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PRELIMINARY NOTES ON THE BEHAVIOUR AND BREEDING OF *GERBILLURUS PAEBA PAEBA* (A. SMITH, 1834) IN CAPTIVITY

by

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Abstract – A captive colony of *Gerbillurus p. paeba* was studied in an outdoor enclosure and observation cages. The general behaviour is discussed and notes on the reproduction and reproductive behaviour given. Increasing the number of light hours and increasing the temperature seem to induce fertility in both males and females. The external parasites found on *Gerbillurus* are listed.

Introduction

The pigmy gerbil (*Gerbillurus p. paeba*) occurs throughout the drier, sandy parts of southern Africa: along the south coast from Alexandria District in the Eastern Cape, westwards to the Cape Flats, thence inland and northwards to South West Africa and the Angolan Namib, the Kalahari and also the sand veld to the north of the Soutpansberg in the Transvaal (Coetzee, 1969).

Little is known about the biology of this species, and difficulties have arisen in trying to breed them in captivity for laboratory studies (Hallett and Keogh, 1971). The object of the present study was to try to establish the possible causes for their poor breeding in captivity. In addition, information was obtained on general behaviour.

Material and Methods

Animals

During January and July 1972 and January 1973 a number of *Gerbillurus p. paeba* were live-trapped in the Kalahari Gemsbok National Park and taken to the University of Pretoria. The animals were first kept in temporary cages and an outdoor enclosure. A total of 60 animals (29 males and 31 females) were used in this study.

Enclosures with breeding boxes

To control this study animals were not only obtained from the Kalahari in January and July, 1972 but the breeding behaviour of *Gerbillurus* was

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also studied in an outdoor enclosure with a total floor surface of 37,6 m². Two types of breeding boxes were used, one being a 20 x 18 x 13 cm wooden box with a 4 cm entrance cut out on one side. To imitate more natural conditions a second type, with similar dimensions to the first, but with the entrance at the end of an 85 cm pipe with a cross section of 5 cm was used (Fig. 1 b). Four breeding boxes, two of each type, were equally distributed in the enclosure and placed in larger low sided boxes filled with 10 cm sand. For laboratory observations four 60 x 30 x 30 cm glass aquaria provided with wooden lids were used. Each was provided with a 20 x 18 x 13 cm wooden breeding box and the floor of these aquaria were covered with 10 cm fine, dry sand (Fig. 1 a). The total observation time was about 200 hours.

Light and temperature regulation

The animals were subjected to a more extended photo-period and higher temperature than that experienced at the peak of the breeding season in the Kalahari. The photo-period was maintained on a 16 hour light, 8 hour dark regime in the experimental room. An average temperature of 25°C ± 5°C was maintained. A time-switch and two 75 watt bulbs were used to simulate daylight. A red light was used to study the behaviour of the gerbils during the dark hours. Two light regimes were used. In one cycle the white light was switched off at 0800 hours and switched on at 1600 hours, enabling the activity of these nocturnal animals to be observed during the day. In the second cycle the lights were switched off at 1800 hours and switched on at 0200 hours to imitate a more natural cycle.

Food rations and water

The gerbils thrived on a diet of millet, oats, sunflower seeds and "Pronutro". Cabbage, lettuce, carrots and potatoes were also provided at times. Water was supplied *ad lib.* in a water bottle with a long spout.

Dissection, Morphology and Histology

Ten of the gerbils collected in the Kalahari Gemsbok National Park in July 1972 and twenty gerbils collected in January 1973 were killed and their mass determined on arrival at Pretoria. The condition of the external sex organs was recorded. The reproductive tracts were dissected out, weighed, slices fixed in Bouin and following routine paraffin wax embedding and sectioning, stained with Delafield's haematoxylin and chromotrope 2R and examined histologically. The uteri of all the females were weighed after preservation. After a month under experimental photoperiodism and increased temperature another 10 gerbils were killed and dissected. The gerbils in the open enclosure were killed and dissected in late winter (August) i.e. after seven months in captivity. A comparison of all the reproductive tracks was then made.

