POST-NATAL DEVELOPMENT OF THE AFRICAN BUSH RAT, *AETHOMYS CHRYSOPHILUS*

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ABSTRACT

This is the first detailed study of the post-natal development of *Aethomys chrysophilus*. Physical measurements were taken from 37 litters consisting of 116 young, and the behaviour of 37 young from 12 litters was observed. The physical development of the young is described and the weight and linear increases analysed. Litter size varied between one and five with an average of 3,1 young per litter for 37 litters. The minimum age of sexual maturity was approximately 82 days, and the shortest interval between litters was 26 days. Major behavioural changes were found at six, 12 and 26 days, and on this basis the post-natal development is divided into Neonatal (0-5 days), Transition (6-11 days), Infantile (12-25 days) and Juvenile (26-82 days) periods. Nipple-clinging dominated the early stages of development and the modifications of the incisors for this purpose are described. The parent-young relationship and mortality of the young are discussed. In addition, the post-natal development of *A. chrysophilus* is compared with that of three other South African murids, namely *Aethomys namaquensis, Thallomys paedulcus* and *Praomys (Mastomys) natalensis*.

This study describes the growth and behavioural development of the African bush rat, *Aethomys chrysophilus*, under controlled laboratory conditions. Although previous data on the post-natal development of *A. chrysophilus* are lacking, developmental studies have been carried out on *A. namaquensis* by Meester (1958) and Meester and Hallett (1970).

PROCEDURE

The colony of partly-inbred (third generation) *A. chrysophilus* was derived from specimens trapped at Tshipise, N. Transvaal in May 1968, and maintained at the Institute for Nutritional Diseases Section of the Medical Research Council in Pretoria. The animals were kept in a constant environment room under controlled conditions of light (0600–1800 h), temperature (± 25°C) and humidity (50% to 60%). They were housed in 44 x 25 x 22 cm cages (plastic base with steel-mesh top), with crushed mealie cob on the cage floor. The animals were fed standard mouse pellets, and water was provided *ad libitum*.

Young were removed from the nipples for measurement and observation by closing the nostrils with the fingers. Standard taxonomic measurements were taken on the day of birth, then daily for 28 days and thereafter at weekly intervals till 20 weeks. In the text the "day of birth" may be referred to as "Day 0", the "first day" after birth as "Day 1", and so on. Weights for the 0 to 28 day period were read to 0,1 g, while those from five to 20 weeks were taken to the nearest gram. Head-body lengths were grouped in 10 mm classes, the tail (anus to tail-tip) was taken to the nearest millimetre, while both the hind foot and ear were read to 0,5 mm.

Growth data are presented in four ways (i) growth tables; (ii) growth curves; (iii) percentages of adult size: determined from eight male and eight female laboratory-bred adults more than one year

old; (iv) instantaneous growth rates (IGR): calculated as by Lackey (1967) using the formula $IGR = \frac{Ln\ m_2 - Ln\ m_1}{t_2 - t_1}$ where Ln m_2 and Ln m_1 are natural logarithms of the measurements taken at times t_2 and t_1. In the present study $t_2 - t_1$ was equal to four days. Smooth curves constructed using these instantaneous growth rate values were then read to give the IGR at any given age (Fig. 3).

The technique adopted in studying the behavioural development of the young was experimental rather than observational. Experimental procedures used to determine normal behaviour patterns for a particular environment (e.g. laboratory cage) which involve handling, have been criticised by Bolles and Woods (1964) on the grounds that subsequent behaviour may be affected. However, in the present study frequent handling for measurement purposes was unavoidable, and the nipple-clinging behaviour of the young made the experimental approach more suitable. Daily observations were made from birth until the young were separated from the adults, usually at about four weeks of age.

Behavioural observations were carried out daily between 0800 and 1800 h on 37 young from twelve litters. Apart from 'cage' observations, the animals were placed in a 16 x 16 x 6 cm cardboard box and observed for ten minutes each day from birth to 21 days. Additional information was derived from the tests described below, which, unless otherwise indicated, were carried out on a flat polished wood surface.

(I) Righting: Young were placed on their backs, and the mode and speed of righting was noted.

(II) Grasp reflex: The ventral surfaces of both fore and hind feet were stimulated with a blunt instrument. The strength of grasp was recorded.

(III) Rooting reflex: The sides of the face were stimulated with the thumb and index finger. A positive response was recorded when young pushed forward in a rooting movement.

(IV) Horizontal bar test: Young were placed on a horizontal aluminium bar, and their agility used as an indicator of muscular co-ordination.

(V) Negative geotaxis: Young were placed facing down a slope of 45°. Turning and moving up the slope indicated the presence of negative geotaxis.

(VI) Cliff-drop aversion: Young were placed on the edge of a table top with their fore feet over the edge. Aversion to the cliff-drop was shown by the young turning and moving away from the edge.

(VII) Contact test: All young from one litter were placed in a group and observed for 60 seconds. Breaking from the group indicated an exploratory urge.

(VIII) Isolation test: Littermates were placed 10 cm apart and observed for 60 seconds. Vocalisation, posture and locomotory movements were noted.

RESULTS

LITTER SIZE AND GESTATION PERIOD

Litter size varied between one and five with an average of 3,1 young per litter (data from 37 litters), which was similar to the figure obtained for *A. namaquensis* by Meester and Hallett (1970) of four young per litter. Sex ratio at birth taken from 116 young was 56 ♂ : 60 ♀. This difference is not significant ($p = 0{,}14$), so that a 1:1 sex ratio can be assumed.

Lactating females produced litters on average every 28,8 days, the shortest interval between births being 26 days. But since gestation may be lengthened if the female is lactating (Pournelle, 1952), the latter figure only approximates the minimum gestation period.

The mean age at which 16 females produced their first litters was 138 days, with a range of 108 to 187 days. The minimum age of sexual maturity, allowing for a 26 day gestation period, was therefore approximately 82 days. *A. chrysophilus* bred throughout the year in the controlled conditions of the laboratory, with no marked peaks of breeding activity.

