J. Anat. (1970), **106**, 2, pp. 349–370
With 25 figures
Printed in Great Britain

A longitudinal study of the growth of the black-hooded rat: methods of measurement and rates of growth for skull, limbs, pelvis, nose-rump and tail lengths

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(*Received* 15 *March* 1969)

INTRODUCTION

The rat is used in experiments on the effects upon growth rate of nutrition or drugs or a changed environment. Curiously enough, however, techniques for the efficient evaluation of growth and development in this animal have scarcely been developed yet. Most investigators content themselves either with the traditional cross-sectional type study, sacrificing rats wholesale at each weekly milestone, or else with longitudinal measurement of body weight only, ignoring all changes of form or body composition. But in the design of most experiments longitudinal methods are enormously more efficient than cross-sectional ones (see Tanner, 1951) wherever the development of non-destructive techniques of measurement permits them to be applied.

The present paper presents reliable techniques for measuring the lengths of body and tail, and the lengths of skull, limbs and pelvis by radiography. Graphs and tables of the rates of growth of these dimensions from birth to maturity are given, and timings of the peak velocities for the various dimensions are compared. A second paper gives details of a method for the assessment of skeletal maturity in the rat, as the most convenient index of tempo of growth (Hughes & Tanner, 1970).

Previous studies on body dimensions of rats are not numerous. Moment (1933) measured body lengths on dead animals, Asling, Simpson, Li & Evans (1954) body length and the lengths of various limb components under anaesthesia, Bernardis & Skelton (1965) nasoanal and tail lengths, Dickerson & Widdowson (1960) body, tail, femur and skull length and Harrison (1963) tail length. De Groot (1963) described a method for measuring tail growth with the aid of a transparent, tail-fitting cylinder marked with a metric scale. Acheson, MacIntyre & Oldham (1959) were the first to describe a comparatively simple, fairly accurate, method for measuring total length and tail length of living rats, using a measuring board calibrated with graph paper. This apparatus was not entirely suitable for our growth studies so the measuring board described below was constructed. This board was used for the measurements of nose-rump and tail length presented here, but subsequently a board incorporating a rack and pinion movement and digital read-out was designed and has been manufactured commercially.

Studies on skeletal dimensions of the rat have been mainly cross-sectional. Hatai

(1907) and Moss (1954) measured skull growth on dry preparations, and Outhouse & Mendel (1933) made an extensive study on skeletal lengths and breadths in this way. Levy *et al.* (1953) looked at various skeletal dimensions in alizarin preparations, and Bernstein & Crelin (1967) used both alizarin preparations and dry bones in studying the growth of the pelvis. Longitudinal radiographic studies on rats have been made by Spence (1940) on skull growth, by Barnes, Sperling & McCay (1947) and Saxton & Silberberg (1947) on tibia lengths and by Harrison (1958*a*, *b*, 1968) on growth of the pelvis. Asling & Frank (1963) described a cephalometric study in which they employed a craniostat to hold the skull.

The way in which animals are positioned in the study described here enables many measurements of skeletal dimensions to be made directly from the radiographs. The technique and results for four such measurements are presented here, and others will be published later.

MATERIALS AND METHODS

Animals

The rats were of a black-hooded strain supplied by the National Institute for Medical Research. They were obtained by the Medical Research Council from the Imperial Chemical Industries' Laboratories in 1930 and have been random-bred since.

Females who had already borne at least one litter were mated overnight with proven males and vaginal smears were examined for the presence of spermatozoa by the staining technique of Lints, Mouravieff & Merckx (1962). Those with a positive smear were caged separately and fed on a diet of Chardex small animal nuts, supplemented with fresh greens and liver, and water ad libitum.

On the day of birth each litter was reduced to eight animals, of which three were male and five female whenever possible. The pups were left with the mother until they showed the first signs of maturing sexually, usually about 55 d post-copulation (PC), and were then placed two/cage and fed Chardex, with supplements, and water ad libitum. The pups were left with the mother for longer than is usually done in laboratories in order to minimize the effect of weaning on their growth, as the usual laboratory weaning at about 42 d PC occurs at a time when growth is proceeding very rapidly. Our procedure accords more closely with the normal behaviour of rats, in which weaning is a gradual, and not a sudden, process (Calhoun, 1962).