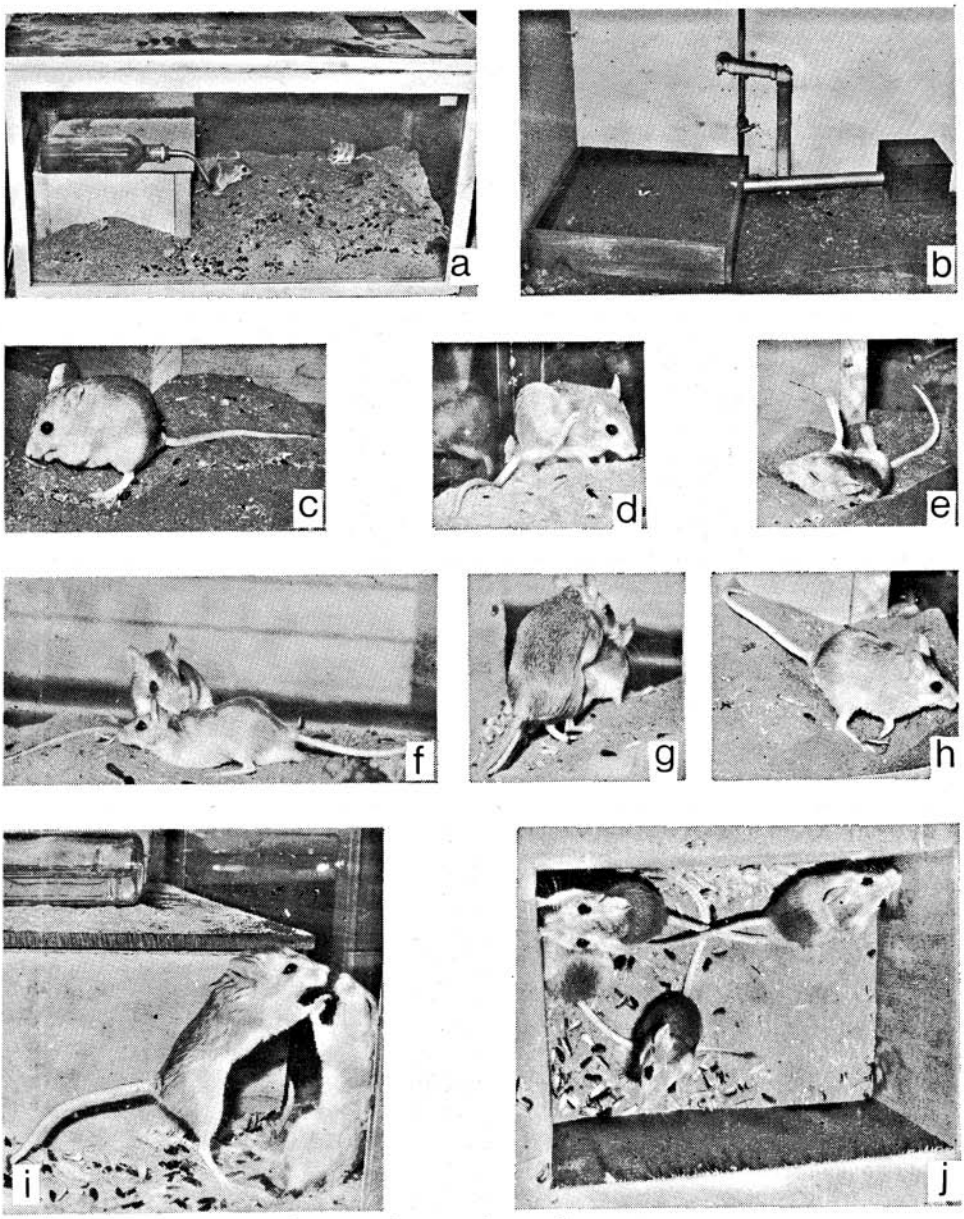

Fig. 1 (a) Observation cage in experimental room.
(b) Breeding box with pipe entrance in outdoor enclosure.
(c) Feeding Posture.
(d) Scratching.
(e) Sandbathing.
(f) Retrieving response female dragging male into nesting box.
(g) Female in oestrus mounting male.
(h) Digging movement.
(i) The upright posture during a conflict situation.
(j) Female with nearly full grown young in breeding box.

Results and Discussion

A. *General behaviour*

1. *Laboratory adjustment*

Adaptation to change in light rhythm was progressive – i.e. the gerbils remained active for longer periods during the hours of red light until after 4–5 days they became completely adjusted to the change of rhythm. Once they had become accustomed to the change the gerbils were active during the period of darkness and slept in their nesting boxes when the "day" lights were switched on. Adaptation was far better to the usual light rhythm (i.e. the period of darkness between 1800 hours and 0200 hours) than when darkness coincided with daylight.

2. *Preference of breeding box*

De Graaff and Nel (1965) studied tunnel systems of *Gerbillurus* in their natural habitat. The tunnels averaged 30 to 40 mm in diameter and 2,5 m in total length. Only a few entrances and blind tunnels are made with the tunnel system being about 15 to 22 cm below the surface. Two female and two male gerbils were released in the outdoor enclosure. Here only those breeding boxes with a tunnel entrance were used. The breeding boxes without tunnel entrances were frequently visited but never slept in. During the summer a breeding box standing in the shade and protected from the rain was used, but during the winter months they changed to a breeding box standing in the sun. Only one breeding box was used at a time and they moved as a group from one box to another. In the observation cages, however, only breeding boxes without any tunnel entrances were provided.

3. *Maintenance behaviour*

3.1 *Feeding*

Feeding occurred mainly during the first hour of activity, although food was eaten throughout the hours of darkness. Feeding involved a variety of movements, but basically the animal crouched and held the food, like a piece of carrot, in its forepaws. Small pieces were bitten off with the incisors, ground between the molars and swallowed. Seeds were shelled by first biting through one edge of the hull, then jerking the head backwards to strip away the edge. The shell was then peeled off by pushing it with the forepaws while the torn edge of the hull was gripped with the incisors. No definite pattern was observed in the feeding on green feed (Fig. 1 c).

3.2 *Drinking behaviour*

Gerbillurus p. paeba normally occur in a semi-desert or desert environment. They can live for indefinite periods of time on air-dried food without access to drinking water. In their natural habitat their diet consists of dry seeds and other dry plant material. The animals in the outdoor enclosure

maintained a normal body weight for seven months without drinking water. In the observation cages, however, water was provided and they drank regularly. Drinking was accomplished by the gerbil standing underneath the water bottle, grasping the spout in the forepaws and licking the orifice. The forepaws were not always used while drinking but were sometimes held in front of the chest. Fighting was observed when drinking water was unavailable for 24 hours. When the bottle was replaced the gerbils crowded around the drinking spout and almost instantaneously random fighting occured which lasted for about 10 minutes.

