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Breeding Biology and Postnatal Development of the African Dwarf Mouse

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Breeding biology and postnatal development are discussed of 27 litters of the African dwarf mouse *Mus minutoides* A. Smith, 1834. The gestation period was 19 days or less, and mean litter size was 4.0 (1—7). The species appears to be relatively social, but males displayed greater intraspecific tolerance than females. At birth young weighed approximately 0.8 g, and were naked and helpless. By 14 days all sensory ablilities had developed and motor abilities were almost perfect. Weaning occurred at 17 days. Sexual activity commenced on day 32, the first successful mating was at approximately 42 days, and first parturition on day 62. Comparison of *M. minutoides* and *M. musculus* shows that whereas some aspects of development are delayed in *minutoides* compared to *musculus* (*e.g.* first appearance of adult behaviour patterns) others (*e.g.* weaning) occur sooner. Development of *M. musculoides* is similar to that of *minutoides*, although weaning occurs sooner in *minutoides* (17 days) than in *musculoides* (24 days). The available evidence suggests that retention of species separation for *minutoides* and *musculoides* is justified. Reproductive strategies of *M. minutoides*, *Praomys natalensis* and *Aethomys chrysophilus* are discussed.

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1. INTRODUCTION

The African dwarf mouse *Mus minutoides* A. Smith, 1834 is the smallest southern African rodent, with an approximate adult mass of 7.5 g, head and body length 70 mm, and greatest skull length 18 mm. Dorsal colour is brownish-buffy, the flanks are orange-buffy, and the ventral surface is pure white. Among southern African rodents it is most closely related to the exotic commensal *Mus musculus*, but it differs from this animal in some physical features and in being independent of human surroundings.

Little is known about *M. minutoides*. Distribution is described by Roberts (1951), Ellerman *et al.* (1953) and Davis (1962, p. 62) who states that it is "generally distributed throughout southern Africa and northwards in Savannah to West Africa". Some natural history notes are recorded by Vesey-Fitzgerald (1966), and Jolly (in Kingdon, 1974) records that it breeds freely in captivity. Brief

accounts exist of captive-born litters (Ansell, 1960; Keogh & Cronjé, 1975). Anadu (1976) has recently described the reproduction and postnatal development of *Mus musculoides* Temminck, 1853 from Nigeria, which may be conspecific with *M. minutoides (i.e. M. minutoides musculoides* — Petter & Matthey, 1975) and is at least closely related, although geographically widely separated from southern African *minutoides*.

M. minutoides minutoides A. Smith, 1834 was abundant during 1973/74 in grassland and disturbed farmland at Thornville Junction, near Pietermaritzburg, Natal. This provided the opportunity for a trapping study of this species from which a number of specimens for subsequent laboratory study of reproduction and postnatal development were obtained. In view of the paucity of information on this animal, the information obtained from the study is here presented.

2. MATERIALS AND METHODS

The animals used in the study were captured in *Themeda*-mixed grassland at Thornville Junction, Natal, in a pit trap and in tunnel traps similar to those described by Meester (1970). The pit trap was 30 cm in diameter and 45 cm deep, while the tunnel traps were 3×4×20 cm and could be triggered by a mass of 5 g. The small dimensions of the latter traps apparently excluded larger rodents, since they yielded only *M. minutoides* and the small shrew *Myosorex varius*.

Captured animals were housed in a sunlit room without temperature control (recorded temperatures: maximum ±25°C at 14h00 in January; minimum ±10°C at 06h00 in July). Compatible pairs of *M. minutoides* were maintained in glass-fronted cages (30×30×30 cm or 60×30×30 cm) which had external nest boxes fitted with removable lids to facilitate removal and examination of young. Floor covering was a beach sand-commercial cat sand mixture and dry grass clippings were provided as nesting material. Mouse cubes, millet and water were provided *ad libitum*. *Tenebrio* larvae (six larvae/animal/week), fresh grass seedheads (*Panicum* and millet) and fruit (apple and tomato) were also provided.

Adults and young over 14 days old were etherized prior to examination to facilitate handling without the possibility of escape. Up to that age young were handled without etherizing. Breeding data were recorded and adult behaviour relating to breeding in captivity was observed under red light.

The physical development of 40 young *M. minutoides* representing nine litters was measured at approximately 18h00 every second or third day from birth (day 0) to 21 days and thereafter weekly until an age of 12 weeks. Standard taxonomic measurements were taken as follows: head-body and tail lengths to the nearest 1 mm; hind foot and ear lengths to the nearest 0.5 mm. Young of each litter were weighed together to the nearest 0.1 g and the mean mass recorded. Measuring commenced on day 0 and day 1 in alternate litters so that from the nine litters combined an approximately equal number of records existed for each day. Following Meester (1960) who inferred mass on a particular day from mass on the preceding and following days, smooth curves were drawn from

available data for each litter and missing values extrapolated from the curves. Development of pelage, digits, eyes, ears and incisors was noted. Length of vibrissae was not accurately measured. Physical growth data were interpreted using curves for means, maxima and minima of standard taxonomic measurements and mass, and in terms of instantaneous growth rates, using the formula of Lackey (1967):

$$IGR = \frac{\ln m_2 - \ln m_1}{t_2 - t_1}$$

where ln m_2 and in m_1 are natural logarithms of mean measurements recorded at times t_2 and t_1. The period $t_2 - t_1$ was taken as four days for this study. *IGR* values recorded in Fig. 4 were obtained by reading smooth curves derived from the formula.