Identification. Each pup had a number marked directly on to its skin with 'Magic Marker' (Speedry Products Ltd., Beckenham, Kent), which needed renewing every other day. When the pups developed fur, at about 35 d PC, their number was painted on to the fur using picric acid made up in 50% alcohol. This was renewed at each weekly examination. When the ears had become large enough to punch, at about 50 d PC, the identification number was punched there.

Age. All ages are given in days after copulation (PC) since the length of gestation is not the same for all litters. It was found in a preliminary study that the variability of lengths and weights at each age was considerably reduced when age was reckoned PC rather than post-birth.

Examination frequency. The animals were examined at 3 d intervals from 23 to 35 d PC, at weekly intervals till 84 d PC and at fortnightly intervals until 210 d PC.

At each examination, the animal was anaesthetized, and nose-rump length, tail length and weight were recorded, and a radiograph taken. When the animals were young, ether was used alone as an anaesthetic, but in older animals a light anaesthesia was induced using intravenous pentabarbital sodium (1 mg/40 g body weight) and completed using ether.

Physical measurements

Apparatus. Measurement of the nose-rump and tail lengths of the animals was done using a specially constructed measuring board, illustrated in Fig. 1.

The length of the board is 28½ in, the width 6 in, the height at the head 3½ in and at the tail 1½ in. At a distance of 16 in from the head of the board is a 'rump-piece' which is an upright board 6 × 2 × ½ in, permanently attached at right-angles to the base. Through the rump-piece are drilled five holes ranging in diameter from ⅛ of an in to $\frac{7}{16}$ths of an in, the bases of which are flush with the surface of the board.

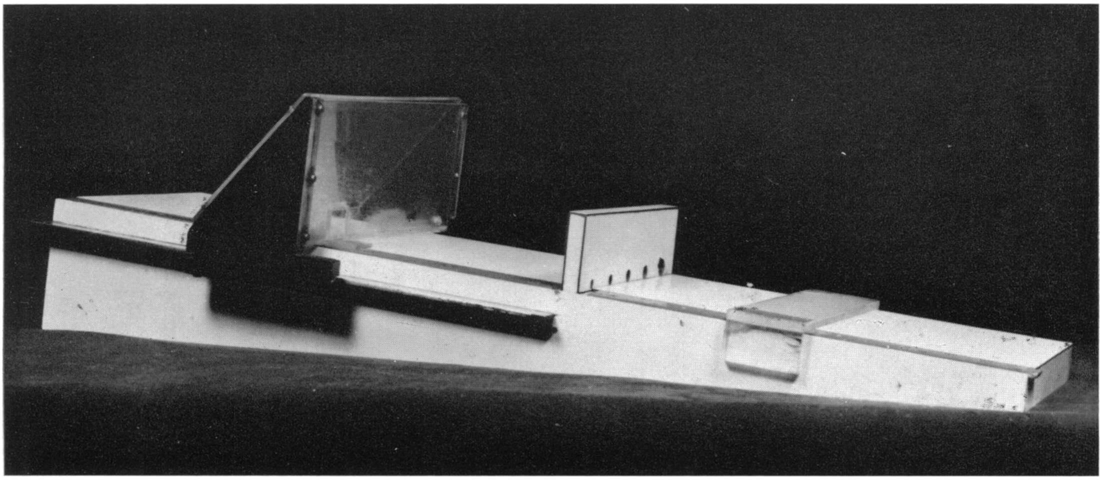

Fig. 1. The measuring board used for nose-rump and tail lengths on living animals.

A metric rule is set into one side of the base-board, measuring to 41 cm at the head end and 32 cm at the tail end. The thickness of the rump-piece and the distance by which the indicators are off-set are allowed for in setting the rule. A rider runs on strips of ½ in angle-iron attached to the side of the base-board so that the nose-rump length may be measured. The rider consists of two triangular pieces of ⅜ in paxalite joined by two pieces of ⅛ in perspex on the vertical and the hypotenuse. Attached to the front end of the rider is a piece of ⅛ in perspex, ½ × ½ in, forming a right-angle with it and running over the scale. On the under side of the perspex is a line which is almost in contact with the scale and eliminates reading errors due to parallax. The rider runs on the angle-iron tracks by means of six ⅜-in ball-races on each upright. Two races are set opposite each other on either side of the angle-iron and the other two races are placed horizontally so that they run against the edge of the angle-iron and eliminate side-to-side movement. In order to measure the tail length a simple perspex rider is used. This consists of two pieces of ⅛-in perspex, 2 × ¾ in, and one of 6 × 2 in. The two smaller pieces are joined one each end of the longer piece and at right-angles to it. On the under side of the rider a line is marked. The rail rider runs directly on the base-board.