MORPHOLOGICAL DEVELOPMENT

The physical development of *A. chrysophilus* described here is in general agreement with the development of *A. namaquensis* described by Meester (1958) and Meester & Hallett (1970); any minor differences may result from the small samples used in their investigations.

Roberts (1951) described *A. chrysophilus* as a medium to large rat with long broad ears and a long scaly tail. The same author described the colouration as " . . . upper parts bright reddish-fawn, strongly sprinkled with black hairs; the cheeks and sides being rather paler, the dark hairs being less numerous and of a browner tint; the whole of the underparts, including the feet and hands, almost pure white; the colour of the upper and lower sides being clearly defined."

PHYSICAL APPEARANCE

(a) Hair proliferation: At birth the dorsal surface of the body showed marked grey-black pigmentation, with a zone of fainter pigmentation extending down the mid-dorsal line from the forehead to the tail base. These areas were covered by short black hairs about 1 mm in length, while longer buff-coloured hairs (± 2 mm) were present along the sides of the body. Vibrissae about 6 mm long were present on the snout.

The ventral body surface lacked pigmentation and was naked, and the viscera were visible through the pink translucent skin. The ears and tail were hairless.

A buffy tinge developed in the weakly pigmented 'posterior head and neck region' on the first day, and joined with the lateral buffy band present from birth. The buff colour spread inwards and backwards into the area of black hairs, so that by the third day the general appearance of the dorsal surface was blackish-brown (2 – 3 mm long). However, the mid-dorsal band was still more black than bluff, and the predominantly black areas on the forehead and near the base of the back were still evident. The sides of the body were mainly buff-coloured.

Finely distributed white hairs appeared on the belly on Day 1. By the seventh day the ventral surface had a dense cover of white hairs, except for the genital region where the cover was sparse. Also by this age, a patch of black hair had developed in front of the eyes, and buff-coloured hair had appeared on the posterior border of the ears.

The dorsal surface was a fairly uniform blackish-brown by Day 18, with hair length approximately 5 mm. The underside was greyish-white, grading to white in the genital region. At 28 days the body colouration was similar to, but duller than, that of the adult.

(b) Toes: The appendages were fleshy at birth and possessed claws less than 1 mm long. Toes of both fore and hind feet were fused, but were all free by Day 4.

(c) Eyes: The eyes were closed at birth, but could be seen clearly beneath the eyelids which were fused. Eye slits appeared between Days 9 and 12. The eyes opened fully between Days 11 and 14, after an average time lapse of two days from the slit condition.

(d) Ears: At birth, the ear pinnae were fleshy and, although never attached to the skin of the face, were folded down over the external auditory openings in about 50% of the young. In most cases they unfolded on the first day, the latest erection occurring on Day 2.

(e) Incisors: Both upper and lower incisors were erupted at birth. Their modification for nipple-clinging is described later.

WEIGHT AND LINEAR INCREASE

The summarized data for increase in weight and linear measurements from birth to 20 weeks are given absolutely and as percentages of adult values in Table 1. These increases, expressed as percentages of adult values, are plotted as growth curves in Fig. 2. Fig. 3 presents the instantaneous growth rate values read from smooth curves as described by Lackey (1967).

Young averaged 4,1 g at birth, and the head-body measured approximately 42 mm. Average lengths (mm) of tail, hind foot and ear were 28,0; 10,6 and 4,1 respectively.

Average measurements from 16 adults were as follows: weight, 117 g; head-body length, 145 mm; tail length, 173 mm; hind foot length, 30 mm; ear length, 24 mm.

TABLE 1

AVERAGE WEIGHT AND LINEAR MEASUREMENTS OF *A. chrysophilus* FROM BIRTH TO 20 WEEKS (PERCENTAGES OF ADULT VALUES IN PARENTHESES)

Age	*Weight (g)*	*Head-body (mm)*	*Tail (mm)*	*Hind foot (mm)*	*Ear (mm)*
Birth	4,1 (3,5)	42 (29,0)	28 (16,2)	10,6 (35,3)	4,1 (17,0)
1 week	7,9 (6,8)	58 (39,8)	50 (28,9)	15,4 (51,3)	7,6 (31,7)
2 weeks	12,8 (10,9)	72 (49,7)	78 (45,1)	20,4 (68,0)	13,9 (57,9)
3 weeks	19,6 (16,8)	86 (59,3)	103 (59,5)	24,0 (80,0)	18,4 (76,7)
4 weeks	26,7 (22,8)	97 (66,9)	115 (66,5)	26,4 (88,0)	20,3 (84,6)
5 weeks	34,0 (29,1)	103 (71,0)	133 (76,9)	27,6 (92,0)	21,1 (87,9)
6 weeks	40,0 (34,1)	112 (77,2)	141 (81,5)	28,5 (95,0)	21,7 (90,4)
7 weeks	44,0 (37,6)	117 (80,7)	151 (87,3)	28,6 (95,3)	21,5 (90,0)
8 weeks	48,0 (40,5)	118 (81,4)	151 (87,3)	28,5 (95,0)	22,1 (92,1)
9 weeks	52,0 (43,9)	122 (84,1)	153 (88,6)	28,9 (96,3)	22,3 (92,9)
10 weeks	54,0 (45,6)	124 (85,5)	157 (90,7)	29,1 (97,0)	22,7 (94,6)
11 weeks	57,0 (48,2)	125 (86,2)	159 (91,9)	29,2 (97,3)	22,6 (94,2)
12 weeks	63,0 (53,3)	128 (88,3)	161 (93,1)	29,2 (97,3)	22,8 (95,0)
13 weeks	62,0 (52,5)	130 (89,7)	162 (93,6)	29,3 (97,7)	23,1 (96,3)
14 weeks	68,0 (57,6)	130 (89,7)	163 (94,2)	29,3 (97,7)	23,4 (97,5)
15 weeks	69,0 (58,5)	132 (91,0)	162 (93,6)	29,3 (97,7)	23,1 (96,3)
16 weeks	71,0 (60,7)	133 (91,7)	163 (94,2)	29,3 (97,7)	23,4 (97,5)
20 weeks	79,0 (67,5)	136 (93,8)	164 (94,8)	29,8 (99,3)	23,4 (97,5)

