LABORATORY AND FIELD OBSERVATIONS ON *ZELOTOMYS WOOSNAMI* (RODENTIA : MURIDAE)

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ABSTRACT

Woosnam's desert rat, *Zelotomys woosnami*, occurs in the arid regions of southern Africa. It is sparsely distributed, asocial and nocturnal, and probably utilizes burrows of other rodents although it can dig well. It has a wide food spectrum ranging from seeds to flesh, and is an agile climber. The litter size of 4,7 and the rapid postnatal development are thought to be adaptations to a short breeding season in the summer months, and to capitalize on seasonally-rich resources in a potentially hostile environment. Minimum period between litters was 31 days.

INTRODUCTION

Woosnam's desert rat, *Zelotomys woosnami* (Schwann, 1906), is poorly known because it is sparse throughout its distribution area of Botswana and the adjacent semi-desert areas. Apart from brief notes in Shortridge (1934), Roberts (1951) and Smithers (1971), no published data are available on any aspect of its biology. Over its extensive distribution area a marked colour variation is found on the dorsal surface, which ranges from a smoke-grey to drab-grey pencilled in black (Smithers 1971).

Since January 1972, during regular trapping sessions, 16 specimens were collected either with Victor or McGill rat snap traps or Sherman live traps in the Kalahari Gemsbok National Park. Here *Zelotomys* has so far been found on the low western bank of the Nossob river, its high eastern bank, on the flat areas covered with *Stipagrostis obtusa* in the wide river loops and in the dune troughs of the NW-SE stretching dunes some 3 km west of the Twee Rivieren rest camp. For further details of the trapping procedure and habitats sampled, see Nel & Rautenbach (1975).

This paper reports on some aspects of the behaviour and breeding of captive specimens and the postnatal growth of two litters kept under laboratory conditions, with additional notes on their biology under field conditions.

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MATERIALS AND METHODS

All 16 specimens so far collected in the Kalahari Gemsbok National Park were of a uniform light-grey colour dorsally. Body measurements and mass of nine of these individuals are available and are lumped with those of 29 specimens (Smithers *in litt.*) from Botswana (Table 1). Mass of only six specimens from Botswana was available.

TABLE 1

Measurements and mass of *Zelotomys woosnami* from the Kalahari Gemsbok National Park and Botswana.

	Total length (mm)	*Tail length (mm)*	*Hind foot length (mm)*	*Ear length (mm)*	*Mass (g)*
n	38	38	38	37	15
Mean ± 1 SD	231 ± 23,7	104 ± 10,8	25,9 ± 1,8	18 ± 1,5	59,8 ± 12,3
SE_m	3,85	1,74	0,29	0,24	3,18
CV	10,3%	10,3%	6,9%	8,2%	20,6%

The mean population mass was significantly higher in summer than in winter ($t_{13} = 2{,}48$; $p < 0{,}05$).

Of six *Zelotomys* trapped during July 1974 and taken to Pretoria, only two, a male and a female, survived until the beginning of 1975. For the purpose of the observations described below these two were housed in a glass aquarium measuring 120 x 50 x 50 cm. A square nest box measuring 20 cm along each side was provided at each end of the aquarium. Each nest box had an opening of 3 x 3 cm and one side of perspex to facilitate observations. The aquarium was placed in a room with constant temperature of 25° ± 5°C and with a reversed photoperiod of 16:8 hour light:dark regime. During "night" two 40 watt red light bulbs were left burning to allow observations.

During observations a stop-watch and a five-key laboratory counter were used. Only five main activities were recorded, viz. face-grooming, body-grooming, tail-grooming, litter-grooming and stretching. These activities comprised 87,5 per cent of the total number of activities seen during 30 hours of observation. Activities falling outside these five categories were noted down separately. The totals registered on the counter for each activity were noted at fifteen-minute intervals together with those recorded otherwise. For final analysis of the data all the activities were expressed as averages per hour, because lumping data into hour intervals gave more meaningful results.

Each activity was recorded separately and its duration was not taken into account, except for litter-grooming where a single infant could be groomed for over a minute. Grooming of individual infants was taken as a separate activity. Sequences such as face-grooming and defecating were recorded as single activities, although they were composed of several distinct actions. If a measured activity, e.g. face-grooming, was interrupted by a short bout of another activity, then every activity was counted separately. If, however, a sequence was interrupted for a second or two and then resumed, it was taken as a single activity.

In recording the development of the young, measurements were taken every second day for forty days. The young were then also checked for the beginning of behavioural responses or morphological developments.