An improved version of this apparatus is available commercially (Holtain Ltd., Brynberian, Crymmych, Pembrokeshire). This has a digital read-out and an inverted V-shape cut out of the rump-piece, which is moveable vertically, so that when the tail has been passed through the hole the rump-piece is allowed to rest on it.

Technique. Although animals can be measured when conscious, far more consistent results are obtained when they are anaesthetized. The anaesthetized animal is gripped by the scruff with the right hand and by the base of the tail with the forefinger and thumb of the left hand. The remaining three fingers of the left hand are placed under the tail in order to hold it out straight and it is then passed through

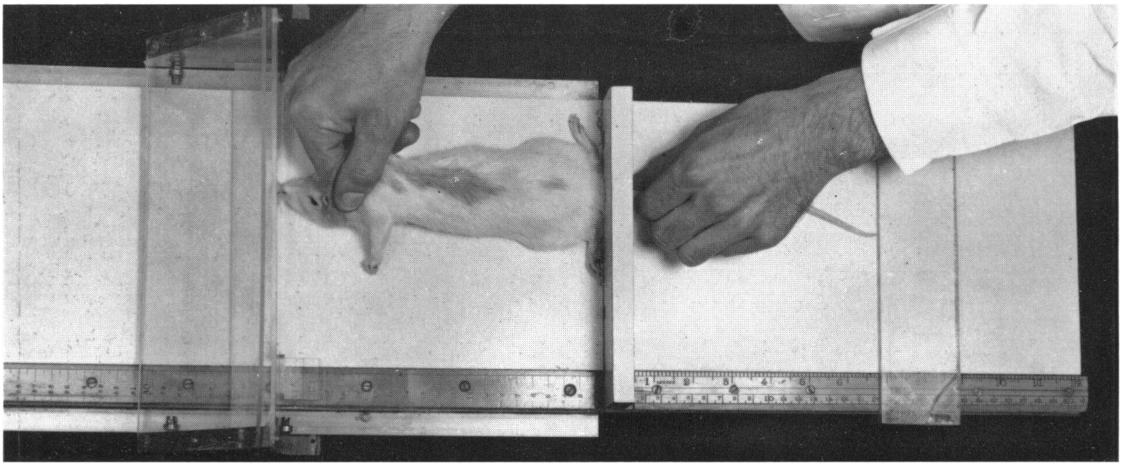

Fig. 2. Measurement of nose-rump length on a living animal.

the smallest hole in the rump-board which will accommodate it. The tail rider is then placed under the distal third of the tail and the base of the tail gripped again with the left hand. The rump of the animal is held tightly against the rump-board by gentle traction on the tail, and the body of the animal is pulled out straight with the right hand. The head rider is allowed to rest against the nose and the nose-rump length noted. This is illustrated in Fig. 2. The scruff of the animal is then released and the right hand is used to draw out the tail at the same time taking the tail rider with it. The tail length is then noted. The left hand does not leave the base of the tail throughout the whole procedure.

Radiographic measurements. A portable X-ray machine with target size 1·4 mm square was used at 48 KVp and 12·5 mA throughout the whole age-range, the length of exposure being varied from 0·25 to 1·25 s. The anode-film distance was constant at 70 cm. To obtain good definition a fine-grain, non-screen film was used.

The anaesthetized animal is placed with its ventral surface in contact with the film in the position shown in Fig. 3. The left manus is gripped between forefinger and thumb and held, pronated, on the film with adhesive tape, so that the humerus is at an angle to the main axis of the body, the radius and ulna are at an angle to the humerus and the digits are slightly separated. The right manus is then gripped, the forelimb supinated, drawn caudally and held in place with adhesive tape. The right hind limb is extended and taped in position and the left hind limb positioned so that the femur is at right-angles to the long axis of the body, the tibia at right-angles to the femur and the foot at right-angles to the tibia. The tail is extended and held in place with tape.