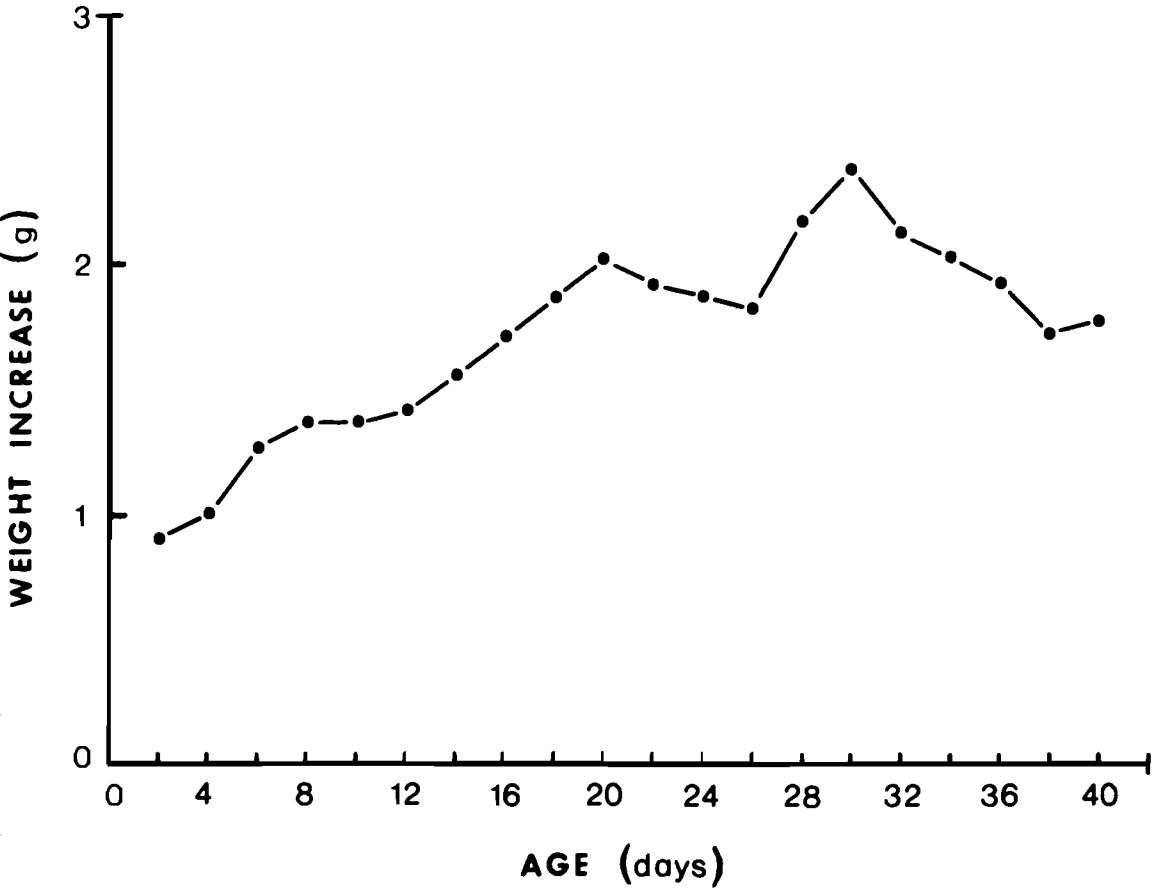

FIGURE 1
Weight increase of young *A. chrysophilus* at two-day intervals from birth to 40 days.
(Values derived from growth curve.)

The weight increases of young *A. chrysophilus* at two-day intervals for the period 0 - 40 days are plotted in Fig. 1. The first break in the curve at Day 20 suggests the onset of weaning. Behavioural changes were evident at this stage in the form of longer periods of detachment from the nipple, perhaps associated with a reduction in maternal milk supply. This increased activity, reduction in maternal milk and probable incomplete adjustment to the utilisation of solid food appears to explain the observed decrease. The sharp weight increase evident at about the 26th day indicates the first efficient use of solid food and the completion of weaning. A similar growth sequence at weaning, also explained by changes in feeding habits and general activity, was observed for the laboratory mouse (MacDowell *et al.* 1930).

At birth, the linear measurements represented greater percentages of the adult values (16,2 – 35,3%) than did weight (3,5%), and they subsequently approached the adult values more rapidly (Fig. 2). However, IGR values for weight were higher throughout (Fig. 3).