Food was provided in the form of Epol rat pellets which were occasionally supplemented by sunflower seeds and millet. Water was supplied *ad lib.* in a drinking bottle and occasionally in a saucer.

RESULTS AND DISCUSSION

Behaviour

Social behaviour

Wild-caught individuals, when placed together in cages, are mutually intolerant and fight. Of a pair, one is usually killed and partly consumed, even where the pair consists of a male and a female, or an adult and a juvenile of the same or of different sexes. Trapping results indicate that individuals are widely spaced, and so far two animals have only been caught once at the same trap station during a particular trapping period. It seems, therefore, that *Zelotomys* is asocial and usually solitary, and that females allow males to approach and cohabit with them only when in oestrus, a characteristic also found in other rodents, e.g. *Desmodillus auricularis* and *Saccostomus campestris*. However, when litter mates are kept together after weaning, intolerance usually fades and successful reproduction may ensue. The two *Zelotomys* that bred in captivity were first allowed to become familiarized through a barrier before they could be put together.

After the first litter was born the male continued to share the nest box with the female until the second litter was born 31 days later; he then moved to the other nest box. This was thought to be due to overcrowding so the first litter was removed, but the male did not return permanently to the nest box containing the female and young. He did, however, frequently cross over for a brief bout of allogrooming. This mutual grooming seemed to have a "reassurance" value to the male as he would afterwards return to his nest box and rest. After a while he would get "restless" and, following repeated false starts, again cross over to allogroom with the female. When the male visited the female he also occasionally groomed the infants. Otherwise allogrooming often occurred between all members of a family but only between two individuals at a time.

General activity

Zelotomys is basically nocturnal. Because perspex-sided nest boxes were used, total active periods could be determined, and not just activity outside the nest box and presumably in nature outside the burrow. How much the red light entering the nest boxes disturbed or changed the activity cycles was not determined. Figure 1 shows that activity outside the nest box has a slight peak in the fourth hour after "nightfall". Presumably, more activity outside the burrow would be found under field conditions than in the laboratory because of the necessity for the animals to forage for food.

Three peaks occurred in activities inside the nest boxes (Figure 1). The first was during the first hour of darkness and was mainly concerned with grooming, eating and defecating. The second peak occurred during the fourth hour of darkness, and the third, a smaller peak, during the sixth hour. From then on activity dropped until the white light came on at "daybreak". A very low level of activity continued into the first hour of "daylight", but the rats soon settled down to sleep. Sleeping was usually done huddled together or lying on their sides.

Zelotomys is active in regular, short cycles. Periods of between five and fifteen minutes (usually about ten) of quiet resting in the nest boxes are followed by about five minutes of activity such as grooming, stretching and feeding, and then a ten-minute rest period. These short cycles are very variable and the rests may continue for over 30 minutes and the periods of activity may be more or less continuous for up to 15 minutes.

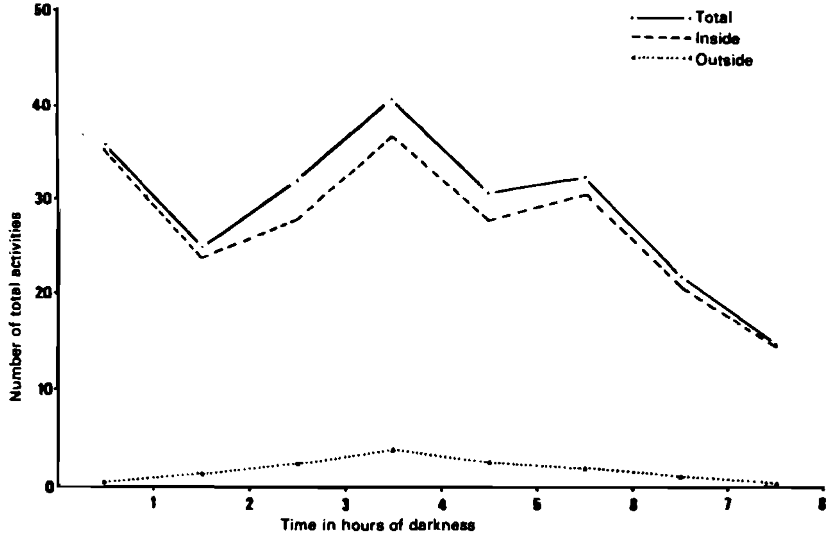

FIGURE 1

Nightly activity cycle, inside and outside the nest box, of *Zelotomys woosnami* kept in captivity.

Grooming

Grooming was the most frequent activity recorded (about 72 per cent) and was therefore broken down into different categories.