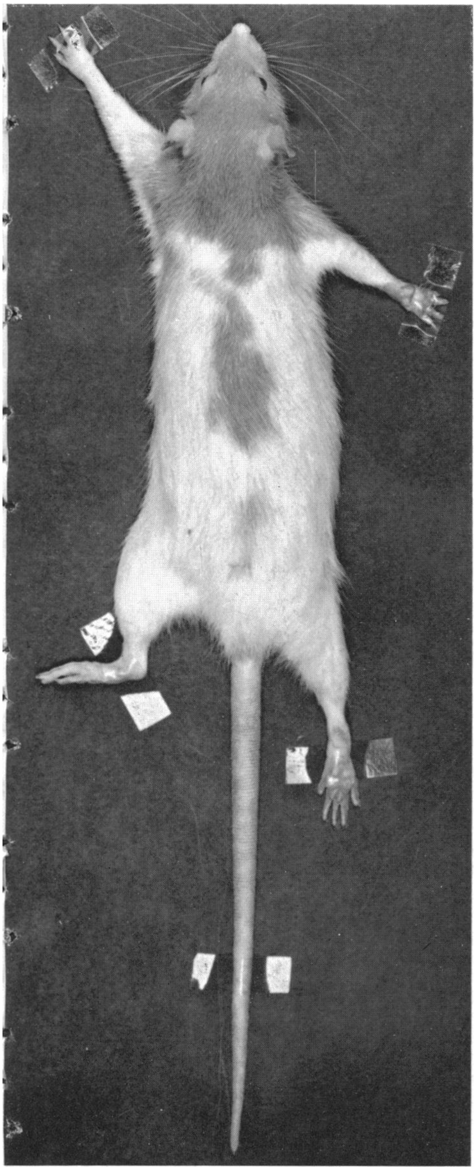

Fig. 3

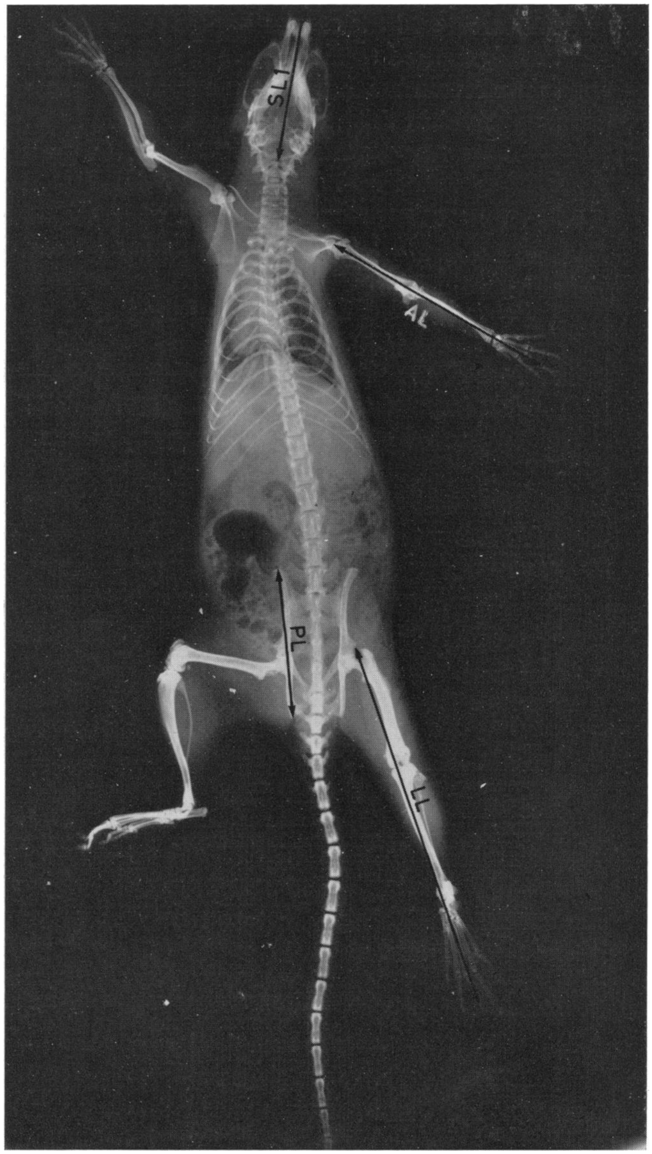

Fig. 4

Fig. 3. Position of the animal for radiographic examination.
Fig. 4. The sites at which skeletal measurements were made.