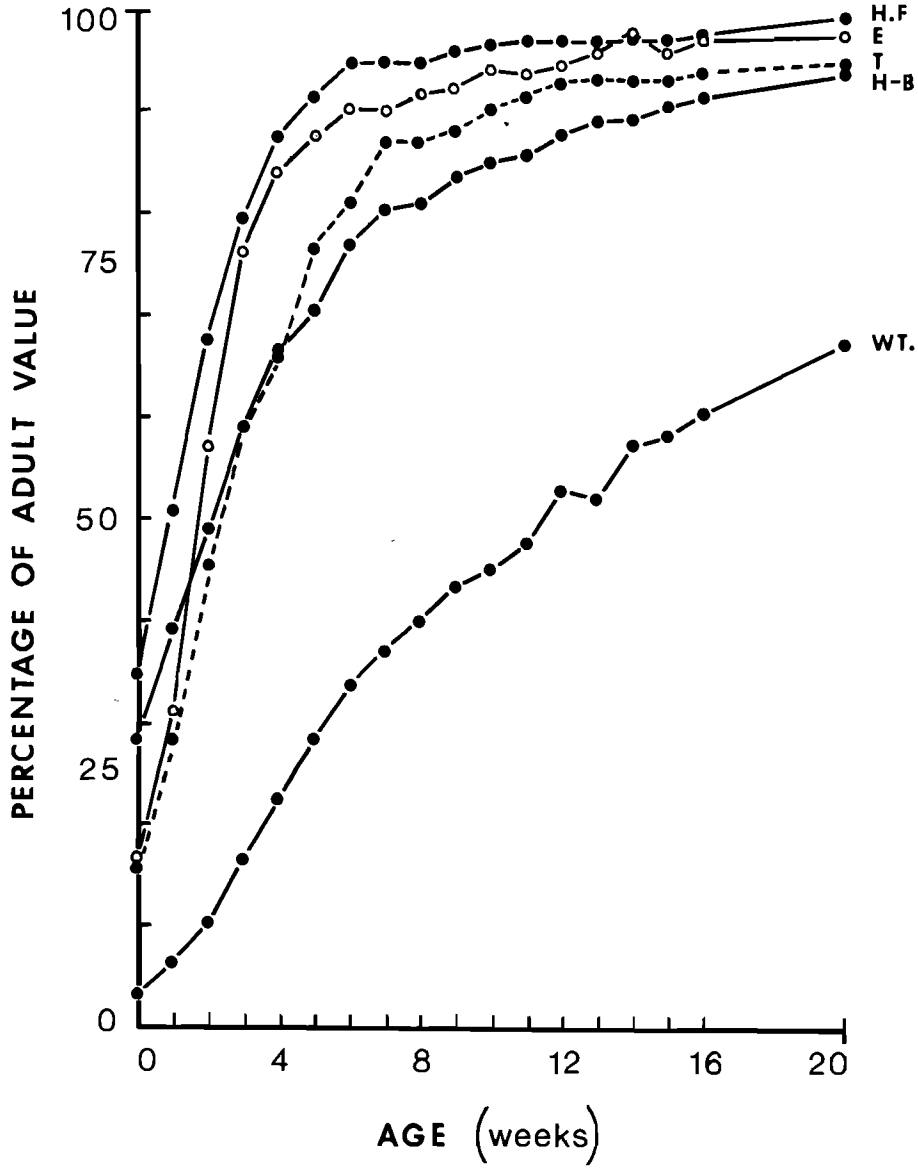

FIGURE 2

Weight and Linear measurement growth curves of *A. chrysophilus* from 0 – 20 weeks, expressed as percentages of adult values. Key to lettering:
WT – weight, H.B. – head-body length, T – tail length, E – ear length, H.F. – hind foot length.

Weight: Young averaged 4,1 g at birth with a range of 3,5 – 4,5 g (Table 1). The IGR of 0,096 in the week following birth was greater than that of any linear measurements (Fig. 3). The IGR value was still relatively high (0,006) at 84 days, when 53,3% of the adult value had been attained (Fig. 2).

Tail Length: Average tail length at birth was 28 mm, ranging from 25 – 30 mm (Table 1). The IGR attained in the first days following birth (Fig. 3) was higher than that of any other linear measurement, and a value of 0,030 was recorded at 21 days. Not until the 34th day had 75% of adult size been attained.

Ear Length: Ear length measured 4,0 – 4,5 mm at birth, with an average of 4,1 mm (Table 1). Growth was extremely rapid and in the first 21 days after birth the ear increased from 17% to 76,7% of adult ear length. In this period the IGR of 0,090 had dropped to 0,020 (Fig. 3).

Hind Foot Length: At birth the hind foot averaged 10,6 mm with a range of 10,0 – 11,5 mm (Table 1). The maximum IGR of 0,055 reached in the first week dropped to 0,016 by Day 21, when 80% of adult hind foot length had been attained.

Head-body Length: The mean head-body length at birth was 42 mm, ranging from the 30 – 39 mm to the 40 – 49 mm size class. The initial IGR of 0,044 was the lowest of all linear measurements (Fig. 3), and growth also proceeded most slowly, so that 75% of adult length was not attained until about 40 days (Fig. 2).

BEHAVIOURAL DEVELOPMENT

The early post-natal life of *Aethomys chrysophilus* was dominated by the nipple-clinging behaviour of the young. This behaviour is characterised by a firm attachment to the nipple which allows the young to be dragged along by the female.

Nipple-clinging has been recorded previously for *A. namaquensis* by Meester (1958) and for *A. kaiseri hindei* by Lawrence (1941). Similar behaviour has been observed in many other species. In the present study, young *Aethomys chrysophilus* attached to the nipples at birth and were not observed detached until 16 to 18 days of age. Attachment was only infrequently observed after weaning at 26 days, and was not recorded after Day 40. Attachment was extremely firm and young could only be removed by blocking the nostrils.

The incisors of both upper and lower jaws were erupted at birth and were specially modified to aid attachment. The tip of each incisor was notched to form two sharp projections (see Fig. 4), which were curved backwards into the mouth. A firm attachment resulted from the grip of these modified incisors on the broad glandular base of the nipple. The modified tips were worn down and disappeared three or four days after the eyes opened, at about 16 days. This may have been due to eating solid food (no records of such intake are available at this age), but is more likely to have resulted from spontaneous grinding of the teeth, which was first observed on Day 12. The loss of the modified tips coincided with the first voluntary detachment of the young on Day 16. Hamilton (1953) recorded that the loss of the modified incisor tips in *Neotoma floridana floridana* was first evident at this age. An almost identical modification of the incisors has been described for *A. kaiseri hindei* by Lawrence (1941). This author also described similar adaptations in *Holomyscus aeta weileri, Neotoma fuscipes annectens, N.f. macrotis* and *N. lepida lepida.*

The ecological implications of nipple-clinging are dealt with in the discussion.