Self-grooming was sub-divided into face-grooming (50 per cent), body-grooming (45 per cent) and tail-grooming (5 per cent). When face-grooming, *Zelotomys* sits on its haunches and starts the sequence by cleaning both forepaws simultaneously, twisting them while pulling them through the mouth. The forepaws are then rapidly brushed a few times through the whiskers, from posterior to anterior, followed by the paws reaching further back with rapid strokes over the eyes and then ears, each time being drawn right down to the whiskers again and intermittently being licked clean. Body-grooming was always preceded by face-grooming but there did not seem to be any preference for dorsal, lateral or ventral grooming, except in the lactating female where ventral grooming was more marked. In the laboratory rat, grooming of the nipple line "increases drastically the week preceding parturition" (Rosenblatt & Lehrman 1963), but it was not stated whether this drastic increase in grooming continued during the time that the young were suckled.

When grooming the hind feet, *Zelotomys* holds the foot with one or both forepaws. This does not occur when the hind claws are being cleaned after scratching. Scratching often occurred, and was always followed by cleaning of the hind claws, by stretching the hind foot forwards and turning the head back so that the claws could be reached by the mouth. This is contrary to what is found in *Peromyscus,* which holds the hind leg while cleaning the claws after scratching (Eisenberg 1968).

Tail-grooming occurred but at a far lower level than head- or body-grooming. When grooming the tail, *Zelotomys* sits on its haunches and feeds the tail past the mouth with both forepaws. This is usually done only once, but occasionally may be repeated twice in succession.

Litter-grooming, which composed a further 15 per cent of total activities, continued for some time, but at a lower level, after the litter mates started grooming themselves. Anal-grooming of young occurred regularly; this behaviour pattern has been shown to promote excretion, the results of which the parent consumes, thus keeping the nest clean (Eisenberg 1968). The male also litter-groomed occasionally.

Allogrooming usually took place when one of the adults returned to the nest box. Occasionally an adult would groom the partner even if neither had been absent from the nest box. Allogrooming was usually directed at the partner's face and mouth whilst the two adults sat on their haunches and held each other up with their forelegs.

Anal-sniffing occurred between all members of the captive *Zelotomys* colony but was most often directed by male at female.

Sand-bathing was never observed although it is very well documented for many other rodents such as *Peromyscus crinitus* (Eisenberg 1968), *Gerbillurus paeba paeba* (Stutterheim & Skinner 1973), *Desmodillus auricularis* (Keogh 1973) and a group of heteromyids (Eisenberg 1964).

Stretching, best described as a comfort activity, occurred frequently and made up a further 15 per cent of the total activities recorded. Stretching usually took place in a corner of the nest box and was often accompanied by a yawn or by licking the wall of the nest box. Stretching usually occurred on entering the nest box, with the adult moving from one corner to the next, stretching in all four corners. This is contrary to the situation found in *Gerbillurus* (Stutterheim & Skinner 1973) where stretching is performed on emergence from the nest box.

Feeding and defecating

When eating, *Zelotomys* picks up the food with the mouth. It then sits on its haunches and holds the food with its forepaws while biting pieces off with the incisors. The food is swallowed after brief mastication. *Zelotomys* hoards some of the food in its nest box. Sunflower seeds were often carried to the nest boxes and immediately consumed but never hoarded. Although most of the eating was done inside the nest box, the adults often ate outside.

Although basically graminivorous (Smithers 1971), *Zelotomys* is also carnivorous. As noted above, when strangers are put together one kills the other. On three out of five occasions the winner ate part of the victim starting at the rectum and pulling the intestines out. Two stomachs of wild-caught specimens were available for comparative purposes. One contained 60 per cent white plant matter (seeds), 20 per cent insects (Coleoptera) and 20 per cent nematodes *(Physaloptera aduensis* females and larvae and *Spirura* sp. female - Verster *in litt.*). The other stomach contained 100 per cent flesh. No hair was present so the source could not be determined. Also, on account of this lack of hair, it is suspected that the specimen had been scavenging. Coprophagy was observed in adults but not in juveniles. It could, however, occur in juveniles because it is an important means of supplying the young with a normal intestinal flora (Ewer 1968).