3.3 *Defaecation and Urination*

In the observation cages only the corners of the cages were used for defaecation and urination. The gerbils defaecated and urinated while standing with the hind feet placed well apart and the tail lifted into the air. The faeces were always dry and hard and about 3 mm in length.

3.4 *Grooming*

Typical grooming activities, i.e. washing, scratching and licking, are discussed together since they are functionally related to the common problem of dressing the pelage, cleaning the digits and genitalia, and removing parasites.

a. *Scratching*

This type of grooming consisted of scratching the head or body with one of the hindfeet (Fig. 1 d). This scratching was sometimes, but not always, interrupted from time to time in order to lick the toes being used for this purpose. The eyes were closed if the head was scratched.

b. *Face washing*

In a typical sequence the animal first licked the forepaws; then the face, head, and ears were cleaned by wiping down simultaneously on both sides of the head. During this operation the animal sat in a crouched position. This rubbing action was always in a forward direction. As in scratching the action might or might not have been interrupted in order to lick the forepaws from time to time.

c. *Licking*

The fur of the belly, the legs and the feet were licked. Licking of the feet sometimes accompanied scratching or face-washing, as noted above, while licking of the belly or legs was independent of the other two types of grooming. Licking always seemed to follow the direction of the pile of the fur (Meester, 1960). The genitalia and perineal region might be licked after copulation. During licking the forepaws were held in front of the body.

d. *Tail washing*

In a complete sequence the tail was grasped with the forepaws, brought up to the mouth, licked and nibbled from the base to the tip.

Table 1

Male reproductive system of *Gerbillurus p. paeba*

No.	External reproductive state	Mass in gram	Testes Mass in gram	Mean diameter of seminiferous tubules, micron	Reproductive state of seminiferous tubules	Reproductive state epididymis
A. *GERBILLURUS* FROM NOSSOB CAMP (JULY 1972) (GROUP A)						
1	Non-scrotal	21,9	0,06	193	Sperms in tubules	Sperms
2	,, ,,	23,5	0,05	201	,, ,, ,,	,,
3	,, ,,	16,3	0,03	201	,, ,, ,,	,,
4	,, ,,	16,6	0,02	162	,, ,, ,,	,,
5	,, ,,	17,8	0,03	181	,, ,, ,,	,,
B. *GERBILLURUS* AFTER A MONTH UNDER CONDITIONS OF EXTENDED PHOTOPERIOD AND INCREASED TEMPERATURES (GROUP B)						
6	Testis enlarged and descended	28,8	0,31	234	Sperms in tubules	Sperms
7	,, ,, ,, ,,	27,2	0,45	233	,, ,, ,,	,,
8	,, ,, ,, ,,	25,1	0,32	235	,, ,, ,,	,,
9	,, ,, ,, ,,	26,1	0,17	201	,, ,, ,,	,,
10	,, ,, ,, ,,	30,3	0,26	230	,, ,, ,,	,,
C. *GERBILLURUS* AFTER SEVEN MONTHS IN OUTDOOR ENCLOSURE (GROUP C)						
11	Testis enlarged and descended	33,6	0,40	209	Sperms in tubules	Sperms
12	,, ,, ,, ,,	37,0	0,39	226	,, ,, ,,	,,

Table 1 (Continued)

GERBILLURUS FROM NOSSOB CAMP (JANUARY 1973) (GROUP D)						
No.	External reproductive state	Mass in gram	Testes Mass in gram	Mean diameter of seminiferous tubules, micron	Reproductive state of seminiferous tubules	Reproductive state epididymis
13	Testes enlarged and descended	23	0,23	210	Sperms in tubules	Sperms
14	,, ,, ,, ,,	21	0,18	208	,, ,, ,,	,,
15	,, ,, ,, ,,	20	0,11	201	,, ,, ,,	,,
16	,, ,, ,, ,,	23	0,26	214	,, ,, ,,	,,
17	,, ,, ,, ,,	23	0,13	233	,, ,, ,,	,,
18	,, ,, ,, ,,	28	0,34	234	,, ,, ,,	,,
19	Non-scrotal	26	0,27	180	,, ,, ,,	,,
20	Testes enlarged and descended	23	0,30	210	No sperms in tubules	No sperms
21	,, ,, ,, ,,	29	0,32	199	Sperms in tubules	Sperms
22	,, ,, ,, ,,	21	0,17	226	,, ,, ,,	,,

e. *Social grooming*

Social grooming consisted of one gerbil lying outstretched with eyes closed in front of the other. The standing gerbil then usually bent forwards and started to lick the prostrate animal on the neck or back. Social grooming usually lasted from 5–10 seconds.

3.5 *Sleep*

Gerbillurus slept intermittently in its nest during the daylight hours. It adopted a curled-up position by sitting on its hindlegs and tucking the head under its body while the tail was generally curled around the feet. This same curled-posture was at times adopted while the animal lay on its side. According to Eisenberg (1968) both positions are typical for rodents. If a pair was sleeping together the one gerbil usually lay on its side while the other gerbil adopted the curled-up posture over it. As the gerbil slept the eyes were closed and the ears were sometimes shaken.

