Postnatal growth and development of the hairy-footed gerbil, *Gerbillurus paeba exilis*

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Received 14 December 1989; accepted 19 March 1991

The growth and development of six litters (21 pups) of captive *Gerbillurus paeba exilis* are described. Growth is slow with mean adult mass (32,4 g) being reached after 102 days, although the youngest sexually mature male and female were 63 days and 84 days old respectively. Physical development is also comparatively slow and weaning is completed after 30 days. Mass, tail length and hindfoot measurements were subject to much less error than head/body length data. Mass values of wild and captive gerbils are compared where possible. Two 'critical periods' in development were pin-pointed, i.e., (i) Day 12, when all the motor abilities developed rapidly, and (ii) Day 17, when the eyes opened and social behaviour followed. Behavioural development was divided into four periods: neonatal, transitional, socializing and juvenile.

Die groei en ontwikkeling van ses werpsels (21 kleintjies) van *Gerbillurus paeba exilis* word beskryf. Groei is stadig en die gemiddelde volwasse massa van 32,4 g is eers op 'n ouderdom van 102 dae bereik, alhoewel die jongste geslagsryp-mannetjie 63 dae oud en die jongste wyfie, 84 dae oud was. Fisiese ontwikkeling is stadig en kleintjies is na 30 dae gespeen. Massa, stert- en agterpootlengte is meer akkuraat as kop- en liggaamslengte. Massas van wilde en mak individue word vergelyk waar moontlik. Twee 'kritieke periodes' tydens fisiese ontwikkeling kan geïdentifiseer word, nl. (i) Dag 12, met die meeste motoriese funksies reeds ontwikkel en (ii) Dag 17, wanneer die oë oopgaan en sosiale gedrag volg. Ontwikkeling van gedrag kan in vier periodes ingedeel word: neonataal, oorgang, sosialisering en jeugdige. Die relatief stadige ontwikkeling van die haarpoot-nagnuis is moontlik te wyte aan die beskerming van ondergrondse neste.

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The hairy-footed gerbil *Gerbillurus paeba exilis* is widespread in southern Africa but is difficult to breed in captivity (Smithers 1971; Hallett & Keogh 1971; Stutterheim & Skinner 1973; Nel 1975; Christian 1979; Nel, Rautenbach, Els & De Graaff 1984). The only information thus far available on growth and development of *Gerbillurus* species in the laboratory is the recent work on *G. p. paeba* (Dempster & Perrin 1989) and on *G. vallinus* and *G. setzeri* (Dempster & Perrin, unpubl.). *G. p. exilis* is an isolated subspecies confined to coastal dunes in the Alexandria dunefield in the eastern Cape.

In this study the growth and physical and behavioural development of 21 *G.p. exilis* pups born in captivity from stock captured in dune slacks were measured. The study formed part of a broad investigation during 1981 and 1982 of the population dynamics, reproduction, feeding habits and habitat utilization of this species in the dunefield (Ascaray 1986). Where possible, laboratory growth data were compared with data obtained from the field study.

Methods

A laboratory colony was started with three males and three females (two of which were pregnant) caught in dune slacks in December, 1980. Light, temperature and humidity were uncontrolled and approximated natural regimes. The gerbils were kept in glass tanks of varying sizes, the smallest measuring 60 × 30 × 30 cm, filled to a depth of approximately 7 cm with beach sand. The gerbils were fed standard laboratory pellets and sunflower seeds, supplemented with oats, *Chrysanthemoides monilifera* berries and lettuce. Water was provided *ad libitum*. Males were removed from cages when females were noticeably pregnant after several incidents occurred where males were wounded or killed by pregnant females.

The following standard measurements were taken from a total of 21 pups (six litters): mass to the nearest 0,1 g; head and body length; tail length and left hindfoot length including the claw. All linear measurements were taken to the nearest 0,1 mm using Vernier calipers. Pups were measured every two days, some beginning on Day 1 (day of birth = Day 0) and some on Day 2, until three weeks old. Thereafter they were measured approximately weekly.

Mass and linear measurements from the six litters were pooled and mean measurements calculated. Since pups were measured every two days beginning either on Day 1 or Day 2, not all possible data were available for any one day. In order to maximize samples sizes for each day, the mass (and linear measurements) of pups that had not been measured on Day 4, for example, were calculated as follows:

$$\text{Mass (Day 4)} = \frac{\text{mass (Day 3)} + \text{mass (Day 5)}}{2}$$

One litter was measured until four weeks of age, three litters until 13 weeks and two litters until 27 weeks of age. Body length was measured only until Day 26; after that time pups developed a typically crouched posture and accurate measurements could not be obtained. Even when the gerbils were etherized, consistent measurements could not be obtained. Other linear measurements were obtained fairly accurately from unetherized gerbils. Wild gerbils were weighed to the nearest 0,5 g with a Pesola spring balance.