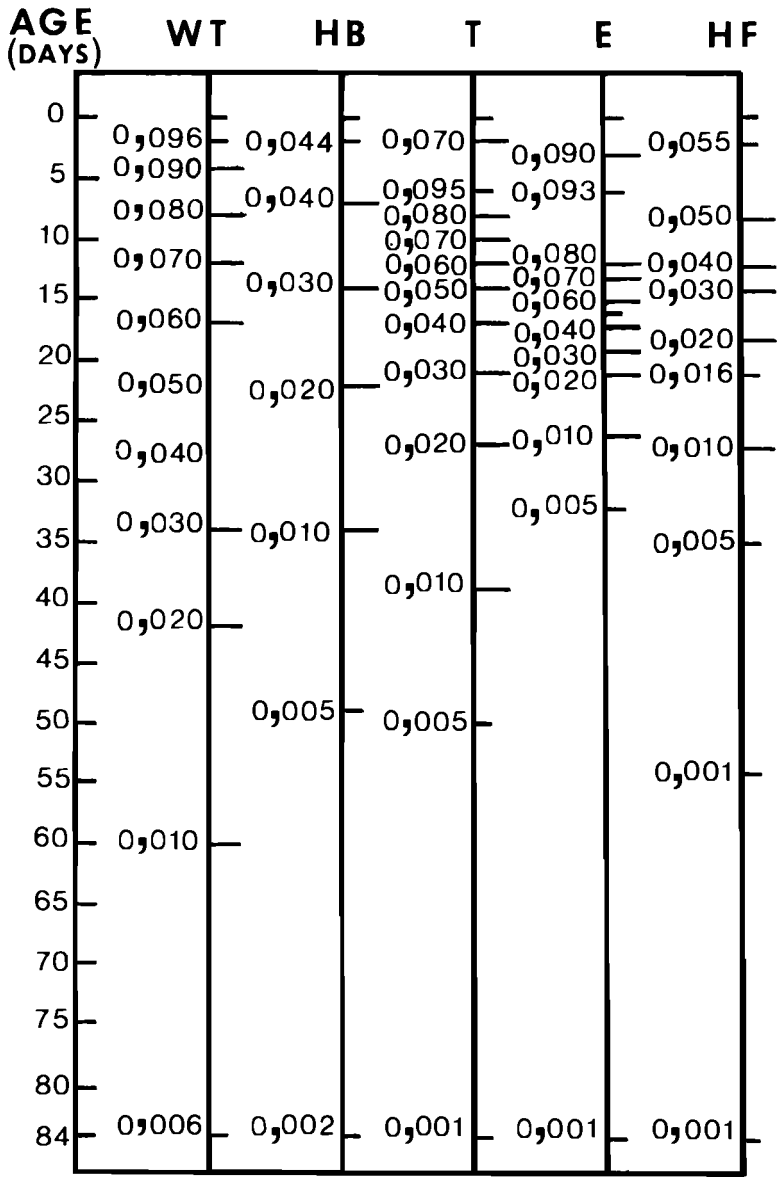

FIGURE 3
Instantaneous growth rates for *A. chrysophilus* from birth to 84 days – Key to lettering : see Figure 2.

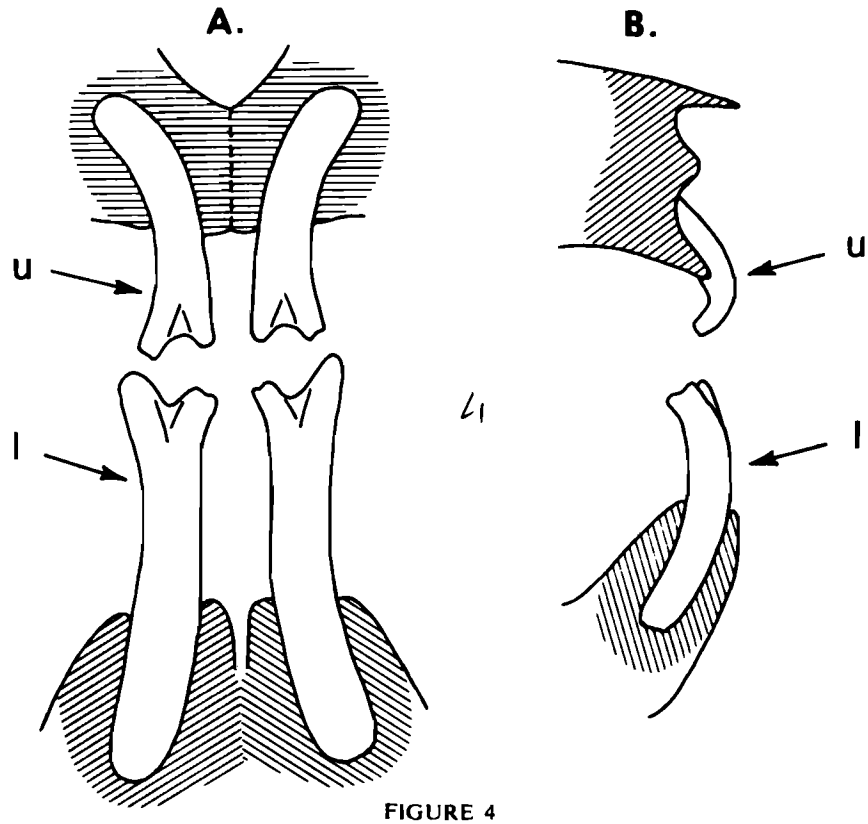

FIGURE 4
Upper and lower incisors of *A. chrysophilus* at 10 days. Key to lettering: A. – frontal aspect (X 20), B. – lateral aspect (X 10), U – upper incisor, I – lower incisor.

An attempt has been made to divide the post-natal behavioural development of *A. chrysophilus* into definitive periods on the basis of changes in social relationships as in Williams & Scott (1953).

Four major developmental stages are described:

1. Neonatal Period (0 – 5 days)
2. Transition Period (6 – 11 days)
3. Infantile Period (12 – 25 days)
4. Juvenile Period (26 – 82 days)

1. NEONATAL PERIOD (birth to 5 days)

Development during the neonatal period appeared to be mainly on the physical level with few behaviour patterns emerging that were not present at birth.

(a) *Sensory:* The eyes and external auditory openings were closed, and the young did not respond to visual or auditory stimuli during this period. Communication between littermates, and from parents to the young appeared, therefore, to be restricted to the thermal, tactile and olfactory levels.