Behavioural development of 77 *M. minutoides* from 20 litters was recorded every two or three days from day 0 to day 21 with an approximately equal number of observations for each day. Righting, negative geotaxis, cliff-drop aversion, contact and isolation tests were conducted (Brooks, 1972). Grasp reflex, rooting reflex and horizontal bar tests (Brooks, 1972) were omitted because of the small size of the young. Response was noted when a bright light was directed at the eyes, and when sucking sounds were made 100 mm from the nest. From 21 days to 12 weeks old litters were observed for two 30-minute periods each week.

3. BREEDING IN CAPTIVITY

From 1 June 1973 to 30 September 1974, 27 litters comprising 108 young were obtained from 12 matings. Litter size varied from one to seven with a mean of 4.0. The sex ratio of 49 young from 11 litters was male: female=22:27. This difference is not significant ($\chi^2=0.32$; $0.5<P<0.7$). Mortality of young up to 12 weeks old was 16.6%.

Of the 12 female *Mus minutoides* concerned, six produced one litter each, and six produced 21 litters between them (Table 1). The minimum period separating two litters from the same female was 19 days. Assuming post-partum oestrus, gestation period is probably about 18 to 19 days. However, gestation may be extended in lactating females (Pournelle, 1952) so that the gestation period may be less than suggested. The mean period separating litters in lactating multiparous females was 22.4 days. Periods of 41, 60, 63 and 116 days between litters (Table 1) were not included in this calculation as they obviously reflected prolonged anoestrus.

Three laboratory bred females produced litters, the first young being born at 62, 110 and 117 days respectively. Mean litter size for the six litters produced by these three females was 4.3 which does not differ significantly from that for the remaining 21 litters (3.7) ($\chi^2=0.45$; $0.8<P<0.9$).

4. BREEDING BEHAVIOUR

Confined *Mus minutoides* females were more aggressive than males, but compatability depended on the circumstances of introduction. Introducing a male to a resident female usually led to attacks on the male. Agonism ceased within 24 hours in most cases but some males were killed by females. Introducing a female to a resident male was usually followed by mutually amicable behaviour within a few minutes, and continued for as long as the pair was kept together.

Mating behaviour was observed on one occasion although intromission was apparently not achieved. Attempted copulation was preceded by intermittent grooming of the female by the male for approximately 15 minutes. Courtship consisted of nuzzling the neck and face of the female while she sat in a hunched position averting her face, apparently

Table 1

Reproductive capacity of female *Mus minutoides* breeding in captivity from June 1973 to September 1974.

Number of females	Litters/ female	Total litters	Total young	Mean litter size	Intervals between litters
6	1	6	30	5.0	
2	2	4	18	4.5	26, (60)
1	3	3	9	3.0	(116), 23
2	4	8	28	3.5	(63), 19, 21, (41), 21, 19
1	6	6	23	3.8	23, 25, 23, 22, 24
12	$\bar{x}$=2.3	27	108	$\bar{x}$=4.0	$\bar{x}$=22.4 *

* Intervals (in brackets) involving extended anoestrus were not taken into account in calculating mean interval between litters.

to avoid contact. Attempts to mount during this period were prevented by the female kicking out with her hind feet. The male was able to mount briefly (1—3 seconds) seven times during an hour's observation, but at no stage did the female adopt the lordosis posture. Except for warding off the male in the initial stages of courtship the female was unaggressive throughout the encounter.

Female *M. minutoides* did not defend the nest until two or three days before parturition. At that stage some females were aggressive when the nest box was opened, vocalizing and biting in defence of the nest. Most females defended the nest when young were present and it was frequently difficult to evict the mother. The male always occupied the nest with the female and young but usually left when the nest box was opened. On one occasion the male assumed the defensive role.

The female occasionally removed young from the disturbed nest to the living area of the cage. Young were carried in the mouth, by only the female, and were deposited under any available cover, in a corner of the living area or next to a feeding dish. Once, after the young had been placed in a corner, the female dug a depression in the sandy floor-covering, placed the young in it, and kicked sand over them until they were partially buried. Whenever young had been carried out of the nest they were returned to it within 30 minutes and usually within 10 minutes. Once, when two litters were present in the cage (26 days and three days old), the female dragged one of the older young (weighing over 50% of her own mass) to the nest. Once a litter of 11 days old was not carried from the nest but driven out by the female. Young at that stage were still blind but highly mobile and capable of returning unassisted to the nest. Young were usually washed by the mother immediately on their return to the nest. Young which the mother removed to the living area were not washed until she returned them to the nest.

Family groups, each consisting of male, female and more than one litter, were occasionally housed in single 60×30×30 cm cages. Parents and siblings (up to eight young from three litters born 19 and 21 days apart) occupied a single nest without apparent ill effects or agonism. In nature, parental *M. minutoides* may not tolerate an earlier litter in the presence of a younger one. Circumstantial evidence of group dispersal was obtained by simultaneously pit-trapping four practically identical *M. minutoides*, judged from their measurements to be about three weeks old. This implies that dispersal may occur at approximately this stage, so that a litter leaves the parental nest at about the time the next is born.

5. POSTNATAL DEVELOPMENT

5.1. Mass and Linear Increase

Growth data are presented in the manner of Kästle (1952). Least deviation from the mean occurred in hind foot length (Fig. 1) — at 21 days the minimum and maximum were respectively 4% lower and 6% higher than the mean. Greatest deviation occurred in mass (Fig. 2), minimum and maximum deviating by 38% and 15% respectively at 21 days. At 21 days, minimum values for mass, head-body, tail and ear length deviated more greatly from the mean than did maximum values, possibly because some young were stunted.