Physical and behavioural development of the pups were

observed at the same time intervals as growth. The physical development of the pelage, limbs, eyes, ears, teeth and reproductive organs was noted. Behavioural observations were made with regard to feeding, locomotion, audible vocalization, grooming, exploration and sexual behaviour. Depth perception was noted by placing the pups near the edge of a surface above the ground and noting their reaction. The righting reflex was tested by placing the pups on their backs on a flat surface and noting whether they were able to right themselves.

Results and Discussion

Growth

Eleven litters comprising 38 pups were born in the laboratory. The first five litters were used to establish a laboratory colony (two litters were eaten by their parents). Baker & Meester (1977) attributed the killing of young *Praomys natalensis* by their parents to disturbance and handling of the litters. However, *G. p. exilis* individuals born in the laboratory appeared to be more tolerant of disturbance, and six subsequent litters (21 pups), five of them born to laboratory-reared females, were measured without mortality or overt ill effect. Litter size was 3,5 ± 1,4 (mean ± *SD*) compared to 4,1 recorded by Nel *et al.* (1984) and 4,6 by Dempster & Perrin (1989) for *G. p. paeba*.

Mass and linear measurements (Figures 1–5) are not all based on the total 21 pups. However, sample size for any one day was never less than five for any of the measurements. Minimum, maximum and mean measurements are shown, to give an indication of variance.

Mass

The increase in mean mass of *G. p. exilis* pups from birth until 193 days (26 weeks) of age is shown in Figure 1. Percentage daily increase in mass from birth until 21 days is depicted in Figure 2. Mean mass on Day 1 was 2,3 g, 7% of the average adult mass. Dempster & Perrin (1989) recorded a mean birth mass of *G. p. paeba* of 1,9 g.

The young grew rapidly until they were 18 days old (Figure 1), but there was a slight decrease in mass on Days 20 and 21 associated with the onset of weaning. Nel & Stutterheim (1973) and Panagis & Nel (1981) recorded a reduction in growth rate associated with weaning in *Desmodillus auricularis* and *Thamnomys dolichurus*, respectively. The percentage mass increase of the *G. p. exilis* pups was highest (22%) on Day 2, and declined with increasing age (Figure 1). Mass increase was less rapid after Day 26 when the pups weighed 50% of adult body mass. It required a further 76 days to reach mean field adult mass. Minimum and maximum values differed from the mean mass by an average 16% and 15% respectively.

It was not clear when to infer that adult mass had been attained as the gerbils increased in mass throughout the study (193 days, Figure 1), although sexual maturity was reached at 60–90 days (asymptote is approximated at about 90 days). Mean mass of adult males recorded during the field study (breeding and non-breeding) was 32,4 g. Female mass values were not used to determine maturity as they are subject to much variation owing to pregnancy (Krebs 1966; Nyton 1974). Adult mass of *G. p. paeba* is given by Christian (1980) as 20–30 g, whereas Smithers (1971) records average mass of 38 males and 38 females from different localities in Botswana as 26,8 g and 26,0 g respectively. De Graaff (1981) records the average mass of 11 males as 27,7 g and eight females as 27,0 g. Neither of the two latter authors makes any distinction between adults and juveniles, while Christian does not state how his figures were derived. A mass of 32,4 g for adult male *G. p. exilis* in the Alexandria dunefield is believed to be accurate, since it is based on a large sample size (181) and specifically

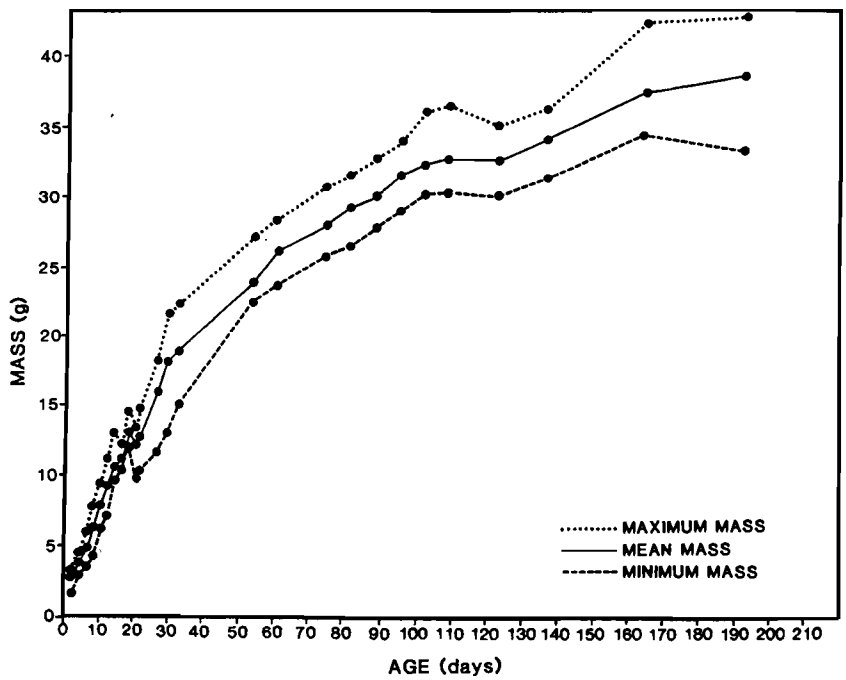

Figure 1 Increase in mass with age of laboratory-bred *G. p. exilis* pups (n = 21).