(b) *Exploration and Vocalisation:* The 'contact test' showed that from birth the young had a strong urge to remain in a group, and showed no tendency to investigate. Weak pivoting movements accompanied by almost continuous squeaking occurred during the 'isolation test'. This reaction could be subdued if the young were placed singly on cotton wool, and they often lay still and quiet in the palm of the hand. These observations suggest that, at this stage, temperature and tactile stimuli may be of greater importance than olfaction in maintaining the group situation.

Vocalisation was infrequent in the normal situation of nipple-clinging, but occurred more frequently in the experimental group situation (contact test). However, squeaking was often persistent when the young were isolated, as described earlier. Young appeared to be deaf throughout the neonatal period, so vocalisation as a means of communication between littermates can be discounted. Squeaking was observed to stimulate parental retrieving, and its role when the young are isolated beyond the range of the visual and olfactory senses of the parents may be important to survival.

(c) *Postural and Locomotor:* When suckling, young normally lay on their back or side. Lounging with the body relaxed when there was insufficient room to lie down, was frequently observed in the 'contact test', and young tended to burrow towards the centre of the group in a rooting movement. When isolated on a flat surface their preferred resting posture was lying with the chin, chest and all four feet in contact with the ground. This position was maintained throughout the 'isolation test' until Day 2 or 3, when pivoting and crawling was observed. Only the fore legs were active in pivoting, which may be defined as a rotation of the body about the fulcrum provided by the hind-quarters.

The torsal twist method of righting was observed, and was effected by the rapid twisting of the body assisted by the head and one of the front legs. The grasp reflex was poorly developed at birth. The response from the fore feet was moderate by Day 4, but that from the hind feet was still weak.

At birth, locomotion was restricted to weak crawling with chin and chest touching the ground. The crawl-walk, in which the chest is held off the ground for short periods, but where the hind legs are not fully extended, was generally developed between Day 2 and Day 5.

Negative geotaxis was present from birth, as indicated by pivoting on the slope. However, the ability to crawl up the slope was not well developed until Day 3 or 4. Young often failed to avoid falling in the 'cliff-drop' test, although intention turning from the drop was present at birth. This failure was probably due to weakness and lack of muscular co-ordination, which was further demonstrated by their inability to cling to the horizontal bar for any length of time during this period.

(d) *Self-Grooming:* The first appearance of face-washing was observed in one neonate on Day 1, when the fore feet were moved simultaneously over the snout. This action was rudimentary in nature and was not repeated. Subsequent attempts at face-washing in this period were generally weak. Ineffectual scratching of the side of the body with one hind foot was recorded on Day 5.

(e) *Ingestion and Elimination:* Young attached firmly to the nipple by means of specially adapted incisors as described above, and were not observed detached from the nipple during this period. The rooting reflex was present at birth, and developed into a positive action by Day 4.

(f) *Social Behaviour:* Social activities were restricted to those behaviour patterns, already

described, that are associated with nursing and maintaining contact with the mother and littermates.

2. TRANSITION PERIOD (6 to 11 days)

The transition period was characterised by the appearance of adult sensory mechanisms and behaviour patterns.

(a) Sensory: The head was moved from side to side in sniffing movements during exploration which suggested an efficient sense of smell. Hearing developed on the 8th day, and young had become hypersensitive to sound by Day 11 when the eyes started to open. In only one litter were the eyes fully open by the end of the period.

(b) Exploration and Vocalisation: The first exploratory movement away from the group in the 'contact test' occurred on Day 6. The frequency of these movements subsequently increased until, by the end of the period, the exploratory urge was fairly well developed. There appeared to be an inverse relationship between the onset and development of exploratory drive and vocalisation frequency. Squeaking ceased in the group situation around Day 6, and was seldom heard in the 'isolation test' towards the end of the period.

(c) Postural and Locomotor: The development of the postural and locomotor patterns during this period was closely associated with increasing efficiency of the hind legs. Lying on the chest was the usual resting posture during the 'isolation test', while in the group situation lounging was more frequently observed. Haunch-sitting appeared on Day 11. This posture releases the fore limbs for activities such as food holding and efficient grooming. The standing posture, with the fore legs used as supports against the wall of the observation box also occurred at this time.

An immediate righting reflex was observed from Day 6. This reflex was too rapid for the exact method to be determined, but it may simply be an accelerated torsal twist. The grasp reflex remained stronger in the fore feet than in the hind feet.

Walking, with hind legs functional and chest held off the ground, developed from the crawl-walk on about Day 6. First attempts were characterised by widely splayed hind legs and low carriage of the head, which resulted in the vibrissae being brushed along the ground. The legs became less splayed and general movement more steady by the end of the period. The ability to climb a vertical wire-mesh screen was moderate by this time.

Pivoting as observed in the earlier period disappeared with the advent of walking. It was replaced by a rotation of the whole body involving both fore and hind legs.

By the end of the period, young were efficient at turning and walking up the slope in the 'negative geotaxis test', and generally avoided the cliff drop. The ability to hang suspended from the horizontal bar developed, but difficulty was experienced in maintaining balance on the top. Agility on the bar at this time appeared to be limited more by muscular weakness than by lack of co-ordination.

(d) Self-Grooming: Face washing while lying on the side or lounging was common from the 7th day, and was first performed while sitting on the haunches four days later. Tooth-combing the fur and licking a littermate's ear were observed on Day 9. Efficient hind leg scratching began on the same day.

(e) Ingestion and Elimination: Young nursed continuously as in the previous period and solid

food offered in the experimental situation was not sampled. Rooting was more vigorous than in the neonate, probably as the result of muscular development. Neither defecation nor urination were observed.

(f) Social Behaviour: The 'contact test' indicated that the young were less dependent on stimulation from littermates within the group, and exploratory sorties became more frequent towards the end of the period. However, contactual behaviour was still marked as young would re-cluster following these short periods of activity.

Social grooming first appeared on Day 9, when one sibling was observed tooth-combing the fur and licking the ear of a littermate. This behaviour developed rapidly so that by Day 11 social grooming and associated activities, such as nudging and sniffing, were common.