Mass curves for two litters with markedly different rates of increase are shown in Fig. 3. Litter *A* comprised a male and a female, and litter

B three females. Both litters displayed irregular mass increase, as did all other litters weighed. Weaning (point 1) in litter *B* appears to have been more rapid than in litter *A*. During weaning, few litters decreased in mass, but none maintained the earlier high levels of mass increase. The female of litter *A* produced her own first litter at 62 days (point 4). Assuming gestation period to be approximately 19 days, sexual activity probably commenced at the break in the curve at six weeks (point 3). At seven weeks the female was observed to be pregnant and was not weighed again until nine weeks, after parturition. Thus the values for litter *A* at seven and eight weeks represent the mass of the male only and are not strictly comparable with those of litter *B*.

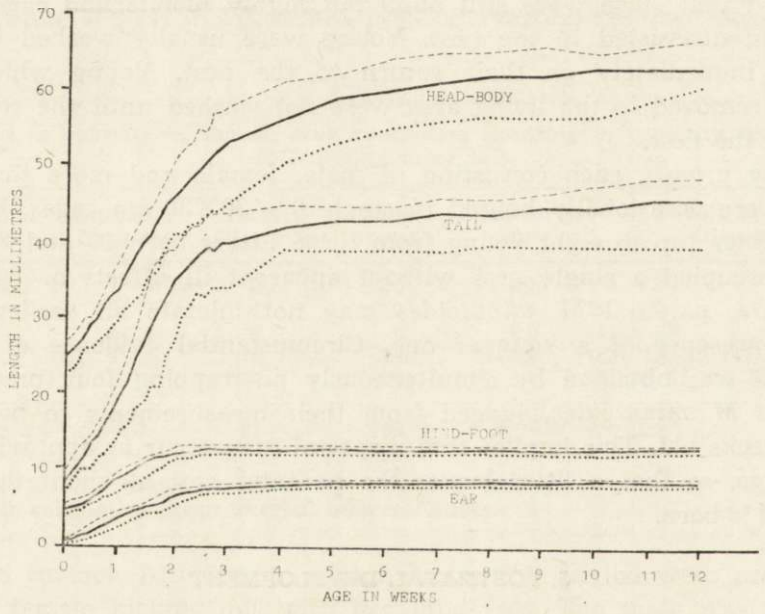

Fig. 1. Postnatal development of *Mus minutoides* from birth to 12 weeks old: minimum, maximum and mean values of linear measurements plotted against time (dotted curve represents minimum; broken curve maximum; solid curve the mean).

Instantaneous growth rate (*IGR*) values (Fig. 4) on day 2 were highest for ear length (0.32) and lowest for head-body length (0.047). Hind foot length most rapidly approached adult value, and by day 26 *IGR* was 0.001. The adaptive significance of rapid development of the hind feet (and presumably of the hands, although their development was not measured) may lie in the need for well-developed locomotor ability at an early age as a predator escape device. In *Dipodomus stephensi* and

Aethomys crysophilus, for which *IGR's* have been calculated by Lackey (1967) and Brooks (1972) respectively, hind foot length also approaches adult length more rapidly than do other dimensions. On day 18 *IGR* for mass was 0.026, and from then until the end of the 56-day period mass maintained the highest *IGR*. Whereas *IGR* for mass was 0.0025 at 56 days, *IGR's* for head-body and tail were 0.0014 and 0.0018 respectively. For hind foot and ear values, *IGR* had fallen to 0.001 by 26 days and 50 days respectively.

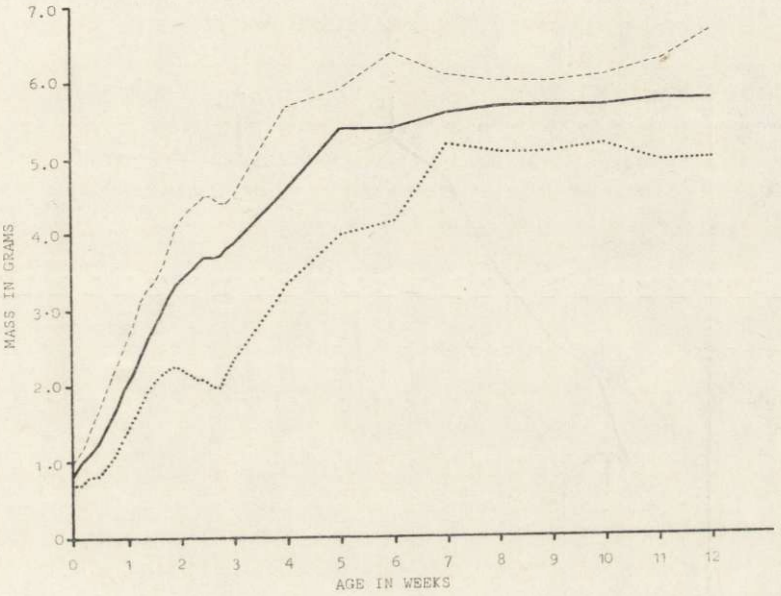

Fig. 2. Postnatal development of *Mus minutoides* from birth to 12 weeks old: minimum, maximum and mean mass plotted against time (dotted curve represents minimum; broken curve maximum; solid curve the mean).

5.2. Physical Appearance

The physical appearance of adult *Mus minutoides* is: brownish-buffy on the top of the face, head, neck and back; pure white below, from the upper lips to the forelegs, lower parts of the flanks and insides of the thighs; orange-buffy (in varying degrees) along the sharply defined border of the white area; tail brown above and buffy below; hands and feet buffy-white (Roberts, 1951, p. 463).