3.6 *Sandbathing*

Sandbathing was observed after the gerbils were provided with dry, loose sand. It occurred each time the lights were switched off and the animals appeared from the nesting boxes. It might have occurred at any time during the active period. The pelage of *Gerbillurus* tended to become oily and matted if sand was not available. Sandbathing was always preceded by a digging movement and consisted of a series of swift movements, during which the animal quickly rolled on to one side and onto its back and with a series of extensions and flexions rubbed the body on the sand. The procedure was then repeated for the other side (Fig. 1 e).

3.7 *Stretching*

Stretching was observed when the gerbils appeared from their nesting-boxes at the beginning of the active period. The stretching movement involved an extension of the body and limbs followed by a flexion. Stretching lasted for at least one to two seconds. According to Eisenberg (1968) the extensions and flexions of the body during sandbathing can be compared with the movements during stretching.

4. *Climbing*

Climbing ability and the spontaneous tendency to climb are closely related and correlate well with the morphology of the animal (Eisenberg, 1968). Climbing was frequently observed in *Gerbillurus* when they were still in their temporary cages before being transferred to the observation cages. Only the forefeet were used for climbing although the hindlegs were used as a support. *Gerbillurus* is not very well adapted to climbing as it cannot grasp with its hind feet. Young individuals (30 days old) readily climbed on to a human hand, or on a bare arm held at 45° from the horizontal.

5. *Nesting*

5.1 *Digging and burrowing*

Activities during the active periods consisted mostly of digging. The layer of sand in the observation cage was too dry and thin to support a burrow therefore, burrowing was absent. The sand in one of the sand-boxes in the outdoor enclosure was occasionally soaked by rain. Shallow burrows were dug but never used for any nesting activities. Digging involved rapid forward and backward forepaw movements until a pile of sand accumulated under the animal. Generally this pile was moved back by one or two simultaneous thrusts of the hindfeet. During the daylight period the entrances to the breeding boxes in both outdoor enclosure and observation cages were closed with sand by means of a few rapid digging movements. Digging was also used for opening the entrance although the snout was sometimes used for pushing the sand out of the entrance (Fig. 1 h).

5.2 *Hoarding*

The gathering of food involves foraging and transport. The food is either carried in the mouth or dragged by holding on with the incisors while pushing with the limbs against the substrate. One may distinguish two main types of hoarding, viz storage inside the animal's home and storage elsewhere. The former is commonly practised by species that have a protective hole and is referred to as "larder hoarding". When food is separately concealed it is called "scatter hoarding" (Ewer, 1968). A few variations of the hoarding behaviour were observed.

a. *Scatter hoarding*

(i) The food that was placed in the observation cage was sometimes covered with sand. The gerbil smelt the food, turned around and covered the food by kicking sand on it with its hind feet. This specific hoarding behaviour was only occasionally observed.

(ii) The female picked up the food with her forefeet, placed it in her mouth by using her front feet, and ran to a corner of the observation cage where the food was spat out. She then turned around and covered the food with sand using all four feet. This was often repeated on the same place. The utilisation of this cache was never observed.

b. *Larder hoarding*

The hoarding behaviour most frequently observed was that of the female gerbil carrying food in her mouth to the breeding box. Food was never seen to be collected by the male. Different kinds of seeds were collected separately and hoarded by the females in the nesting box. Food like lettuce was always collected last and dragged into the nesting box by holding on with the incisors. When all the visible food was collected the female scratched with her forefeet in the sand, in search of food possibly concealed beneath the sand.

5.3 *Nest building*

Only females were observed transporting nesting material. The material, which consisted of cotton wool provided for this purpose, was dragged by the incisors into the breeding box. When no nesting material was provided a rough nest was built with seed hulls. The assembled material was generally arranged in a cup-shaped structure. Pushing movements with the forepaws and the nose and moulding of the nest cup by turning movements of the body were frequently observed. Disturbances sometimes led to the nesting material being removed from the nesting box. A peculiar behaviour of filling the nesting box with sand a few days before giving birth was observed. At birth this sand had, however, already been removed again.

6. *Social behaviour*

6.1 *Retrieving response*

The retrieving response was only observed once when a female grabbed the male by the scruff of the neck and dragged him into the nesting box (Fig. 1 f).

6.2 *Agonistic behaviour*

During conflict situations between two strange animals the following behaviour patterns were noted:

a. *Approach*

Approach is the direct movement of one animal towards the other. Whilst approaching the animal moved with a tense, elongate posture, including forward directed pinnae and a rigid tail. Lateral and rear approaches caused the approached animal to turn and face its opponent and all approaches resulted in either combat or retreat (Spickett, 1971).

b. *Retreat*

Retreat usually consisted of the gerbil turning around and running away. An escape leap was sometimes observed. The escape leap is an erratic jump to avoid being attacked.

c. *Attack*

An attack occurred as a rapid lunging of the attacking animal at its opponent. Attacks occurred suddenly and without any apparent warnings.

d. *Combat*

Upright and horizontal fighting postures were observed. In the upright posture the gerbils stood on their hindlegs and struck each other with the forepaws (Fig. 1 i). This pattern resulted in no real damage to either animal but was rather defensive in character (Eisenberg, 1968). In the horizontal posture the body was elongated and kept close to the ground while approaching the other animal. Actual rushes and biting followed.

e. *Reaction to intruders*

A male gerbil was released into an observation cage where a female had been isolated for two months. The female immediately attacked the male when he tried to enter the breeding box, then closed the entrance with sand and chased the male until he jumped on to the box. A submissive attitude was never observed in the male. After six hours the male was still on top of the breeding box and was attacked by the female each time he tried to smell her genitalia.