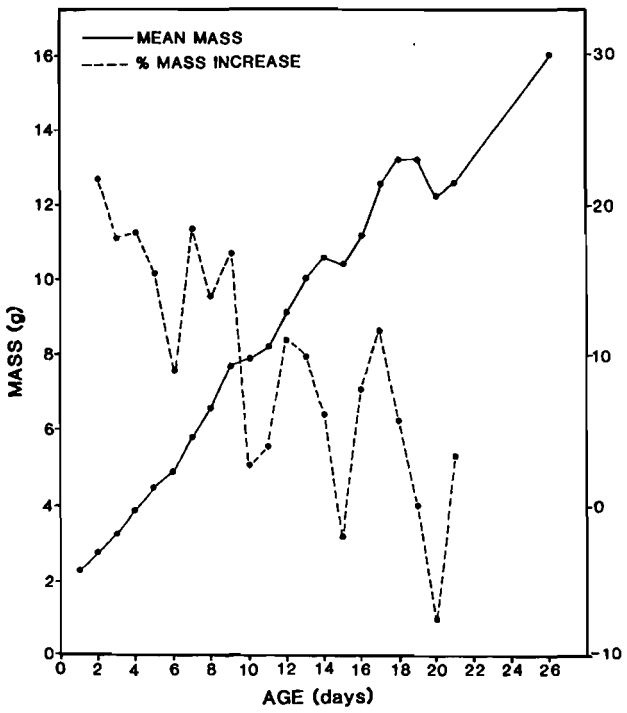

Figure 2 Mass and percentage mass increase of *G. p. exilis* pups from birth to weaning.

it is based on a large sample size (181) and specifically excludes juveniles. This seems significantly higher than other subspecies and may have ecological or phylogenetic implications. *G. p. exilis* pups in the laboratory reached this mass after approximately 102 days.

Linear measurements

Increases in head and body length, tail length and hindfoot length of *G. p. exilis* pups are shown in Figures 3, 4 and 5. Morris (1972) states that body length is difficult to measure accurately since the body can be stretched out to a variable degree, while Jewell & Fullagar (1966) have found head/body length almost impossible to standardize among observers working on dead rodents. Mean head/body length of the gerbil pups on Day 1 was 29,6 mm, or approximately 31% of adult size. By Day 26 average head/body length was 65,0 mm. Average head/body lengths of *G. p. paeba* are generally 93–97 mm (Smithers 1971; De Graaff 1981). Assuming a mean adult head/body length of 94 mm for *G. p. exilis* in the Alexandria dunefield, the pups appear to have completed about 67% of their growth by Day 26.

Jewell & Fullagar (1966) found tail length to be subject to much less error than head/body length as is reflected by the smoother curve in Figure 4. Mean tail length on Day 1 was 13,3 mm, or 11% of the adult length. Growth of the tail appears to have been completed by Day 102, when the

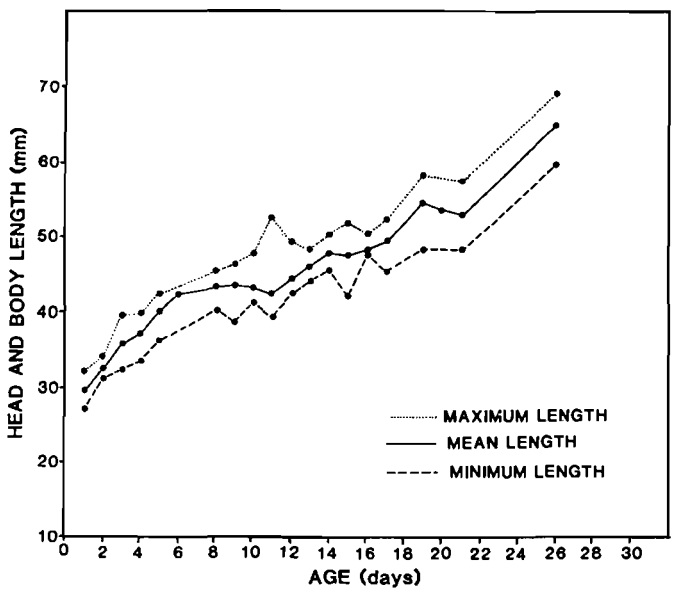

Figure 3 Increase in head and body length of laboratory-bred *G. p. exilis* pups (n = 21).