The times of appearance of physical characters reported here (Fig. 5) are not fully in agreement with previous accounts (Ansell, 1960;

Keogh & Cronjé, 1975). However, Ansell reared only one litter and Keogh and Cronjé did not handle the young, so that differences observed may be due to less detailed observation in the previous studies. In the present study physical appearance developed as follows:

Young were born bright pink with translucent skin through which the abdominal viscera and cranial sutures were visible. Vibrissae were approximately 1 mm in lenght at birth and by day 21 measured approximately 15 mm. Greyish pigmentation appeared in the interscapular region on day three or four and by the following day (four or five) the dorsal regions of the head, body and tail were pigmented. By day five

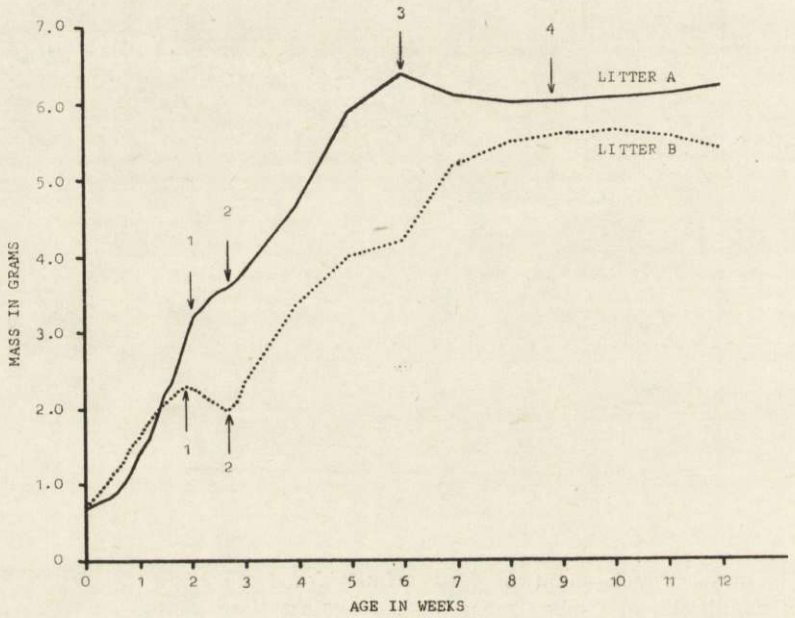

Fig. 3. Mass curves for two extreme litters of *Mus minutoides* from birth to 12 weeks old to illustrate differential mass increase in different litters (1 indicates onset of weaning; 2 improved utilization of solid food; 3 sexual activity; 4 birth of first litter).

or six pigmentation was darker and extended down the flanks. The cranial sutures were obscured by this time but the viscera remained visible. Unpigmented hairs appeared dorsally on the body on day five or six. By day nine a fine brownish-buffy pelage had appeared dorsally, extending down the flanks, and sparse white hairs had appeared ventrally. The viscera were no longer visible. By day 14 young were complete miniatures of the adults except that the orange-buffy on the

flanks was almost entirely lacking. Eruption of incisors occurred between days seven and nine, the upper incisors appearing on the day following the lower. The five pairs of mammae (three pairs pectoral, two inguinal) became apparent in females between days 10 and 12. Therefore it was convenient to sex young on day 12, after the mammae had appeared and before the ventral pelage was complete. Claws were lacking at

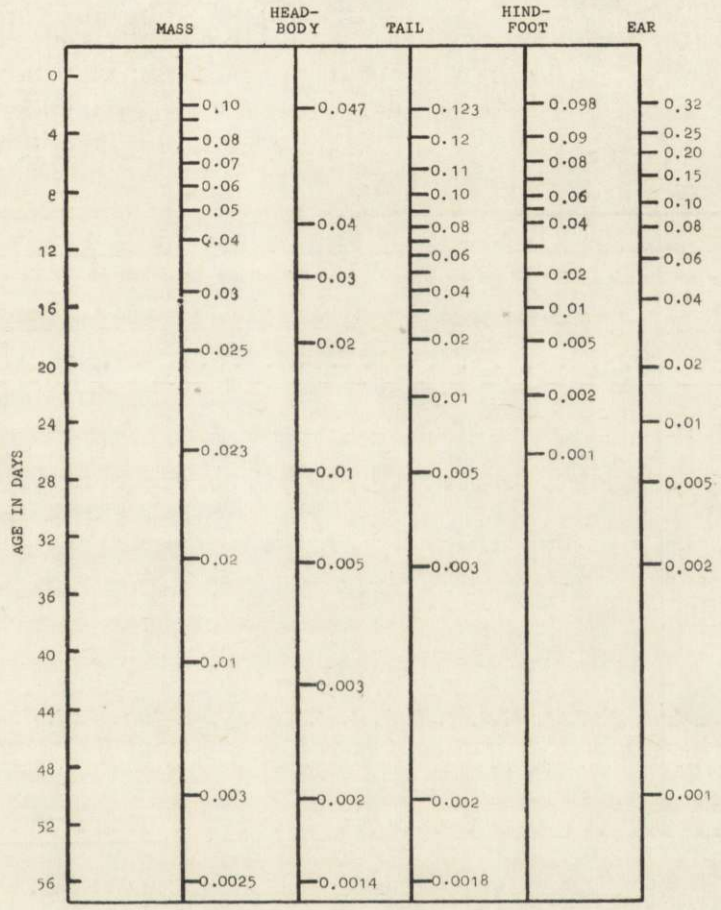

Fig. 4. Instantaneous growth rates of *Mus minutoides* from birth to 56 days old.

birth but were apparent by day four. Toes were at first fused; foretoes were separate by day six or seven and hind toes by day seven or eight. Ear pinnae were fleshy and folded over the meatuses at birth. They unfolded by day three or four remained somewhat fleshy until days eight to 10. The meatuses opened between day 12 and 14. Young were born blind with eyespots visible through the eyelids. The dark

area representing the eye had a lighter spot in the centre until day two when the spot disappeared. Eye-slits appeared between days 10 and 12 and the eyes opened fully between days 12 and 14.