The female was then removed and another female released in the observation cage. This female immediately adopted a submissive attitude (a lowering of the body and cringing towards one side) when the male approached her. The male sniffed her genital region and attempted copulation but the female turned on her back and pushed him away with her front paws. This was repeated several times. After an hour the animals moved into the breeding box and did not appear until the next active period.

f. *Spontaneous fighting*

Three different situations were observed:

(i) Spontaneous fighting occurred when the water bottle was replaced after water had not been available for 24 hours (see 3,2).

(ii) Two females were released in an observation cage. Random fighting immediately started and no submissive attitude was adopted by either animal. Fighting still occurred after an hour and the gerbils were then separated.

(iii) When only a single piece of lettuce was placed in the observation cage it stimulated aggressive behaviour. This consisted of one gerbil carrying the food in the mouth and dragging it by holding on with the incisors and being chased by the other gerbil.

g. *Development of dominance*

Under stable conditions obvious signs of dominance or submission were absent. However, during conflict situations, behaviour patterns were observed which indicated the position of dominance. In a dominance-subordination relationship one animal is able to establish a superior social respect with respect to another. Established groups of gerbils having a dominant member show little difference in individual behaviour, but the dominant member can displace subordinates if there are competitive interactions (Eisenberg, 1968). The following situations were observed:

(i) Aggressive behaviour towards the male by the female was observed before parturition. The male adopted a submissive attitude each time and the female attacked him. Aggressive behaviour, 19 days before parturition, was observed in one case.

(ii) A male and a female were released in an observation cage. The female immediately entered the breeding box and prevented the male from entering by biting him on the nose. He adopted a sub-

missive attitude each time the female left the breeding box but was nevertheless frequently attacked by the female. After an hour the intervals between fighting became longer and after two hours the male was allowed to enter the breeding box without any aggressive behaviour from the female.

(iii) During aggressive behaviour indiscriminate mounting occurred. A dominant female mounted a female that had adopted a submissive attitude several times. Mounting occurred from any position and never lasted longer than a second.

(iv) A female (female No. 1) was released in an observation cage where another female (female No. 2) had been isolated for a month. Ten minutes afterwards a female (female No. 3) slightly bigger than females 1 and 2, was released in the same cage. Both intruders were immediately attacked by female 2 and chased until they jumped on top of the breeding box. No aggressive behaviour was noted between females 1 and 3, although female 1 adopted a submissive attitude towards female 3.

h. *Displacement activity*

Tinbergen (1951), as referred to by Hallett and Keogh (1971), has given the characteristics of displacement activity as incomplete behaviour patterns (usually) which seem irrelevant or out of the functional context in conflict situations. The following would, therefore, appear to be displacement activities observed in *Gerbillurus:*

(i) When the gerbils were caught and returned to the observation cage, vigorous digging occurred. During these digging movements the gerbil moved forewards and therefore could not have performed any specific action.

(ii) Drumming occurred when three female gerbils were fighting for dominance in the observation cage. Drumming consisted of a rapid pounding with the hind feet on the sand. According to Hallett and Keogh (1971), drumming could have been a threat attitude but drumming by a male was also observed when this specific male was not allowed into the breeding box. The male repeatedly tried to return to the breeding box but was every time chased out again by the female. Drumming was only observed in a situation of conflict.

(iii) While defending her breeding box a female gerbil suddenly stopped fighting and started to collect food. This hoarding was incomplete because the food was only carried from one corner of the observation cage to another corner. No food was buried in the sand or carried to the breeding box. The female then started fighting again without any preliminary warning.

7. *Stereotyped Motor Reactions*

Stereotyped behaviour was frequently observed and occurred in both sexes.

7.1 *Straight pathway*

A stereotyped forward and backward walking along the glass of the observation cage was frequently observed, particularly in females. This straight pathway could be an automatized attempt to get out of the cage or enclosure (Meyer-Holzaphel *in* Fox, 1968). It is the simplest and most basic form of all stereotyped behaviour. The more excited or aroused an animal is the more quickly it seems to walk to and fro.

7.2 *Oval circuits*

Animals kept in very small, square cages with homogenous walls tend to walk around in their cages instead of going back and forth along one wall. If the cage is rectangular the path has an oval form (Meyer-Holzaphel *in* Fox, 1968). These oval circuits were only made by male animals. One specific male ran in a clockwise direction around the nesting box, jumped on top of it, ran to the other side, only to jump off again. This was repeated several times in succession. The male maintained this clockwise direction without variation.

7.3 "*Weaving*"

Weaving consisted of a rhythmic sideways swinging of the head. Weaving was only observed in female gerbils. According to Meyer-Holzaphel, as quoted by Fox (1968), weaving is elicited by the same motive as in the other stereotyped reactions, i.e. an attempt to escape.

8. *Exploratory Behaviour*

8.1 *Exploring a new environment*

When released into the observation cage the gerbils began to explore their surroundings and continued doing so for at least an hour. This exploratory behaviour started after a brief initial period of hesitancy when the animal was prone to become rigid and moved with a tense, elongated posture, expanded forward-directed pinnae and a straight tail. The posture and gait changed as the animal continued to explore the unfamiliar surroundings and gradually became familiar with the new environment. When the nesting box was discovered the gerbils immediately went inside. From the nesting box more confident explorations were made. After about twenty minutes the gerbils remained for longer periods in the nesting box. Eventually the passage leading to the nesting box was closed with sand. No further movements were observed until the next active period.