When positioning the animal it is necessary to ensure that the limbs which are extended, i.e. the right side of the animal, are positioned so that true dorsi-ventral views are obtained. This is done by placing a slight traction on the limbs and ensuring that pes and manus are flat on the film. The left fore and hind limbs provide true lateral views of the bones when positioned as described.

The X-ray beam is centred to the third lumbar vertebra, i.e. midway between the iliac crest and the caudal border of the dorsal part of the rib cage. (In practice, the tube is centred to the middle of the film and the animal positioned so that the third lumbar vertebra lies over the centre.) The radiographic appearance of an animal positioned in this way is illustrated in Fig. 4.

The measurements marked in Fig. 4 were made on the radiographs with a caliper reading to 0·1 mm (Tanner & Whitehouse, 1955). A mounted magnifying glass or low-power microscope was used when the animals were small.

Skull length 1 (*SL* 1). The anterior border of the foramen magnum to the tip of the nasal bones.

Pelvis length (*PL*). The tip of the iliac crest to the distal surface of the pubis.

Leg length (*LL*). The dorsi-lateral articular surface of the acetabulum to the distal surface of the third proximal phalanx.

Arm length (*AL*). The articular surface of the glenoid cavity of the scapula to the distal surface of the third proximal phalanx.

Reliability of radiographic measurements

To estimate the reliability of the radiographic measurements, a series of whole-body radiographs of animals in the age-range 23–140 d PC was measured by three observers, two experienced and one inexperienced. The former two measured the series twice each, the latter once only. The average within-observer S.D. of differences between duplicates was 0·35% of the mean value for arm length, 0·41% of the mean for leg length and 0·43% for pelvis length. The S.D. of differences between observers averaged 1·2% for arm length, 0·92% for leg length and 1·05% for pelvis length.

RESULTS

The results are shown in Tables 1–4 and Figs. 5–20. The numbers of animals at each age diminish gradually from a few days after birth onwards. Thus the data are 'mixed longitudinal'. The efficiency of various ways of estimating means and S.DS of size attained at each age and of rate of growth from one age to the next in such data have been discussed by Tanner (1951). The most efficient ('minimum variance') estimates of these parameters are a little cumbersome to compute and have the possible disadvantage that the formulae assume the existence of certain relationships within the data. When the numbers drop as little from one age to the next as in our data the simpler methods used below are very nearly as efficient (Tanner, 1951), and in fact we have compared both series of estimates for nose-rump and tail lengths and found differences in the mean distances and velocities of the order of 1–2% only.

The means and S.DS of each measurement at each age ('distance curves') have been calculated simply from the data available at the age in question, in a cross-sectional manner. The means and S.DS of rate of growth ('velocity curves') have been calculated as 'actual increments'; that is the increment from one examination to the next was calculated for each individual rat present on the two occasions and these increments were used to compute the statistics.

There is probably a bias introduced by the diminution of numbers, since the reduction was caused by animals dying. The growth of animals in the period before death was in some cases less than that of animals not about to die; thus the survivors represent a progressively healthier group. The bias is very small however. We have examined weight and leg length of the 'pure longitudinal' series constituted by animals surviving to 140 d and these curves do not differ significantly from the curves for the larger group given below.