No chasing, fighting or sexual behaviour was observed in this period.

3. INFANTILE PERIOD (12 to 25 days)

Opening of the eyes was accompanied by several behavioural changes, and was considered the most significant event of the period. Behavioural activities in general were performed with improved efficiency, and in most cases were adult in nature by weaning at about 26 days.

(a) Sensory: The olfactory function became increasingly important as indicated by vigorous sniffing of littermates and objects placed in the observation box. Hearing was acute, and over-reaction to auditory stimuli was general up to Day 18. The eyes opened fully between the 11th and 14th days, and with the development of sight, all the major sensory mechanisms had become functional.

(b) Exploration and Vocalisation: Young seldom remained together in the 'contact test' for more than about 30 seconds, but moved away to explore the surroundings. The frequency and duration of such explorations increased with age. The animals responded to the 'isolation test' by immediate exploratory sorties.

Vocalisation was restricted to a squeak in reaction to pain, and teeth-chattering when provoked.

(c) Postural and Locomotor: Most of the adult postural and locomotor patterns not directly associated with fighting or sexual behaviour had appeared by Day 12. Muscular co-ordination improved and the young became progressively stronger throughout this period, so that by the end most activities were performed with adult efficiency.

The hind legs became less splayed and adult walking was achieved by Day 20. The ability to stand on the hind legs without support from the fore legs, and to climb upside-down on a wire mesh screen, had developed mid-way through the period. Jumping only became efficient in the latter stages.

As soon as the eyes opened the young would walk while attached to the nipple instead of being dragged. The specialised incisor tips were lost at about Day 16, which may explain why young were occasionally dislodged from the nipple at this time when the female was handled.

Muscular co-ordination as tested on the horizontal bar showed marked improvement between the 11th and 14th days. The ability to climb from an inverted hanging position to the top surface was developed.

(d) Self-Grooming: Grooming movements became deliberate, and were performed with adult co-ordination.

Washing of the face, head and neck region was effected by simultaneous movements of the paws, and the fur was combed with the teeth. Hind leg scratching of the lateral and ventral body regions, as well as the ear, was common. The only new development was the licking of hind feet and claws following scratching.

(e) Ingestion and Elimination: Young were first observed voluntarily detached from the nipple about five days after their eyes opened, that is between 16 and 18 days. Investigation of the cage took place, and the time spent nursing became gradually less until weaning at about 26 days. The rooting reflex lessened in intensity as weaning approached. Suckling was observed occasionally up to Day 40.

In the experimental situation, young would nibble mouse cubes as soon as the eyes were open, but the eating of solid food in the cage was not seen until Day 18. Seeds and small fragments of mouse cube were held in the forepaws in the adult manner while being eaten.

Urination in the observation box was first observed on Day 17, and defecation two days later.

(f) Social: Young were frequently seen away from the mother or littermates after Day 18. Nevertheless, the contactual urge remained well developed, as resting periods were invariably spent in family groups, with the mother, the young and often the adult male lounging together.

Sibling care in the form of social grooming was common. Serious fighting was not observed in this period, although certain behavioural activities associated with fighting had developed by Day 19. These activities included boxing, and a defensive haunch-sitting posture with the fore legs held up in front of the body, accompanied by teeth-chattering.

Sexual behaviour, apart from genital sniffing, was not observed.

4. JUVENILE PERIOD (26 to 82 days)

This period covered the time between weaning and the onset of sexual maturity.

(a) Sensory: Over-reaction to sound disappeared early in this period and the eyes increased greatly in size. Sensory mechanisms appeared otherwise unchanged.

(b) Exploration and Vocalisation: These behaviour patterns were similar to those of the previous period.

(c) Postural and Locomotor: Increase in strength and efficiency of muscular co-ordination enabled all postural and locomotory activities to be performed in the adult manner mid-way through the period.

(d) Self-Grooming: No change was observed.

(e) Ingestion and Elimination: Young suckled occasionally up to 40 days, but from weaning at 26 days were dependent on water and solid food.

(f) Social: Most of the young to be retained were separated into heterosexual pairs at about 28 days. These animals invariably rested in contact with one another, and social grooming was common. Chasing and fighting were not observed.

(g) Sexual: Testes generally became scrotal between 49 and 63 days, while the majority of females became perforate between 56 and 70 days. No sexual behaviour was observed. Earliest sexual maturity for either male or female, derived from sixteen successful brother-sister pairings, was 82 days.

PARENT-YOUNG RELATIONSHIP

(a) Feeding: The female nursed the young continuously up to 16 or 18 days, and before this time young were never seen detached from the nipple. It was not possible to make observations during the night, but that young frequently changed their nipple of attachment during the night was established by toe-clipping. Young were not toe-clipped until Day 5, and from this time frequent movements from nipple to nipple were recorded. In litters of four or less these movements were restricted to the four inguinal mammae, the two pectoral mammae only being utilised when the litter size was greater than four.

Maternal care while the young were actively suckling was restricted to occasional sniffing and licking.

(b) Grooming: When returned to the cage after examination, young were groomed extensively, and usually by both parents. The female would then pull the young beneath her body to assist their re-attachment. Mouth carrying was not common and was restricted to nervous females. In such cases young were gripped by any part of the body and carried round the cage before being dropped and pulled beneath the body.

(c) Protection: The male was generally docile and made no attempt to protect the young. The female, on the other hand, would bite aggressively at a prodder in defence of the young.

INJURIES AND MORTALITY

A mortality rate of 10,3% was recorded from the 17 litters that were observed up to 20 weeks of age. Young were particularly vulnerable during the 0–3 day period. Scratches from the female's claws were often inflicted while the young were being detached, and two young were eaten alive by the parents as a direct result of their injuries. A further three young from this age group were eaten, but their cause of death was not established.

Mortality in the second week was restricted to a single runt which died naturally on Day 13. It was removed from the cage. There were no further deaths up to the age of 20 weeks.