8.2 "*Observing*" *posture*

The observing posture consisted of the gerbil rising on its hind legs with the forefeet pulled up in front of the body while at the same time testing the air by sniffing. This behaviour was resorted to every time the animal came out of the nesting box and lasted for 2–5 seconds. Both sexes adopted this posture.

B. *Reproduction and Reproductive behaviour*

1. *Mating behaviour*

Mating behaviour includes those patterns associated with copulation. It is generally displayed in a male-female encounter although mounting amongst female groups and females in oestrus mounting males were often observed (Fig. 1 g).

1.1 *Conditions of copulation*

Copulation took place only in the observation cages and was only permitted by females in oestrus. No copulation was observed to take place in the temporary cages or in the outdoor enclosure.

1.2 *Courtship behaviour*

During oestrus the female is very active and usually runs up and down in the cage with the tail lifted off the ground. The male would chase the female and when she stopped running he sniffed her genital region. Urination by the female would induce the male to smell the spot and become highly excited. Mounting usually took place after smelling of the genital region. If mounting was not tolerated by the female the following avoidance behaviour was observed:

a. The female kept on running and shook off the male.
b. The female turned round and started biting the male.
c. The female turned over on her back and pushed him away with her front paws.

1.3 *Quantative descriptions of copulatory events*

According to Eisenberg (1967) as quoted by Dewsbury (1972), the copulation pattern of gerbils generally resembles that of laboratory rats and hamsters. During copulation the male clutched the female's thorax with his front paws and simultaneously rubbed his nose against her back. Gerbils have a multiple intromission pattern with each intromission lasting about 3 to 6 seconds. No lock and no thrusting was observed.

1.4 *Behaviour accompanying copulation*

At the conclusion of a mount the male and female separated temporarily and washed their genital areas. After washing, the male usually ran around the female before copulating again. This procedure was repeated several times.

2. *Gestation period and the oestrous cycle*

According to Hallett and Keogh (1971) the gestation period of *Gerbillurus paeba coombsi* is 23 days. Only in one instance was the gestation period determined for *Gerbillurus p. paeba.* Mating took place on 30th May and a litter of three was born on 25th June. This implies a gestation period of 26 days (three days longer than for *Gerbillurus paeba coombsi*). However, fertilization need not have occurred on 30th May and could have taken place later.

The pattern of breeding behaviour of a given mammal is a manifestation of the frequency with which the oestrus cycle is repeated. During oestrus the vulva was pinkish and thrown into folds. According to Measrock (1953) external signs are not a reliable criteria of oestrus in the gerbil. In *Gerbillurus p. paeba* unsuccessful mating was noted on 28th April. Mating was again noted on June 8th. The oestrus cycle could thus have been repeated every 41 days but an abnormal anoestrus could have occurred.

3. *Maternal behaviour*

3.1 *Pre-parturitional behaviour*

Parental care patterns were only observed in the female gerbil because in two cases the female showed aggressive behaviour towards the male. The males were then removed. In the third case the young were presumably eaten by the female, or the male, or both. A few days before parturition an increased tendency to nest building by the female was observed. The breeding box was covered on the outside with sand by means of a backwards scratching movement. A day before parturition the female was very nervous and tried to get out of the observation cage. Parturition itself was not observed.

3.2 *Interaction between the female and the young*

After parturition the female remained for long periods in the breeding box and left the young only for eating, drinking, urination and defaecation. For the first eleven days the young were completely covered with cotton wool before the female left the breeding box. The entrance of the breeding box was also closed each time she entered or left. Brooding was frequently observed and consisted of the mother crouching over the young while they suckled. Nipple-clinging was not observed in *Gerbillurus*. Aggressive behaviour was noted on the first day. The female habitually left the nest to attack the person opening the breeding box. As the young grew older the female became less aggressive.

As the young became independent the mother spent less time in the breeding box. Grooming of the young was frequently observed during the first few days. In grooming the young female clutched the young in her forepaws and licked them. According to Eisenberg (1968) licking the genitalia is vital for the litter during the first few days of life, since this stimulates normal urination and defaecation.

The young left the breeding box for the first time on the 19th day – at a stage when solid food was readily taken. Initially they left the breeding box only for short periods and were frequently herded back to the entrance by the female. From the 25th day a normal adult cycle was adopted. The male was returned two months after he was removed but was attacked by one of the young. Four months after birth there was still no sign of aggressive behaviour by the female towards the young and *vice versa* (Fig. 1 j).

4. *Litter size*

Hallett and Keogh (1971) give the litter size for *Gerbillurus paeba coombsi* as two to three (an average for three litters).

In *Gerbillurus p. paeba* the litter size varied between three (two litters) and five (one litter). Litter sizes collected from *Gerbillurus p. paeba* in the Kalahari Gemsbok National Park varied between two and five with a mean of 4,1 (13 litters) (Nel, *pers. com.*).

5. *The effect of an extended photoperiod and increased temperature on fecundity*

5.1 *Male reproductive system*

During July 1972 gerbils were collected near Nossob Camp in the Kalahari Gemsbok National Park. Of these, five males were killed and dissected immediately on arrival at Pretoria (Group A, Table 1).