5.3. Behavioural Development

The behavioural development of the laboratory mouse *M. musculus* is divided into natural periods, based on major changes in social relationships, by Williams & Scott (1953). Except as otherwise stipulated the criteria employed by Williams and Scott were used in this study to divide the behavioural development of *M. minutoides* into the following periods: Neonatal period (0—4 days); Transition period

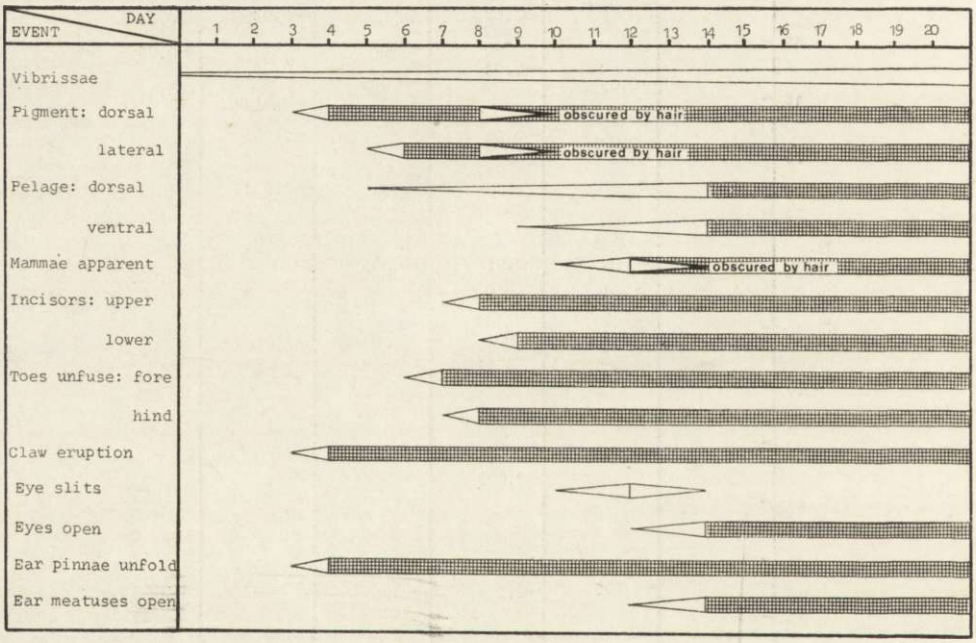

Fig. 5. Physical development of *Mus minutoides* from birth to 21 days old (shaded bars represent fully developed physical characters; unshaded wedges the appearance or disappearance of the character)

(5—11 days); Socialization period (12—17 days); Juvenile period (18—42 days) (Figure 6).

5.3.1. Neonatal period (0—4 days)

The upper limit of the neonatal period was defined as day four, the day preceding the appearance of body hair in over half of the litters

studied. To separate the neonatal and transition periods in *M. musculus* Williams & Scott (1953) used not only the appearance of body hair, but also evidence from a study by Hall & Whiteman (1951, in Williams & Scott, 1953) of hearing ability at five days. In the present study the first apparent response to sound was observed only on day 12, so that this event is not used to mark the end of the neonatal period. However, in their study Williams and Scott found that until day 11 reaction to auditory stimuli was not definite. With this in mind it is possible that *M. minutoides* responded to sound earlier than day 12 but that until then the response was not clearly apparent or recognised.

The most significant features of the neonatal period were that young were almost completely helpless throughout, and behaviour was little more complex by the end of the period than at birth.

Young were blind and the ear meatuses were closed; they responded to neither a bright light shone on the eyelids nor auditory stimuli. When held in the hand they were less restive than when placed in a glass dish, probably due to the hand more effectively simulating the nest environment with its strong thermal and tactile stimuli. It is likely that thermal, tactile and olfactory communication was possible at or soon after birth as in *M. musculus* (Williams & Scott, 1953). Squeaking occurred virtually at random, some litters vocalizing when the mother left the nest, others on her return to it. Lightly pinching the tail or feet elicited loud squeaking.

Young usually lay on the belly or side, but when suckling some lay on their backs. They were unable to move on a flat surface until day three when feeble crawling was possible. However, from birth slight mobility was observed in the nest and by day three young were able to pull themselves about over their littermates. Pinching the tail or feet caused young to fling their bodies around in a violent escape reaction. Even when four days old young were insufficiently mobile to participate successfully in the negative geotaxis test or to avoid falling in the cliff-drop aversion test (Brooks, 1972).

Contact and isolation tests (Brooks, 1972) indicated lack of an exploratory urge. Young placed in contact with one another did not move from the group, but if isolated they would move about (once this became possible at day three) until the group was re-established.

Social behaviour was resticted to feeding from the mother and huddling or pushing against littermates. No agonistic behaviour was observed.

5.3.2. Transition Period (5—11 days)

The lower limit of the transition period was defined by the appearance of body hair at five days, and the upper limit of 11 days by the opening of the eyes on day 12 in more than half the young studied. The transition period was characterized by improved sensory and motor abilities.