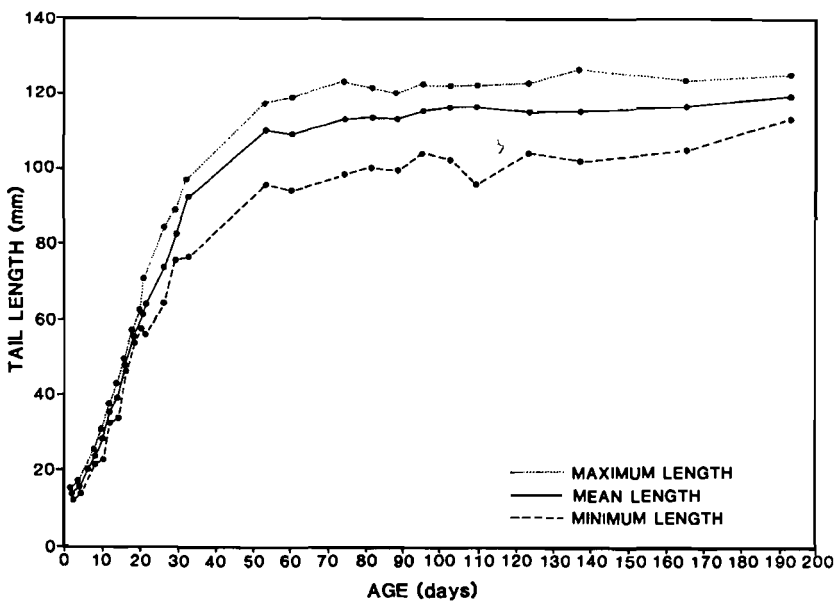

Figure 4 Increase in tail length with age of laboratory-bred *G. p. exilis* pups (n = 21).

mean tail length was 116,5 mm. Smithers (1971) gives tail lengths ranging 102–125 mm for Botswana specimens of *G. p. paeba*. De Graaff (1981) quotes mean values of 109 mm for males and 110 mm for female *G. p. paeba*. Again, neither author specifies whether these are adult measurements only, so that a strict comparison is impossible.

Hindfoot length of the gerbil pups at birth was 7,7 mm, approximately 27% of adult size. The hindfoot reached its maximum length after approximately 53 days (Figure 5), when the mean length was 28,1 mm. Smithers (1971) gives an average value of 27,0 mm for Botswana specimens (range: 25–29 mm), while De Graaff (1981) gives mean values of 26 mm and 27 mm for *G. p. paeba* males and females respectively.

Comparison of laboratory and field growth

Growth, as represented by an increase in mass, may be influenced by several factors, such as the time of year litters are born and by population density (Delany 1976). Retardation of growth and even mass loss during unfavourable times of the year have been reported for several mammal species (Morris 1972; Davis 1973; Chidumayo 1980). Young born late in the breeding season may be influenced by unfavourable environmental conditions. Since laboratory conditions are generally much more constant than field conditions, growth in the laboratory and in the field may be quite different.

Growth in the field and the laboratory could not be directly compared in the present study, since live individuals in the field could not be aged. However, mass at weaning appears to be similar for captive and wild individuals. Weaning is complete at 30 days of age in *G. p. exilis*. The mean mass of captive gerbils at 30 days was 18,5 g (range: 13,7–21,8 g). The nine smallest individuals (< 20 g) captured in the field had an average mass of 17 g (range: 13–19 g).

Wild individuals underwent several fluctuations in mass before reaching average adult size. The growth of eight wild individuals is represented in Figure 6. Only males and non-parous females were used, thus eliminating any fluctuations owing to pregnancy. All eight gerbils were trapped for the first time as juveniles. After an initial period of regular growth, most individuals experienced changes in mass of several grams over three weeks. These fluctuations were possibly due to lower temperatures and/or a poorer food supply during the autumn and winter months. The sharp rise in mass of individuals from June 1981 – July 1981 may be due partly to the attainment of reproductive status, which is a distinct seasonal event. Large mass fluctuations did not occur in captive individuals, presumably as a result of the more constant conditions.

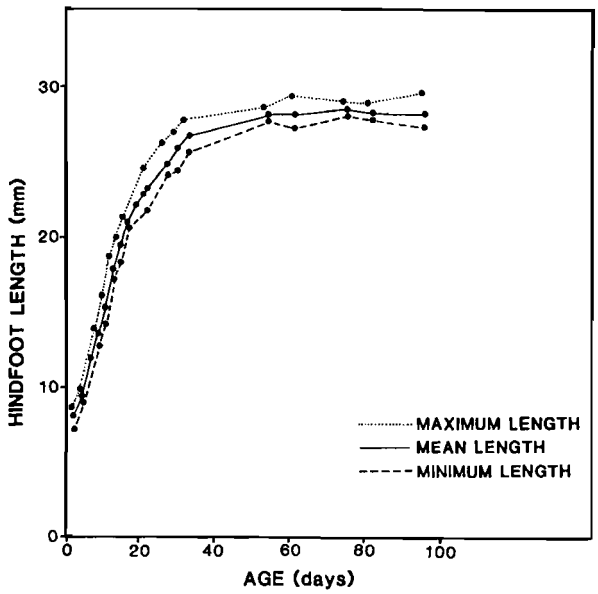

Figure 5 Increase in hind-foot length with age of laboratory-bred *G. p. exilis* pups (n = 21).