The following information was obtained:

Mean mass of animals: 19,2 g
Mean testes mass: 0,038 g
Mean diameter of seminiferous tubules: 187 micron

Five males (Group B, Table 1) were kept under conditions of an extended photoperiod and increased temperature. They were killed and dissected after a month and the following information was obtained:

Mean mass of animals: 27,5 g
Mean testes mass: 0,30 g
Mean diameter of seminiferous tubules: 226 micron

During January 1973 another ten males were collected near Nossob Camp. These were subsequently killed and dissected and the following information was obtained:

Mean mass of animals: 23,7 g
Mean testes mass: 0,23 g
Mean diameter of seminiferous tubules: 211 micron

According to Skinner (*pers. comm.*) the internal diameter of the seminiferous tubule is an indication of the reproductive state of the male animal. There was an increase of 17,2 per cent in respect of the internal diameter of the seminiferous tubules after one month under conditions of an extended photoperiod and increased temperature. A 43,2 per cent increase in total mass and a 90 per cent increase in the testes mass also occurred. The effect of increasing the number of light hours and increasing the temperature would, therefore, seem to improve fertility in male *Gerbillurus*.

A difference of 0,07 g in the mean testes mass and 11 micrometres in he mean diameter of the seminiferous tubules was observed between the males collected in January 1973 (Group D) and the males collected in July 1972 (Group A).

5.2 *Female reproductive system*

The classification of Measrock (1953) was used to classify the reproductive state of the female gerbils, i.e. :

(i) Non-parous females
Females which have not previously produced any litters. This was evident from the small nipples.
a. Non-adult (pre-pubertal) females.
These had very low uterus mass and the vaginal orifice was usually closed.
b. Adult females.
These had attained puberty as shown by the increase in uterus mass and the condition of the ovaries.

(ii) Parous females
These were adult females which had already produced one or more litters and were recognizable by the presence of long nipples.
a. Females in di-oestrus cycle.
During the di-oestrus cycle (pro-oestrus and met-oestrus) the vaginal orifice was open.
b. Pregnant females.
Visible pregnancies were those in which the embryos were already implanted.
c. Lactating females.
Gerbils were classified as lactating only if milk could be exuded from the nipples.
d. Anoestrus females.
These were identified fairly easily by the low mass of the uterus, the closed vaginal orifice and the complete inactivity of the ovaries.

A total of 10 females, collected near Nossob Camp during July 1972, were divided into two groups of five. The first group (Group E, Table 2) was dissected at the same time as Group A (Table 1) of the males. The second female group (Group F, Table 2) after a month of an increased number of light hours and increased temperatures, was dissected at the same time as Group B (Table 1) of the males. The following information was obtained from females (Group E, Table 2):

Mean mass of animal: 19,4 g
Mean uteri mass: 0,042 g

The following information was obtained from females (Group F, Table 2):

Mean mass of animals: 28,4 g
Mean uteri mass: 0,074 g

From the ten females (Group G, Table 2) collected in January 1973 near Nossob Camp, the following information was obtained:

Mean mass of animals: 24,0
Mean uteri mass: 0,04 g

According to Measrock (1953) the mass of the uterus is a good indication of reproductive activity in female gerbils. In the females a 32,6 per cent increase in the uterus mass and a 31,6 per cent increase in the total mass was found after a month under conditions of extended photoperiod and

Table 2

Female reproductive system of *Gerbillurus p. paeba*

No.	Age	External reproductive state	Mass in gram	Uterus mass in gram	Reproductive state of the ovaries
A. *GERBILLURUS* FROM NOSSOB CAMP (JULY 1972) (GROUP E)					
1	Parous	Anoestrus	15,3	0,05	Primordial and primary follicles present
2	,,	,,	22,8	0,06	,, ,, ,, ,, ,,
3	Non-parous	,,	18,4	0,03	,, ,, ,, ,, ,,
4	,, ,,	,,	21,9	0,04	,, ,, ,, ,, ,,
5	,, ,,	,,	18,6	0,03	,, ,, ,, ,, ,,
B. *GERBILLURUS* AFTER A MONTH UNDER CONDITIONS OF EXTENDED PHOTOPERIOD AND INCREASED TEMPERATURE					
6	Parous	Anoestrus	25,8	0,08	Primordial, primary and secondary follicles present
7	Non-parous	,,	26,7	0,08	,, ,, ,, ,, ,, ,,
8	Parous	Di-oestrus	30,6	0,09	,, ,, ,, ,, ,, ,,
9	,,	Anoestrus	29,3	0,06	Primordial and primary follicles present
10	Non-parous	Di-oestrus	29,5	0,10	Primordial, primary and secondary follicles present
C. *GERBILLURUS* AFTER SEVEN MONTHS IN OUTDOOR ENCLOSURE					
11	Parous	Anoestrus	40,0	0,09	Primordial and primary follicles present
12	,,	,,	38,0	0,07	,, ,, ,, ,, ,,

Table 2 (Continued)