Young remained blind with the ear meatuses closed. There was no response to a bright light shone on the eyelid until eye slits appeared on day 10 (in those animals whose eyes were fully open on day 12). Then the head would be averted or the young would move off. There was no apparent response to sound throughout the period. Sniffing the air and littermates was first observed on day seven. Young held in the hand did not attempt to escape until day nine or 10. Squeaking became less frequent toward the end of the period although some litters still squeaked loudly when disturbed. Pinching the tail or feet elicited squeaking until day nine or 10. Thereafter response was directed entirely toward escape.

Righting on a flat surface, following wriggling about on the back and a final torsal twist, became possible on day five. Crawling was still slow at this stage but improved until day seven or eight. On day eight or nine walking commenced, jerky at first, with the legs splayed, but improving rapidly to day 11 when jerky but rapid running was possible. Haunch-sitting was first observed on day six. The negative geotaxis test did not yield positive results, with movement up or down the slope apparently being undertaken at random. By day seven or eight young usually avoided falling in the cliff-drop aversion test.

The contact test indicated lack of an exploratory urge before day eight or nine. After that young still tended to huddle together although occasionally one would break off and wander a short distance before seeking the group again. By day 11 they would run around the observation area, but eventually huddle together after one to two minutes. This movement probably represented escape reaction rather than exploratory urge. When deliberately isolated, young over eight to nine days old would move about at random for up to roughly one minute, then re-establish contact with the group. The mother spent relatively long periods (30 minutes or more) out of the nest. During these periods young remained piled up in the nest in close contact with one another. When the mother was in the nest her young spent most of the time suckling and were seldom observed away from the group. Physical contact between young involved a great deal of jostling for position at the teats, especially when the female returned to the nest.

Face-washing with the hands was first observed at seven days (one

individual) but by day 10 or 11 self-grooming was frequent, consisting of washing the face, ventral body surface, hind limbs, feet and tail. A single young of 11 days old, which had been removed from the nest to be photographed, was observed holding a millet seed in its hands, apparently attempting to dehusk it. Apart from this, ingestive behaviour was limited to suckling. Young usually attempted to escape once locomotor abilities were sufficiently developed. However, one young of 11 days old attempted to bite when cornered.

5.3.3. Socialization Period (12—17 days)

An alternative and possibly preferable name for this period is the Infantile period (Brooks, 1972). The lower limit is at opening of the eyes which occurred in most young on day 12. The upper limit is completion of weaning, taken to be day 17. Young were not observed to suckle after day 16 and the curve for mean mass of young (Fig. 2) indicates that weaning probably occurred on day 17 in most litters. The majority of behavioural changes during this period were related to opening of the eyes and improved locomotor ability. However, young did not leave the nest of their own accord until day 14 or 15 and were seldom observed outside the nest box until day 16, presumably after weaning had commenced.

In most young the eyes opened on day 12 and all had the eyes fully open by day 14. Response to auditory stimuli was first observed on day 12, and consisted simply of starting. Sniffing of the air and littermates was common. Squeaking was much reduced although some young squeaked loudly when captured for measurement.

During this period young developed efficient locomotory abilities. By day 13, when relased on a flat surface, they were difficult to recapture. By day 16 they were able to climb up the sides of the cage in the course of exploratory activities, making use of cracks and other small footholds. All locomotor and postural patterns were accomplished with adult proficiency by the end of the period. Young were highly mobile, although they were seldom observed out of the nest box until day 16.

The contactual urge, still apparently strong at the beginning of this period, seemed to have declined by day 16 to 17. Young spent much time with the parents in the nest but when in the living area no attempt was made to form groups. Littermates were often sniffed, but such contact was normally brief. By the end of the period self-grooming was accomplished with adult efficiency. On day 16 young were first observed to clamber up the side of a feeding dish and enter it to feed on millet. Suckling was not observed after day 16. Frantic attempts

to escape from the hand were made during the first few days but by the end of the period attempts to escape were less frenzied.

5.3.4. Juvenile Period (18—42 days)

The beginning of the juvenile period was the first day after weaning was complete. The end was marked by sexual maturity, shown in this study to occur at 42 days or less (see Postnatal Development: Mass and linear increase). The juvenile period was characterized by behaviour patterns which were largely adult in nature.

Sensory mechanisms appeared unchanged and there was no apparent overreaction to sound. Some juveniles squeaked when captured for measurement, but otherwise no vocalization occurred. No change in posture or locomotion was observed from the previous period except that as juveniles became larger they were better able to reach certain hand — and footholds (*e.g.* a water bottle attached to one wall of the living area) so that climbing ability improved.

In most cases juveniles continued to occupy the nest with the parents, even when a subsequent litter was present (see Breeding Behaviour). However, when sufficient bedding was available some litters moved out of the parental nest and constructed their own in the living area. This occurred late in the juvenile period. Self-grooming was performed in the adult manner as it had been by the end of the previous period. Juveniles fed exclusively on solid matter and were observed drinking from a water bottle soon after weaning. Juveniles initially made vigorous attempts to escape when captured but by day 25—30 their response to capture was more calm. *M. minutoides* bred in captivity rarely attempted to bite. Genital sniffing was occasionally observed in juveniles from 32 days on.