Physical development

At birth the young were naked and pink in colour (Figure 7). The sutures of the skull, and the viscera, were visible through the translucent skin and the only hair present was in the form of vibrissae. The eyes and ears were closed and

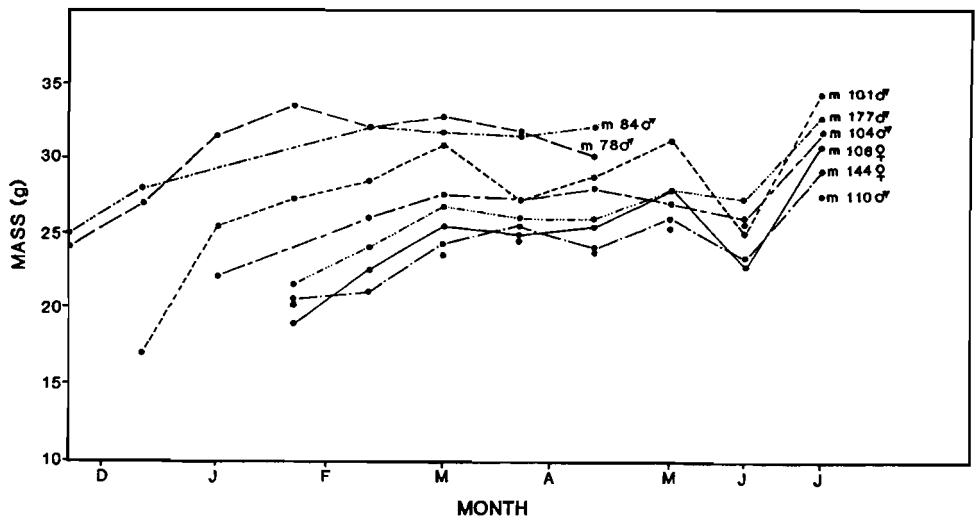

Figure 6 Growth of wild *G. p. exilis* individuals. Time intervals between samples = 3 weeks.

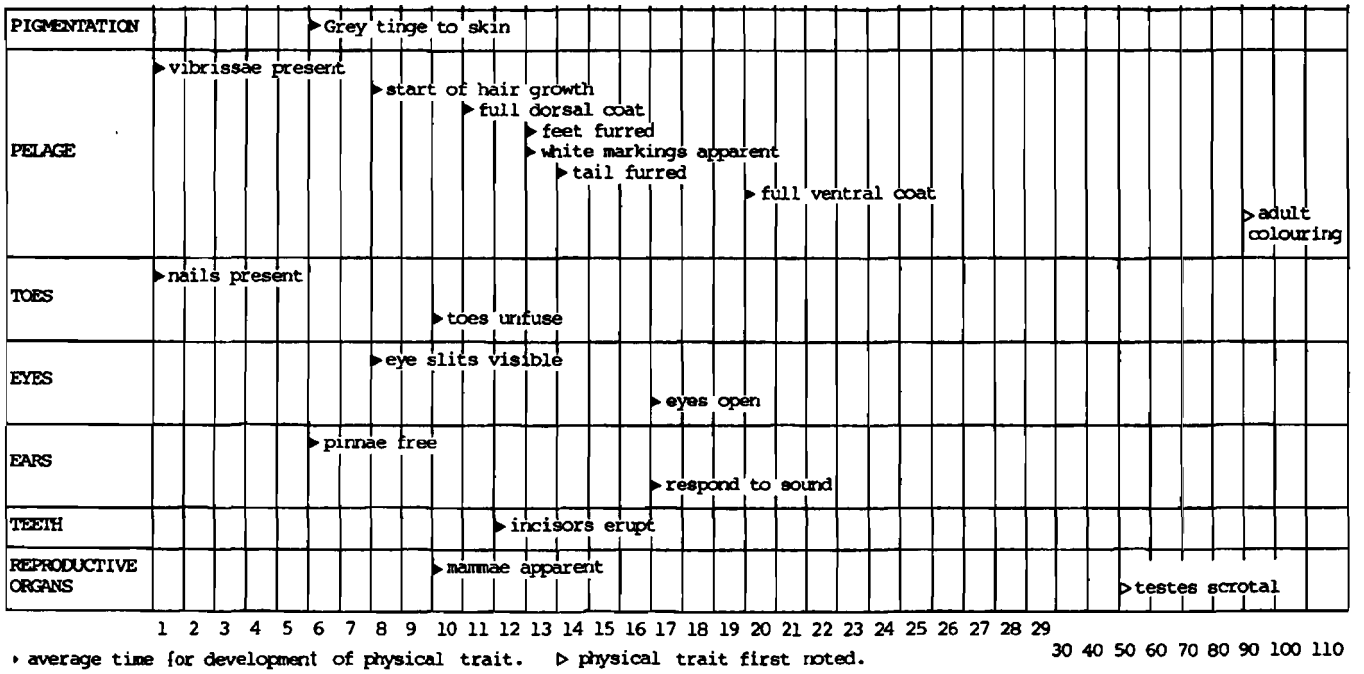

Figure 7 Physical development of laboratory-reared *G. p. exilis* pups.

no teeth were present. The toes were fleshy and fused together.