G. *GERBILLURUS* FROM NOSSOB CAMP (JANUARY 1973) (GROUP G)					
No.	Age	External reproductive state	Mass in gram	Uterus mass in gram	Reproductive state of the ovaries
13	Non-parous	Anoestrus	22	0,05	Primordial, primary and secondary follicles present
14	,, ,,	,,	18	0,02	Primordial and primary follicles present
15	Parous	,,	26	0,04	Primordial, primary and secondary follicles present
16	Non-parous	,,	23	0,04	,, ,, ,, ,, ,, ,,
17	,, ,,	,,	23	0,03	,, ,, ,, ,, ,, ,,
18	,, ,,	,,	25	0,05	,, ,, ,, ,, ,, ,,
19	Parous	,,	24	0,03	,, ,, ,, ,, ,, ,,
20	,,	,,	22	0,01	Primordial and primary follicles present
21	,,	,,	28	0,05	Primordial, primary and secondary follicles present
22	,,	Pregnant	28	0,75	Corpus lutea present

increased temperature. No secondary follicles were found in the ovaries of the gerbils from Nossob Camp (Group E) but were frequently observed in the ovaries of gerbils (Group F) after a month in the experimental room. After one month in the experimental room two of the females (Group F) were in a state of oestrus but no visible pregnancies were observed. However, breeding did occur in gerbils who had been under extended photoperiod for a longer time. The effect of increasing the number of light hours and increasing the temperature would therefore seem to induce fertility in the female *Gerbillurus* as well. The females collected during January 1973 (Group G) appeared to be in a non-breeding condition although one pregnancy was observed.

6. *The effect of space on fertility*

After seven months the gerbils in the outdoor enclosure were killed and dissected. The mean diameter of the seminiferous tubules in the males was 217 micrometres and showed all stages of the spermatogenic cycle (Group C, Table 1). The females (Group C, Table 2) were in a state of anoestrus but the uterus mass indicated an active reproductive state. However, the cold winter months could have inhibited breeding activity. Only four gerbils were released in the open enclosure and this number is insufficient to allow for definite conclusions.

C. *External parasites*

During July 1972 a few external parasites were collected from *Gerbillurus* which were trapped at Nossob Camp. There were:

Mites:

Androlaelaps oliffii (Zumpt)
Androlaelaps marshalli (Berlese)

Fleas:

Xenopsylla philoxera (Hopkins)
Xenopsylla piriei (Ingram)

Summary and Conclusions:

A captive colony of *Gerbillurus p. paeba* was studied in an outdoor enclosure and observation cages. The gerbils thrived on a diet of millet, oats, sunflower seeds and "Pronutro".

Adaptation to change in light rhythm was far better to the usual light rhythm than when darkness coincided with daylight. A breeding box with a tunnel entrance was preferred by the gerbils. Feeding occurred mainly during the first hour of activity. The animals in the outdoor enclosure maintained a normal body weight for seven months without drinking water.

Typical grooming activities, i.e. washing, scratching, licking and social grooming, were observed. Sandbathing occurred each time the lights were switched off and the animals appeared from the nesting boxes. *Gerbillurus* is not very well adapted to climbing as it cannot grasp with its hind feet.

Activities during the active period consisted mostly of digging. During the daylight period the entrances to the breeding boxes were closed with sand. "Larder hoarding" and "scatter hoarding" were observed. During conflict situations between two strange animals agonistic behaviour was observed. In the normal behaviour patterns of *Gerbillurus* dominance-subordination relationships were absent. Stereotyped motor reactions in *Gerbillurus* consisted of a straight pathway, oval circuits and "weaving". An observing posture was resorted to every time the animal came out of the nesting box.

Copulation was only permitted by females in oestrus. *Gerbillurus* have a multiple intromission pattern but no lock and no thrusting was observed. The gestation period in *Gerbillurus p. paeba* was noted as 26 days with an oestrus cycle repeated every 41 days. Before parturition the females showed aggressive behaviour towards the males. Nipple-clinging was not observed. The young left the breeding box for the first time on the 29th day. Four months after birth there was still no sign of aggressive behaviour by the female towards the young. The litter size varied between three (two litters) and five (one litter). Increasing the number of light hours and increasing temperature seem to induce fertility in the male and female gerbil.

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REFERENCES

COETZEE, C. G. 1969. The distribution of mammals in the Namib Desert and adjoining inland escarpment. *Scient. Pap. Namib Desert. Res. Stn.* 40: 23–36.

DEWSBURY, D. A. 1972. Patterns of copulatory behaviour in male mammals. *Quart. Rev. Biol.* 47: 1–33.

DE GRAAFF, G. and J. A. J. NEL 1965. On the tunnel system of Brant's Karroo rat, *Parotomys brantsi* in the Kalahari Gemsbok National Park. *Koedoe* 8: 136–139.

EISENBERG, J. F. 1968. Behaviour patterns. *In* KING, J. A. 1968. *Biology of Peromyscus (Rodentia)*. Spec. publ. No. 2, The American Soc. of Mammalogists.

EWER, R. F. 1968. *Ethology of mammals*. London: Logos Press.
FOX, M. W. 1968. *Abnormal behaviour in animals*. London: W. B. Saunders.
HALLETT, A. F. and H. KEOGH, 1971. Laboratory Behaviour and breeding of *Gerbillus paeba coombsi* (Roberts) kept in captivity. *S. Afr. J. Med. Lab. Technol.* 17: 45–47.
MEASROCK, V. 1953. Growth and reproduction in the females of two species of Gerbil, *Tatera brantsi* (A. Smith) and *Tatera afra* (Gray). *Proc. zool. Soc. Lond.* 124: 631–658.
MEESTER, J. 1960. Early post-natal development of multi-mammate mice *Rattus* (*Mastomys*) *natalensis* (A. Smith). *Trans. Mus. Mem.* 24: 1.
SPICKETT, A. M. 1971. Intra-specific aggression in two species of *Aethomys*. Unpublished Ms.