Figure 2 shows that of the three eating peaks the main one occurs during the fifth hour of darkness. The main peak for defecation is during the first hour but a small peak does occur during the fifth hour which corresponds with the main eating peak. Defecating took place in both nest boxes although they preferred the box with the largest nest. A specific corner was used for defecation. This corner was located by its position in the box and not by the pile of scats. When the box was turned slightly so that the pile of faecal pellets became displaced to another position, the original position was chosen in preference to the pile of scats. In both boxes the scats were piled against the perspex side, the opposite end to that used for nesting. A specific fixed action pattern was seen in defecating. The rat would approach, smell the scats and then turn around and move backwards a step or two so as to be over the pile, one to five pellets being expelled per defecation. The last pellet was displaced by a "pump-handle" action of the tail, and on moving away the rat usually displayed an inguinal drag. Urination often accompanied defecation.

Digging

In the wild, *Zelotomys* lives in burrows (Figure 3). These burrows are thought to be dug by other rodents, e.g. *Tatera* (Shortridge 1934) or *Desmodillus* (Roberts 1951). But, although the sand in the cage was fairly shallow, i.e. 10 mm, *Zelotomys* did show that it was capable of active digging. Most of the digging occurred in corners of the cage or box.

The digging sequence started with several true digging or substrate-loosening motions in which the forefeet were used alternately. The forefeet were then used in unison to "clear" by pushing the sand under the abdomen. After "clearing" two or three times with the forefeet, the hind feet were employed in unison to "clear" what had accumulated. "Clearing" by the hind feet seemed to be triggered by the amount of sand that had accumulated under the abdomen, but was also seen to occur when digging was attempted in the corner of a plastic bag, where there was no sub-abdominal substrate accumulation. This digging sequence is very similar to that found in *Peromyscus polionotus* (Layne & Ehrhart 1970) except that *P. polionotus* showed powerful hind foot "clearing" that blasted the sand a distance of 60–65 cm. Power strokes were seen in *Zelotomys* but they were not as strong.

Nest-building

Only a minimum amount of nesting material was normally supplied because the captive *Zelotomys* made nests which obscured the behaviour. When a surplus of nesting material in the form of "wood wool" and cotton wool was supplied, it was all pulled into the nest box,

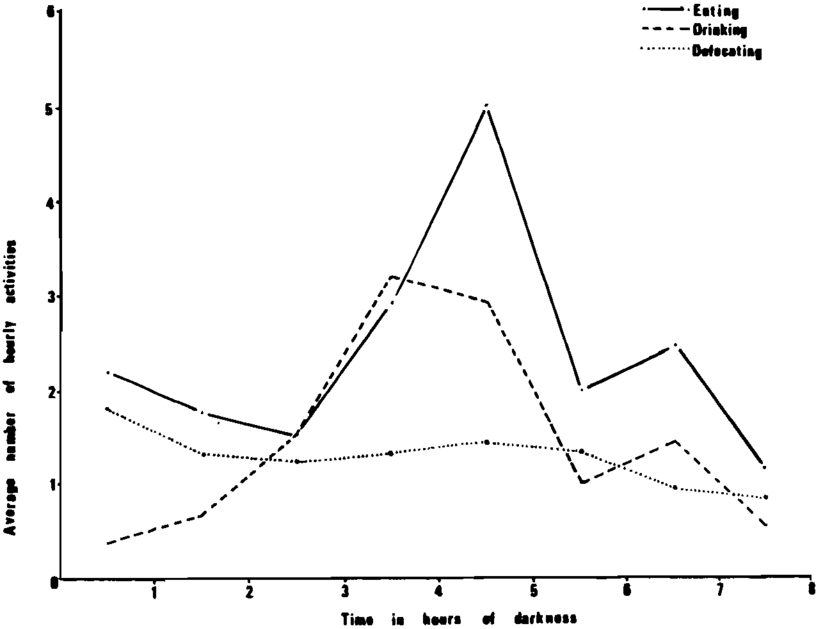

FIGURE 2

Eating, drinking and defecating cycles of *Zelotomys woosnami* kept in captivity.

shredded, and a deep cup-shaped nest made by the female pushing her head into the pile of material and then moulding the cavity. The male was also involved in nest-building but not as actively as the female; the same applies to *Aethomys chrysophilus, Praomys (Mastomys) natalensis* and *Rhabdomys pumilio* (Stiemie & Nel 1973).

When the first litter was born the female initially moved to the other nest box every time the young were removed for measuring. Immediately after the young were placed in the nest she would return and transfer them, and the nest itself, to the other nest box. This occurred several times until the female got used to being disturbed; thereafter, even when the young of the second litter were measured, this behaviour ceased.