A grey pigmentation became visible on the dorsal surface of the body on Day 4 in one litter and was present by Day 5 in the other litters. By Day 7 the dorsal and ventral surfaces of the pups' bodies were covered with very sparse, spiky hairs and the internal organs were no longer visible through the skin. By Day 10 all the pups had a thick, glossy covering of buff dorsal fur, while their ventral surfaces and the upper sides of the feet and tail were covered with sparse hairs. The ventral surfaces of the feet were naked. From Day 11 (average: Day 12) the characteristic white markings on the sides of the body and on the cheeks became noticeable. Feet were fully furred dorsally on Day 12, and tails on Day 13. Muzzles were the last to become haired, usually by Day 19. By Day 10 the white ventral hair was very dense. Although the pelage was complete by 21 days of age, the pups were easily distinguished from adults by their colouring. Adult *G. p. exilis* had a reddish tinge to the dorsal fur, while juveniles were a buff colour. The first time pups were noticed to have acquired the adult colouring was on Day 79.

Nails were present at birth. The toes began to separate from Day 7 onwards, the outermost toes of the fore- and hindfeet separating first. By Day 10 the toes of all pups were unfused. The hindlegs were large and ungainly from Day 12, but by Day 22 they once more looked in proportion to the body.

By Day 8 the eye slits were dark and very noticeable. The eyes of most pups began opening on Day 14 and all had eyes fully open by Day 17. However, in one litter the pups' eyes only began opening on Day 17 and were fully open on Day 22.

The ear pinnae, which were fleshy and folded at birth, unfolded on Days 5–7. Pups began responding to sound on Day 15, with all pups' ears being open by Day 17.

Incisors became visible as early as Day 9 in one litter, but were erupted by Day 13 in all pups.

Mammae became apparent in young females on Day 10. A female gave birth to a litter on Day 105: subtracting 21 days gestation, gives the age of successful mating of this female as 84 days. The first pup with scrotal testes was recorded on Day 53. The first successful mating of a male pup, which had been housed with females from birth, took place at 63 days of age. This suggests sexual maturity at 60–90 days. The earliest recorded age at breeding of 84 days for female *G. p. exilis* is considerably greater than ages recorded for other species in southern Africa. Brooks (1974) found the mean age at reproductive maturity to be 65 days in female *Rhabdomys pumilio*. Baker & Meester (1977) found that female *Praomys natalensis* can mate successfully from 54 days, and *Mus minutoides* is reproductively active at 42 days (Willan & Meester 1978).

Behavioural development

Behavioural development has been seperated into the four natural periods described by Williams & Scott (1953) for house mice, and adopted generally (Brooks 1974; Baker & Meester 1977; Willan & Meester 1978; Brooks & Htun 1980; Panagis & Nel 1981). These four periods are: neonatal, transitional, socialization and juvenile period.

The neonatal period is characterized mainly by physical development, with little development of behavioural patterns taking place (Figure 8) (Williams & Scott 1953). In *G. p. exilis* pups, it extends from birth to Day 6. At birth the pups exhibited little movement except for a feeble crawling action and were unable to right themselves. They emitted faint squeaking noises. Dempster & Perrin (in press) recorded ultrasounds (50–60 kHz) made by *G. vallinus* and *G. setzeri* pups. From Day 3 onwards, the young crawled actively when removed from the nest, still dragging their