6. DISCUSSION AND CONCLUSIONS

6.1. Reproduction

The reproductive strategy employed by *Mus minutoides* appears to be largely determined by its small size, and is characterized by a short gestation period and relatively low litter size. The relationship between adult mass and gestation period, in which smaller animals have shorter gestation periods, is borne out by that of *M. minutoides* (18 or 19 days). *Praomys natalensis*, with adult mass 60 g to 70 g, has a gestation period of about 23 days (Meester, 1960), and *Aethomys chrysophilus* (adult mass over 100 g) has a 26-day gestation period (Brooks, 1972). However, litter size apparently bears no simple relation to adult mass

Litter size of *M. minutoides* ($\bar{x}$=4.0 for this study) is considerably less than for *P. natalensis* ($\bar{x}$=10.4 — Baker & Meester, 1977), but greater than for *A. chrysophilus* ($\bar{x}$=3.1 — Brooks, 1972). At parturition an average *M. minutoides* litter weighs approximately 43% of adult mass while the figure for *P. natalensis* is approximately 37%. This difference is not significant (χ^2=0.45; p=0.5), but the figure of approximately 11% of adult mass for a litter of *A. chrysophilus* (Brooks, 1972) is significantly different from that of *M. minutoides* (χ^2=18.9; $p<0.001$). Whereas *M. minutoides* and *P. natalensis* are probably both at the limit of their physical reproductive ability, *A. chrysophilus* probably is not. This difference may be explained by the fact that when disturbed *A. chrysophilus* young are dragged by the mother's nipples whereas young of the other two species are carried in the mouth. Meester & Hallett (1970) suggest that nipple-dragging is of high survival value. High survival of *A. chrysophilus* young, in conjunction with reduced litter size and relatively advanced age at weaning (25 days) and sexual maturity (82 days) (Brooks, 1972), probably serve to maintain fairly stable population levels of this species. *M. minutoides* and *P. natalensis*, on the other hand, probably have higher mortality of young, but this is compensated for by greater reproductive potential, evidenced by greater litter size and earlier onset of sexual maturity (*M. minutoides:* 42 days in this study, and *P. natalensis:* 54 days — Baker & Meester, 1977).

6.2. Postnatal Development

Physical and behavioural development of young mammals are, of necessity, closely linked, certain physical developments acting as precursors to behavioural phenomena. In *Mus musculus* (Williams & Scott, 1953) early development is largely physical with no patterns of socialization emerging which are not present at birth. Similarly, young *M. minutoides* almost doubled their weight during the neonatal period (0—4 days), but remained virtually helpless, and socialization was dominated by the thermal, tactile and olfactory stimuli of the nest environment (Fig. 6).

The rapid development of motor abilities during the transition period (5—11 days) culminated in the ability to run fairly efficiently by day 11. However socialization was limited to suckling and huddling with littermates as in the neonatal period. The first appearance of adult behaviour patterns, reported by Williams & Scott (1953) to occur in *M. musculus* during the transition period, were not observed in *M. minutoides*. This may in part reflect the apparent inability of *M. minutoides* to hear until day 12.

The ability to hear on day 12, and opening of the eyes by day 14, together with near-perfect locomotory abilities, led to a rapid change in the patterns of social behaviour during the socialization period (12—17 days). Young left the nest of their own accord and the contactual urge was reduced. Exploration occurred frequently by the end of the period. Weaning occurred relatively early and was complete by day 17. *M. musculus* (Williams & Scott, 1953) and *Aethomys chrysophilus* (Brooks, 1972) suckle until day 25, and *Praomys natalensis* until day 20 (Baker & Meester, 1977). It would seem significant that all these species have a post-partum oestrus and that lactation in each case is shorter than gestation period, so that an earlier litter is weaned

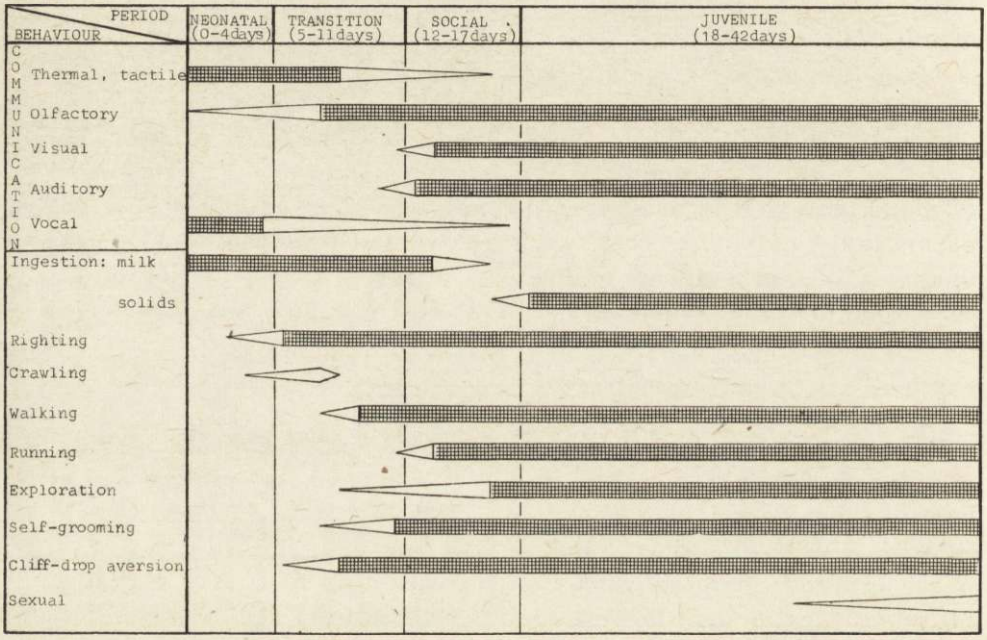

Fig. 6. Behavioural development of *Mus minutoides* from birth to sexual maturity at 42 days old (shaded bars represent fully developed behavioural patterns; unshaded wedges the appearance or disappearance of the behaviour).

before a later one is born. Weaning occurs earlier in *M. minutoides* than in the other three species. This may be related to the high metabolic demands of the unborn young, which weigh 43% of adult mass at parturition. Similarly, a *P. natalensis* litter weighs approximately 37% of adult mass, and suckling is three days shorter than gestation period. On the other hand, weaning in *A. chrysophilus* occurs only a day before

parturition, which may relate to the fact that the unborn litter weighs only approximately 11% of adult mass.

