. The behaviour pattern occurs similarly in *T. splendens* and *H. argenteocinereus* (Jarvis 1969), but in *H. glaber* occurs almost exclusively, in the toilet area, prior to, during and after urination and defaecation.

Tooth-sharpening

Tooth-sharpening is seen in all the bathyergids (Jarvis 1969; N. C. Bennett, pers. obs.). The tooth-sharpening behaviour is essentially the same in all the mole-rats and takes place when the animal is drowsy and usually preceeds "sleep".

In *C. hottentotus*, there was no animal which tooth-sharpened more than another. However, after recruitment had occurred in a *C. damarensis* colony "frequent workers" sharpened their teeth significantly more than "infrequent workers" (Bennett 1988). These frequent workers were the two recent litters and a small adult animal. It is possible that the frequent workers, the animals that do most digging, had a greater rate of incisor growth compared to the rest of the colony or that their activities were blunting their incisors.

BRETT (1986) noted that when *H. glaber* dug through very hard soil they had to make frequent stops to sharpen their incisors.

Coprophagy

Autocoprophagy occurs in all the southern African bathyergids (*C. hottentotus*: KINLOCH 1982; *G. capensis*: BENNETT, pers. obs.; *B. suillus*: J. U. M. JARVIS, pers. comm.). Coprophagy is undertaken to enhance the digestion and absorption of food, (particularly of cellulose) which do not readily yield their nutrients. The available literature on the subterranean rodent families Geomyidae, Ctenomyidae and Spalacidae make no mention of these rodents practising coprophagy.

To my knowledge allocoprophagy, involving pups and other colony members, is unique to the social Bathyergidae. Allocoprophagy includes both begging faecal material directly from the anus of a conspecific and the consumption of a voided pellet, picked up in the toilet area.

Coprophagy is commonly undertaken in *H. glaber* (JARVIS 1981); weaning pups beg faeces from other colony members, begging for them with mewing cries and tugs of the donor's anus. When very gravid, the breeding female of *H. glaber* has difficulty in doubling up to reach her anus. She begs faeces from other adults and subadults engaged in autocoprophagy in the nest area (JARVIS 1991). Unlike the gravid *H. glaber*, pregnant reproductive cryptomyids do not appear to beg faeces from other colony members. However, the pups of *C. hottentotus* and *C. damarensis* beg faeces from their mothers after weaning. Allocoprophagy at this age may allow the transmission of valuable gut fauna from the parent to the offspring, as well as providing the weaning pups with easily assimilable food.

Toilet behaviour

The exact function of grooming in the toilet area and the subsequent smearing of a fluid on exit from this region is unknown. It appears to occur mainly within the social bathyergids (JARVIS 1981).

The marking agent may serve as an indicator in the same way as urination within the burrow is believed to act as an orientation marker (KINLOCH 1982). The marking of the section of the burrow leading away from the toilet area and the actual entrance may well act as a cue for orientation within the particular region of the burrow system. The frequency of marking may well inform each animal of the degree of use of this part of the system.

Smear marking may familiarise each mole-rat with the odour of other colony members. This would allow members of the colony to differentiate between conspecifics and intruding individuals. Marking could be of importance in expressing the internal sexual status of each animal, the urine merely reflecting the corresponding plasma hormone concentration, in this respect the reproductive pair of *C. hottentotus* were found to smear mark significantly more frequently than non-reproductive colony members. In contrast there was no significant tendency for any one animal to urinate any more frequently than another. The second focal area in the burrow system which receives frequent visits and could be involved as a site of the release of a chemical which initiates suppression of reproduction in the females other than the reproductive females, is the toilet area. Mole-rats entering the communal toilet area not only urinate and defecate in this area but also smear mark and groom. This area, as well as the nest therefore exposes colony members to each others' semiochemical signals and will serve to inform each other of the sexual status of colony members and impart a general group odour. If reproductive suppression of colony members by the reproductive female has a chemical component, then the toilet area would be an opportune site in which to effect this control. It is possible that chemicals, such as volatile hormones or pheromones, are released at the toilet areas in the urine by the reproductive female.

The advantages of having colonies in which reproduction is limited to a single female seem to mainly relate to inclusive fitness and the associated benefits of altruistic behaviour (Rasa 1977). For example food sharing, an altruistic behaviour is exhibited by the colony, despite the unequal involvement of the colony members in the various burrow maintenance activities. This is a strong indication of differential participation in burrowing and food harvesting occurring in the natural environment. *Cryptomys hottentotus* colonies involve a reduction in individual reproduction to an extent that only one female in the colony is reproductive. This offers some of the strongest evidence for the phenomenon of kin selection.

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Zusammenfassung

Aspekte des Sozialverhaltens einer in Gefangenschaft gehaltenen Kolonie des südafrikanischen Graumulls Cryptomys hottentotus

Das Verhalten von Graumullen *(Cryptomys hottentotus)* in einer Laborkolonie wurde qualitativ und quantitativ untersucht. Die Kolonie bestand aus einer reproduktiven und einer nichtreproduktiven Kaste. Die nichtreproduktiven Tiere ließen sich in „Arbeiter" und „Gelegenheitsarbeiter" einteilen. Das Ausmaß der geleisteten Arbeit stand in keinem direkten Verhältnis zur Körpermasse der Tiere.

Die beobachteten Verhaltensweisen ließen sich drei Hauptkomplexen zuordnen: Bauinstandhaltung, Interaktionen und Individualverhalten. Bei der Analyse sozialer Interaktionen wurden Alter und Klassenzugehörigkeit berücksichtigt. Arbeitergruppen unterschieden sich in ihrer Grabaktivität nicht signifikant von anderen. Jungtiere trugen häufiger Nahrung ein als Adulte.

Eine positive Korrelation zwischen den Verhaltensweisen des Initiators und denen des Empfängers wurde in folgenden Fällen festgestellt: gegenseitige Genitalpflege; Kampfspiel; naso-anale Kontakte und Beschnuppern des Urogenitalbereichs. Das reproduktive Paar pflegte sich nur gegenseitig. Gegenseitige Fell- und Genitalpflege, naso-anale Kontakte sowie Kampfspiele traten bei Jungtieren häufiger auf als bei Adulten. Viele der Verhaltensweisen scheinen eher vom Alter abhängig zu sein als von der Klassenzugehörigkeit.

In der Kolonie gab es einen abgegrenzten Toilettenbereich, in dem reproduktive Tiere signifikant häufiger markierten als andere Koloniemitglieder.

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