DISCUSSION

The major events in the early post-natal development of *A. chrysophilus* are presented in Table 2, distinguishing between the Neonatal (0–5 days), Transition (6–11 days), Infantile (12–25 days), and Juvenile (26–82 days) periods on the basis of three critical ages at six, 12 and 26 days. At six days walking and exploratory movements first developed, while at 12 days the eyes of most young opened and solid food could be taken. The Juvenile period extended from weaning at 26 days to sexual maturity at about 82 days.

The early post-natal development was dominated by nipple-clinging, and the modification of the incisor tips of the young for this behaviour is described above. The major adaptive role of nipple-clinging appears to be in keeping the young in contact with the maternal milk supply for the maximum length of time. A secondary advantage may be in allowing the young to escape with the mother from the nest situation, but it is unlikely that the routine transportation of young outside the nest would be of survival value. Some species which exhibit nipple-clinging are able to

detach the young. *Neotoma floridana floridana* treads on the young while turning in small circles (Hamilton 1953), and according to Richardson (1943) the young of *Neotoma albigula* are grasped by the incisors and twisted from the nipple. In the present study, toe-clipping established that young *A. chrysophilus* frequently changed nipples during the night. Also, circumstantial evidence suggests that the adult leaves the young in the nest during normal activity periods. Smithers (personal communication) stated that young *A. namaquensis* were never transported into traps, and Horner and Taylor (1968) reported no instance of rodents entering traps with unweaned young. Donat (1933) stated that one *Neotoma fuscipes annectens* often came out at dusk without her offspring. Therefore, it may be that nipple-clinging young are normally left in the nest during the activity periods of the adult, and would only benefit from being dragged to safety if the female was disturbed while nursing in the nest.

The ages at which some major developmental events occur in three South African murids, namely *A. chrysophilus* (present study), *Thallomys paedulcus* (Meester & Hallett 1970) and *Praomys (Mastomys) natalensis* (Meester 1960) are presented with relevant reproductive data in Table 3. Comparison of these data may illustrate how the post-natal development of nipple-clingers (*A. chrysophilus* and *T. paedulcus*) differs from that of more 'conventional' species such as *P. (M.) natalensis*. Weaning occurs earliest in *P. (M.) natalensis*, although physical and behavioural development is retarded for most of the pre-weaning period as compared with the other two species. This is particularly with regard to the eruption of incisors, and development of hearing and sight. Early eruption of incisors may be directly associated with nipple-clinging behaviour (Meester & Hallett 1970), but the earlier occurrence of the other events in *A. chrysophilus* and *T. paedulcus* is difficult to explain. *A. chrysophilus* is not fully weaned until 26 days, although it appears as physically and behaviourally developed as *P. (M.) natalensis* at 21 days when the latter is weaned. The significance of continued maternal care (as in *A. chrysophilus*) beyond the age when the animal could be independent may be of survival value by allowing for a longer period of learning.

P. (M.) natalensis becomes sexually mature at an earlier age, has a slightly shorter gestation period and a greater litter size than the other species (Table 3). This appears to be compensated for in *A. chrysophilus* and *T. paedulcus* by more continuous nursing and increased protection afforded by the female's body which result from nipple-clinging. The survival rate of *A. chrysophilus* in the present study was high, with over 89% of young surviving to 20 weeks.

Also, Davis (1963) ascribed the high survival rate (over 80%) of *Mystromys albicaudatus* to the habit of clinging to the nipple until weaned. However, the survival rate of *P. (M.) natalensis* (over 88%) from birth to weaning was also high (Meester 1960), so the value of nipple-clinging may be obscured by the artificial environment of the laboratory, which is designed to minimize mortality.

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TABLE 2

TIMES OF OCCURRENCE OF SOME MAJOR EVENTS IN THE EARLY POST-NATAL DEVELOPMENT OF BEHAVIOUR OF *A. CHRYSOPHILUS*.

Behaviour \ Age (days)	NEONATAL 0-5	TRANSITION 6-11	INFANTILE 12-25	JUVENILE 26-82
TACTILE	Present from birth			
OLFACTORY	Present from birth			
AUDITORY	(2) Ear pinnae unfold	(8) Hearing →	(11) Hypersensitive (18)	
VISUAL	Eyes closed at birth	(9) Eye slits (12)	(11) Open (14) →	
INGESTIVE	Suckle at birth	(Experimental) (12) Eat solid food (18) (Observational)	(16) (18) Voluntary detachment →	(26) Weaned →
CONTACTUAL (contact test)	Strong →	Less strong →	Weaker →	Still present →
EXPLORATIVE (Isolation test) +Contact test		(6) Break from group →	Increased →	
VOCAL	In group (6)	Isolation (11)	Reaction to pain →	
LOCOMOTORY	Crawl (3)	(6) Walk →	More efficient →	
	(2) Crawl walk (6)			
GROOMING	(1) ..... (7) Face wash (11) On haunches →			
	(5) ..... (9) Scratch, lick, toothcomb →			

TABLE 3

REPRODUCTIVE DATA (*a*) AND TIME OF OCCURRENCE OF CERTAIN DEVELOPMENTAL EVENTS (*b*) IN *A. chrysophilus* (PRESENT STUDY), *T. paedulcus* (MEESTER & HALLETT 1970) AND *P.(M.) natalensis* (MEESTER 1960)

	*A. chrysophilus**	*T. paedulcus*	*P.(M.) natalensis*
(*a*)		REPRODUCTION	
Young per Litter	3,1	2,7	8,5
Number of Litters	37	23	19
Age at birth of first Litter ..	108	107	77
Interval between Litters ..	26	26	24
(*b*)		DEVELOPMENT	
Ear pinnae unfold	0–2	0–1	1–2
Incisors erupt	0	0–1	9–11
Toes loose	1–4	3–4	5–7
Response to sound	8	9	12–14
Eyes open	11–14	11–15	15–16
First unattached	16	15	0
Efficient walking	13	15	(11–13)†
Weaned	26	28–31	19–21

* Section (*b*) from 12 Litters.

† Datum in parenthesis from Meester & Hallett (1970).

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