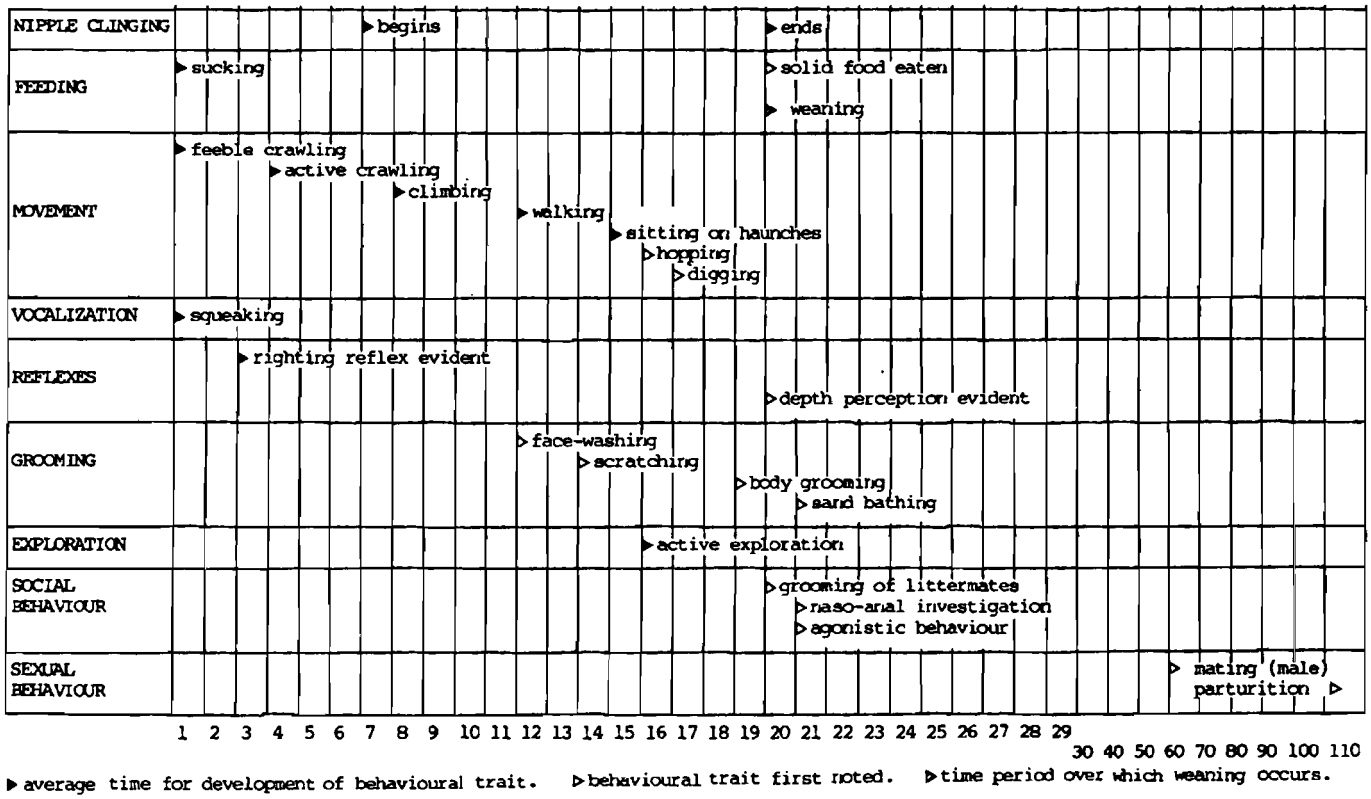

Figure 8 Behavioural development of laboratory-reared *G. p. exilis* pups.

bodies on the ground. At an average age of three days the pups could right themselves. On Day 5 the grey tinge preceding hair growth was visible and by Day 6 the ear pinnae were free. Suckling occurred throughout the neonatal period. No behavioural patterns developed during this period that were not present at birth, except for the appearance of 'nipple-clinging' in some pups, although most pups first exhibited this behaviour in the transition period. This may not have been true nipple-clinging, but rather a consequence of disturbance of suckling females.

The transition period includes the development of body fur, responding to audible sound, walking and running (Williams & Scott 1953) and ends just before the eyes open. It extends from Day 7 to Day 13 in *G. p. exilis* pups. Suckling continued during this period, and the average time for the appearance of 'nipple-clinging' behaviour, which was present throughout this period, was Day 7. Stutterheim & Skinner (1973) and Dempster & Perrin (1989) state that nipple-clinging does not occur in *G. p. paeba*. Their statement may have been prompted by the fact that nipple-clinging is not evident at birth and that *G. p. paeba* mouth-carries as well as nipple-clings, as does *Tatera brantsii* (Meester & Hallett 1970). However, it is likely that what was observed in this study was not true nipple-clinging but reaction to disturbance.

Several behavioural developments, notably walking and grooming, accompanied the physical changes which occurred during this period. Climbing developed before walking and was common on Day 8. The average time for the development of walking was Day 12. The first grooming behaviour in the form of face-washing occurred as early as Day 12, although pups frequently overbalanced while attempting to wash. At first, the fore-paws were passed over the muzzle; as this behaviour became more developed (during the socialization period), the fore-paws were licked and passed over the head and the face. Hearing did not develop during the transition period in *G. p. exilis*, the average time for response to sound being Day 16. However, the boundary between the transition and socialization period could be regarded as the time when eyes begin to open (Day 14), or the time when they are fully open (Day 17). The former definition was arbitrarily used in this study.

The socialization period begins with the opening of the eyes and ends with weaning. During this period exploratory behaviour increases and social interactions with litter mates occur (Williams & Scott 1953). It began on Day 14 in *G. p. exilis* and ended on Day 30, when weaning was finally completed. Most pups' eyes began to open on Day 14 and were fully open on Day 17. Depth perception was noted first on Day 20. By Day 16, most pups were actively exploring their surroundings. On Day 14, pups could sit on their haunches without falling over and on Day 16 hopping was observed for the first time. Hopping appears to be the most common method of locomotion in *G. p. exilis* when moving long distances, as evidenced by tracks on the study grid. During this period face-washing became more accomplished, and body grooming was noted for the first time on Day 19. Scratching of the head and body with the hind-toes was first noted on Day 14. Sandbathing, as described by Stutterheim & Skinner (1973), was seen for the first time on Day 20. Digging was observed on Day 17. Social interactions with litter mates included grooming of litter mates, first observed on Day 19, and naso-anal investigations of each other (Day 20). The first agonistic behaviour was seen

on Day 21. Two pups 'lunged' vigorously at each other's faces, with much squeaking, but no wounds were inflicted.