In the wild, two nests were found in a burrow system excavated in the Kalahari Gemsbok National Park (Figure 3). These were respectively 55 and 40 cm below the soil surface, with nest chamber dimensions of 14 x 10 x 10 cm and 14 x 16 x 15 cm respectively. Both nests were rather shapeless and consisted of finely-shredded "Kortbeenboesmangras", *Stipagrostis obtusa.*

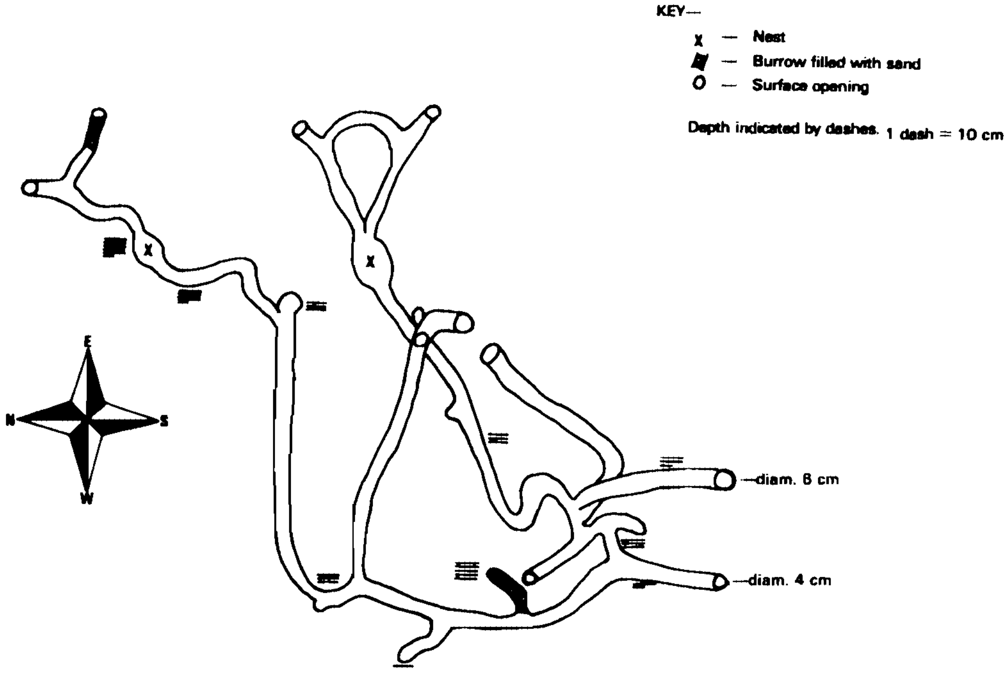

FIGURE 3

Burrow system of *Zelotomys woosnami* in the Kalahari Gemsbok National Park.

Tree-climbing

Zelotomys was thought to be terrestrial by Smithers (1971), but during our observations proved quite adept at climbing branches placed in the cage. The adults did not climb often but the juveniles climbed regularly. Although the tail is not prehensile, it is used for balancing when climbing, often aiding the balance by being pushed against a side branch and partly wrapped around it. *Zelotomys* seemed to prefer branches of 15 mm diameter or more, but often climbed to the highest point which was about 0,8 m above ground level on a branch of only 5 mm diameter. Slipping and falling did occur, but became less frequent as the rats grew older and more practised.

When stationary on a thick branch (more than 15 mm) the rats usually stood parallel with the branch, but if the branch was thin (less than 15 mm) they usually aligned themselves at right angles to the branch axis and used their tails to keep their balance.

They were also seen to jump from one branch to another for distances of between 15 and 20 cm. When descending the stem (30 to 40 mm thick) the rats always went head first and dragged the wide-spread hind legs behind them in much the same way that a squirrel does when descending a tree trunk. Only branches with fairly rough bark could be climbed as foothold was gained by the nails. The fore-foot digits were not opened so as to grasp the branch in climbing, but the hind-foot digits were extended when climbing down the stem.

In infant *Zelotomys* a cliff response or edge effect was seen for the first time on the 14th day, two days before the eyes opened. Ewer (1968) suggests that this cliff response in juveniles might be present in species that, when full grown, would be climbers. However, *Desmodillus* also shows a cliff response (Nel & Stutterheim 1973) but is most unlikely to be a climber. Shortridge (1934) reported that *Zelotomys* burrows are often found in the close vicinity of large trees (e.g. camelthorn - *Acacia ereoloba*), and in the Kalahari Gemsbok Park this was also the case. Being trapped in the vicinity of trees does not necessarily mean that a rodent would utilize such trees, but the above observations do seem to suggest that *Zelotomys* may be partly scansorial.