The juvenile period (18—42 days) is characterized by rapid perfection of adult behaviour patterns, and by approximately six weeks old, when sexually mature, it was difficult to distinguish young *M. minutoides* from their parents. This is in general agreement with the other species under discussion here, except that *M. minutoides* more rapidly approaches full adult size.

Table 2

Comparison between reproduction, postnatal development and adult size of *Mus minutoides* and *M. musculoides* (data from Anadu, 1976).

	minutoides	*musculoides*
Number of young per litter at birth	4.0 (1—7)	3.0 (1—5)
Age at sexual maturity	62 days *	70—84 days
Minimum interval between litters	19 days	22 days
Development of pigment	3—4 days	3 days
Appearance of visible hair	5—6 days	6 days
Opening of eyes	12—14 days	14 days
Unfolding of ear flaps	3—4 days	4 days
Opening of meatus	12—14 days	11 days
Loosening of toes : fore	6—7 days	6 days
Loosening of toes: hind	7—8 days	
Eruption of claws	4 days	5 days
Eruption of incisors	7—9 days	8—10 days
Mammae visible	10—12 days	8 days
Age at weaning	17 days	24 days
Mass at birth	0.8 g	0.8 g
Adult mass	7.45 g	6.0 g (at 60 days)
Head-boody length at birth	25.0 mm	26 0 mm
Adult head-body length	69.5 mm	63.3 mm (at 60 days)
Tail length at birth	9.0 mm	8.0 mm
Adult tail length	50.1 mm	41.1 mm (at 30 days)
Hind foot length at birth	4.6 mm	—
Adult hind foot length	13.2 mm	13.0 mm (at 30 days)
Ear length at birth	0.8 mm	3.0 mm
Adult ear length	9.5 mm	9.0 mm (at 50 days)

* Age at first birth in captivity.

A comparison between postnatal development in *Mus minutoides* and *Mus musculoides* is of some interest. Anadu (1976) describes morphological development and reproductive patterns in *musculoides*, and some interesting similarities and differences emerge (Table 2). *M. minutoides* appears to be slightly the larger and heavier form, with tail slightly longer in proportion. It appears to reach sexual maturity earlier, although this comparison is not entirely valid as age at girth of first litter

in *minutoides* (62 days) is compared with a loosely defined »age at sexual maturity« of 70—84 days in *musculoides*. On the other hand, *musculoides* achieves maximum size and mass at 60 days, while even at 84 days *minutoides* has not achieved adult size. Litter size is fractionally larger in *minutoides* although there is a great deal of overlap, the minimum interval between litters is shorter, suggesting a shorter gestation period, and young are weaned a week earlier than in *musculoides*. Development of young shows considerable similarity, but in *minutoides* development of response to sound, loosening of the claws and appearance of nipples are slightly delayed compared to *musculoides* in which, on the other hand, incisors erupt slightly later. Weaning in *musculoides* occurs only at 24 days, as compared with 17 days in *minutoides*.

It is not immediately clear what is the significance of the differences noted. The two forms represent either different species (Anadu, 1976) or different subspecies (Peter & Matthey, 1975). In addition they are geographically widely separated, and although they occupy a broadly similar habitat, *i.e.* grassland savanna, they can be expected to occupy slightly different microhabitats. Too little is known of geographic and ecological variation in reproduction and postnatal development of small mammals to permit reliable taxonomic conclusions on these data, but the available evidence appears to suggest that species separation should be retained for the moment.

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BIOLOGIA ROZRODU I ROZWÓJ POSTNATALNY *MUS MINUTOIDES*

Streszczenie

Obserwowano rozwój postnatalny *Mus minutoides* A. Smith, 1834, na przykładzie 27 miotów, uzyskanych od 12 par hodowanych w laboratorium. Długość ciąży *M. minutoides* trwa około 19 dni. Średnia ilość młodych w miocie wynosi 4 (od 1 do 7) (Tabela 1). Samce są mniej agresywne niż samice i zwykle nie biorą udziału w bronieniu gniazda i młodych. Gatunek wykazuje natomiast względną socjalność.

Wzrost rozmiarów i ciężaru ciała w okresie pourodzeniowym jest szybki, ale niejednostajny. Młode po urodzeniu są gołe i bezbronne, ale po 14 dniach są już w pełni sprawne, choć jeszcze mniejsze od dorosłych. Karmienie trwa do 17 dnia życia. Aktywność płciowa rozpoczyna się w 32 dniu po urodzeniu, pierwsze sku-

teczne kojarzenie przypada na 42 dzień życia, a pierwszy miot urodził się w 62 dniu życia młodej samicy (Ryc. 1—5).

Porównując rozwój pourodzeniowy u *Mus minutoides* i *M. musculus* wykazano, że np. u *M. minutoides* później wykształca się wzorzec behawioru właściwy dorosłym a np. okres karmienia przez matkę trwa krócej u *M. minutoides* niż u *M. musculus* (Tabela 2, Ryc. 6). Dyskutuje się także podobieństwa i różnice w strategii rozrodczej u *M. minutoides, Praomys natalensis* i *Aethomys chrysophilus.*