The determination of the time of weaning presents difficulties, as suckling does not stop abruptly, but gradually lessens and eventually ceases altogether. Baker & Meester (1977) defined weaning in *Praomys natalensis* as the time when solid food was first eaten; however, some suckling was observed subsequent to that. Weaning was observed to occur over a period of 12 days in *Desmodillus auricularis* (Nel & Stutterheim 1973). *G. p. exilis* pups were seen to hold empty seed husks and scraps of paper in their forepaws on Day 19, but definite ingestion of solid food was not observed until Day 20. This was regarded as the beginning of weaning. The mass loss which the pups underwent on Days 20 and 21 (see Figure 1) appears to be associated with weaning. 'Nipple-clinging', which had gradually been lessening, was observed for the last time on Day 20. Suckling became less frequent before solid food was eaten, but nevertheless continued after Day 20. Infrequent suckling was observed until Day 30, which marked the end of weaning.

The juvenile period is characterized by initiation of some adult behaviour patterns, with the exception of sexual and parental behaviour (Williams & Scott 1953). It begins on day 30 in *G. paeba* and ends with the attainment of sexual maturity. The end of this period is difficult to establish with the limited data available, but it may occur as early as Day 53, when the first male with scrotal testes was observed. The first successful mating (i.e. resulting in a litter) of a male pup occurred on Day 63. Males appear to reach sexual maturity before females.

A between-species comparison of developmental characteristics (Table 1) shows that *G. p. exilis* pups develop slowly compared with the other species, with the exception of *Desmodillus auricularis*. The slower development of *Gerbillurus* species may be due to the fact that they bear young in protected underground nests. Nel & Stutterheim (1973) also refer to the survival value of underground nests.

The growth rate of *G. p. exilis*, up to 90 days, was 0,3 g/day, while that of *G. p. paeba* was 0,4 g/day (Dempster & Perrin 1989). The slower growth rate of *G. p. exilis* is unlikely to be the reason for its slower development (Table 1), since Neal (1990) found that post-natal growth rate of neonates was independent of development rate from conception, both in altricial and precocial species. Although the growth rates of *G. vallinus* (0,4g/day) and that of *G. setzeri* (0,7g/day) differed, the rate of physical and behavioural development was similar in the two species (Dempster & Perrin, in press).

Conclusions

G. p. exilis bears small litters of altricial young. Growth is comparatively slow. Although most physical attributes are present 20 days after birth, it takes 60–90 days to reach sexual maturity and 102 days to reach mean adult field mass. Of the physical measurements, mass is the most accurate, with head/body length being the most difficult to measure accurately. Generally, the Alexandria dunefield subspecies *G. p. exilis* appears to be larger than *G. p. paeba* specimens mentioned by Smithers (1971) or De Graaff (1981). Although captive and wild individuals appear to be similar in mass at weaning, wild individuals experience large fluctuations in mass after weaning, whereas the mass values of captive gerbils are much more constant, possibly as a result of their more uniform environmental conditions.

Physical and behavioural development are also slow, with weaning beginning at three weeks and lasting approximately 10 days. The most important periods in the development of gerbil pups are: (i) approximately Day 12, when the motor abilities become well developed and walking, running, sitting up, grooming and scratching behaviour all appear within a few days and (ii) the opening of the eyes on Day 17, after which exploration and social behaviour follow rapidly. Meester (1960) found two similar 'critical periods' in the development of multimammate mice and Brooks & Htun (1980) note that behavioural development in *Rattus exulans* proceeds rapidly once the eyes have opened.

Males seem to reach sexual maturity before females, both sexes taking considerably longer than many other *Gerbillurus* species to reach maturity. Despite relatively slow sexual development, *G. p. exilis* females can produce up to three litters per breeding season (Ascaray 1986).

Acknowledgements

We thank Dr R. Randall, and two referees for constructive criticism. This study was made possible by funds from the

Table 1 Comparison of development in seven rodent species

	Mean age of appearance (days)						
	1	2	3	4	5	6	7
Developmental character	*Mus minutoides*	*Thamnomys dolichurus*	*Praomys natalensis*	*Rhabdomys pumilio*	*Desmodillus auricularis*	*Gerbillurus paeba paeba*	*Gerbillurus paeba exilis*
Walking	8–9	7	9	8	15	7–14	12
Eyes open	12	10	15	7	22	–	17
Beginning of weaning	–	19	20	10	21	15	20
End of weaning	17	26	–	16	33	30	30

Sources: 1. Willan & Meester 1978; 2. Panagis & Nel 1981; 3. Baker & Meester 1977; 4. Brookes 1974; 5. Nel & Stutterheim 1973; 6. Dempster & Perrin 1989; 7. This study.

Department of Environmental Affairs and Fisheries and a C.S.I.R. bursary.

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