Breeding and Postnatal Development

The present observations confirm that the breeding season for *Zelotomys* is during the warm-wet months of December-March (Shortridge 1934; Smithers 1971). In the present study the litter sizes were 5, 4 and 5, with a mean of 4,7; while Smithers (1971) recorded litters of 11, 5 and 5. The mean litter size of the six litters is thus 5,8; but this figure is perhaps too high due to the effect of the one large litter in the small sample. The sex ratio of male: female was 43:57 per cent in the 14 infants born in captivity.

The minimum period between litters was 31 days, indicating a post-partum oestrus, but the minimum age at birth of the first litter has not been determined.

Development of young (Figure 4)

At birth (Day 0) the young are pink and have a dorsal grey tinge due to the start of hair proliferation. Vibrissae are present, the eyes are closed and the pinnae are folded over forwards. The toes are fused for half their length.

Hair proliferation

By Day 2 the eyebrows start erupting and the dorsal grey tinge gets darker. The dorsal proximal part of the tail also shows a dark tinge. Hair eruption takes place by Day 6, resulting in a dorsal grey pelage and a ventral white pelage in a fairly uniform coat.

Ears

The ear pinnae which are folded forward over the external auditory meatus at birth stand upright by Day 2 but are still thick and fleshy. The external auditory meatus opens on Day 14.

Incisors

The incisors erupt between Days 10 and 12, with the lower incisors erupting slightly before the upper ones, similar to *Desmodillus auricularis* (Nel & Stutterheim 1973) and *Mystromys albicaudatus* (Hallett & Meester 1971).

Mouth

At birth the margins of the mouth are almost totally fused together. The only open portion is right in the middle where a small orifice (diameter 1-1,5 mm) permits suckling. By the time the incisors erupt on Day 10, most of the mouth is open but there is still fusion near the corners.

Toes

The toes which are only half fused at birth are completely loose by Day 4. This corresponds with the condition in *Aethomys chrysophilus* (Brooks 1972).

Eyes

From Day 10 a visible crease is present across the eye but it only opens on Day 16 or 17.

Physical growth

The increase in mass and percentage mass is shown in Figure 5. In common with most other rodents the percentage mass increase reaches a peak a few days after birth (in this case on Day 4) and thereafter shows a progressive decline. At 40 days a young *Zelotomys* already weighs about 80 per cent of the adult mass. *Desmodillus auricularis*, on the other hand, has only reached 50 per cent of the adult mass by the age of 40 days. These percentages are rough approximates, especially in the case of *Zelotomys* where very few adult mass values are known. Male and female growth values were averaged because they were very similar

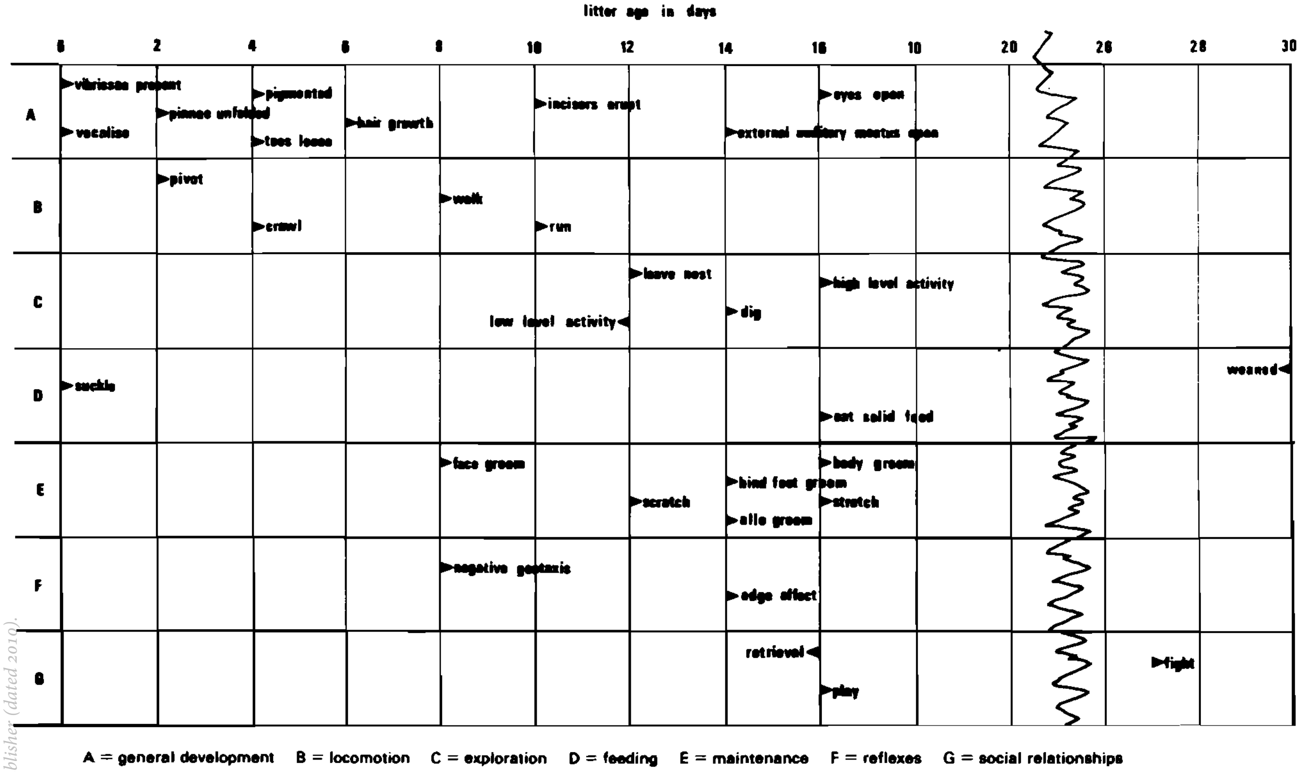

FIGURE 4
Developmental stages (physical and behavioural) of captive *Zelotomys woosnami*.

(Figures 5 & 6). The only difference in growth between the sexes is that males tended to be heavier than females towards the end of the 40-day observation period, although there were exceptions.

Development of behaviour

Figure 4 shows the stages in the development of behaviour patterns in *Zelotomys*. The definition of various actions follows Evans (1970). Day 16 marks the beginning of the high activity level. This corresponds to opening of the eyes, the beginning of play and the end of retrieval. Playful mounting was first seen on Day 38.

Parent-young relationships

The retrieval response in the female is fairly well developed. The young were replaced at the entrance of the nest box after being weighed and measured, whence they were pulled inside by the male or the female, or on one occasion, by a 35-day-old juvenile from the previous litter. When retrieved from the nest-box entrance, an infant was grabbed by the nearest part, be it head, body, limb or tail. It was then briefly groomed before the next youngster was retrieved. For transporting it was grasped on the middle of the back. This manner of transporting young occurs in many rodents (Ewer 1968). Meester & Hallett (1970) report a case of a male *Praomys (Mastomys) natalensis* which regularly carried young around in its

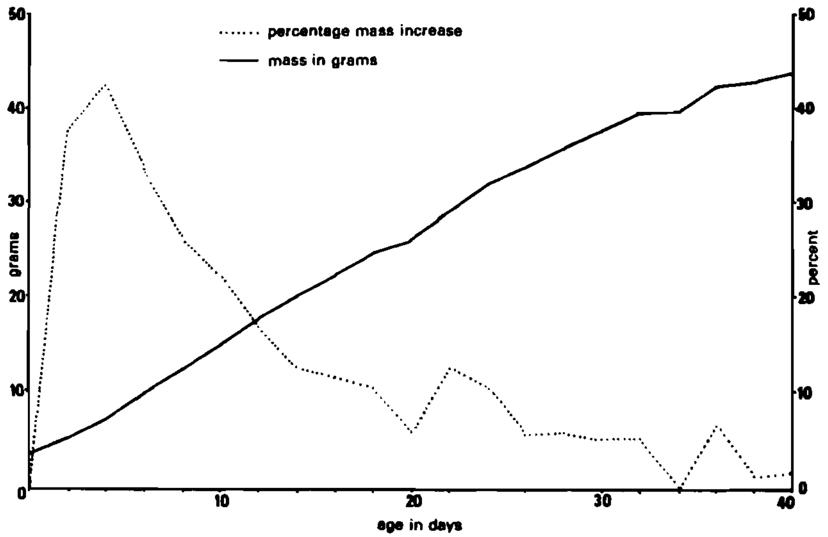

FIGURE 5

Mass and percentage mass increase in developing *Zelotomys woosnami* kept in captivity.

mouth. Choate (1972) states that in *Lemniscomys griselda* both sexes retrieve displaced young. In *Zelotomys,* however, the female did most of the retrieving.

Nipple-clinging was not observed. When the nest box was removed the male and female fled. The young could be handled from the day of birth and the female did not respond to human smell by eating the young, as is seen in some other rodents such as *Praomys natalensis* and *Rhabdomys pumilio* (Choate 1972). The male, as well as older litter mates when present, often groomed the infants. Sparring occurred between the mother and young, and between the young themselves, and consisted of standing on the hind legs and beating each other with rapid fore-paw strokes. Up to Day 16 the female always lay on top of the suckling young but from then on she usually lay on her side, presumably because the infants were too large (average mass 22 g).

Nest-leaving

The lowest recorded mass of a *Zelotomys* trapped in the field, i.e. outside the burrow, is 42 g. This is equivalent to an age of 35 days. In the litter studied the young first let the nest on Day 12 but only did so regularly after Day 16.

CONCLUSIONS

From all accounts, and as trapping in the Kalahari Gemsbok Park and Botswana (Smithers 1971) show, *Zelotomys* is an arid-area species never present in high numbers. Its exact ecological requirements are thus still rather obscure and, anatomically, the species shows neither adaptations to digging (e.g. big feet) or to tree climbing. Yet, both of these dimensions of the habitat seem to be utilized. *Zelotomys* digs, although under natural conditions perhaps preferring the disused tunnels of *Tatera brantsii* and *Tatera leucogaster,*

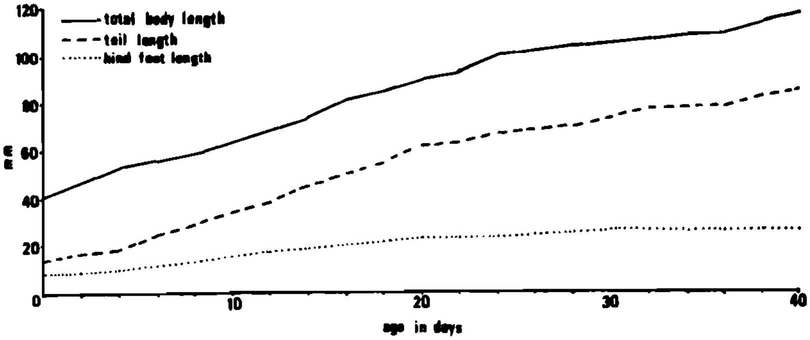

FIGURE 6

Increase in total body length, tail length and hind foot length in developing *Zelotomys woosnami* kept in captivity.

and it is well capable of climbing trees. This ubiquitous nature would allow *Zelotomys* to coexist with other rodents in arid areas, where arboreal and scansorial rodents are especially scarce. The food niche also seems to be wide, from seeds to flesh - again this would allow food requirements to overlap, rather than directly compete with, those of other sympatric rodents.

From field and laboratory observations, it appears that *Zelotomys* is normally asocial and aggressive. In confinement, and especially between litter mates, this antagonism declines.

Meester & Hallett (1970) suggest that nipple-clinging is present in rats with small litters and early incisor eruption. *Zelotomys* has relatively large litters and late incisor eruption (Day 10) and nipple-clinging does not occur. Burrowing rats usually have a small litter size (Nel & Stutterheim 1973) as is seen in *Tatera brantsii* and *Desmodillus auricularis* (both two per litter). Nipple-clinging surface-nesters also have small litter sizes, as mentioned previously, but non-nipple-clinging surface-nesters have relatively large litters as is seen in *Rhabdomys pumilio* which has an average litter size of 5,8 (Meester & Hallett 1970). The reason for the large litter size in *Zelotomys* is obscure, but an ecological study might show that because it lives in an arid habitat and has a low overall density, the reproductive rate is constantly being inhibited by adverse conditions. A large litter size and rapid development of the young would enable this species to take advantage of unpredictable and perhaps short-lived favourable conditions.

Most of our data on numbers and developmental time can be interpreted in the framework of the *r* and *K* continuum (Pianka 1970). *Zelotomys woosnami* shows the *r* correlates of inhabiting an area with a variable and rather unpredictable climate (especially rainfall), having a low population density, relatively large litter size, and a rapid developmental rate. To these correlates can perhaps be added the wide habitat and food niches. Other attributes, e.g. large body size, the possibility of multiple breeding (i.e. having a post-partum oestrus) and long lifespan do not fit the theory of *Zelotomys* being *r*-selected.

All these factors, however, point to *Zelotomys* being adapted to exploit a xeric and potentially hostile environment. The breeding season is short (December - March) and rapid growth will permit young to mature sufficiently during the rainy season when the energy potential in plant foods in high. In these aspects *Zelotomys* agrees with a mesic species such as the white-throated wood-rat *Neotoma albigula venusta* (Schwartz & Bleich 1975) but contrasts with the xeric adapted *Peromyscus floridanus* (Layne 1966).

The density-limiting factors are not known, but it was only in 1974, when the Kalahari Gemsbok Park had a four-times higher than normal rainfall, that *Zelotomys* was trapped in any numbers. Before that only one specimen had been caught.

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