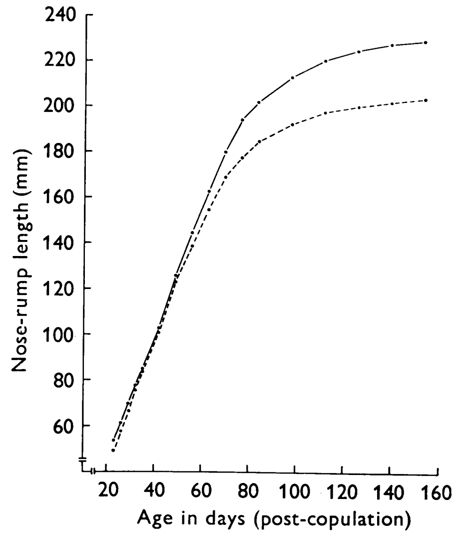

Fig. 5

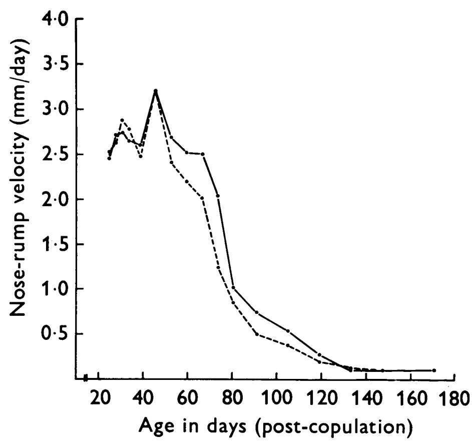

Fig. 6

Fig. 5. Nose-rump length of male and female animals. Male, ———; Female, - - - -.

Fig. 6. Nose-rump length velocity of male and female animals. Male, ———; Female, - - - -.

Nose-rump length (Figs. 5, 6; Tables 1, 2)

Males are larger than females from birth onwards, though the difference only becomes statistically significant at about 50 d PC. It increases from then till the completion of growth (at about 200 d PC in these rats) at which time males are about 12% larger.

The shape of the velocity curve is similar for both sexes. The velocity rises from 23 to 30 d PC, drops to a trough at 40 d PC, rises markedly to a peak at 45 d PC and then declines. This decline has a 'shoulder' on it, however, the drop in velocity being partly arrested between 50 and 55 d. This lessened deceleration is less marked for females than males and coincides with sexual maturation (vaginal opening is at 54 d PC on average and testicular descent at 50 d PC on average). It probably represents the equivalent of the adolescent growth spurt seen in man and some other primates (Tanner, 1962). In the rat there is not an actual acceleration of growth, only a diminution in deceleration. From 60 to 100 d the male velocity is significantly greater than the female.

Table 1. *The mean and* S.D. *of physical measurements at each age in days post-copulation*

	Nose-rump length (mm)				Tail length (mm)		Total length (mm)		Weight (g)	
Age	N	Male	N	Female	Male	Female	Male	Female	Male	Female
23	71	53·14	48	50·43	20·30	19·70	73·45	70·13	9·98	9·53
		2·74		3·83	2·26	1·98	4·54	5·49	1·35	1·16
26	68	61·21	47	59·38	29·63	28·19	90·82	87·49	13·83	12·97
		3·56		4·50	3·92	3·64	7·05	7·63	1·89	1·90
29	68	69·47	45	67·91	37·21	36·56	106·68	104·69	17·86	17·09
		4·83		3·87	4·43	3·39	9·03	7·35	2·50	2·15
32	65	77·65	42	76·67	45·52	44·93	123·32	121·59	22·29	21·41
		5·35		4·68	5·31	4·76	10·33	9·11	3·08	2·85
35	62	85·27	38	85·11	52·37	53·03	137·65	138·11	28·07	26·05
		6·27		3·94	6·18	5·02	12·02	8·44	3·78	2·59
42	60	103·42	36	102·28	69·50	70·82	172·95	173·10	38·19	37·06
		7·14		4·12	7·78	6·43	13·01	9·61	5·12	3·71
49	56	126·42	36	124·57*	89·06	90·49	215·48	215·04	61·20	58·29
		8·01		4·92	9·83	9·57	16·01	13·05	8·12	5·98
56	53	145·32	36	141·42*	111·93	113·54	257·25	255·01	93·59	85·22†
		8·13		5·74	13·15	10·80	19·05	14·96	13·07	9·42
63	51	162·73	35	156·70‡	130·44	130·50	293·17	287·20	131·04	114·53
		8·10		7·27	16·59	13·10	21·19	17·86	15·17	11·85‡
70	47	179·75	33	170·56	143·03	142·35	322·55	312·91	163·18	132·89
		8·47		5·96‡	18·39	12·93	23·49	16·74*	19·52	11·33‡
77	46	193·92	32	178·69	156·35	152·89	350·27	331·58	200·30	149·23
		9·49		5·34‡	20·63	12·76	25·22	16·98‡	22·42	13·48‡
84	45	201·93	31	184·81	165·69	160·15	367·62	344·67	229·06	162·92
		7·68		5·40‡	21·35	12·54	25·32	16·43‡	23·71	14·03‡
98	45	212·27	29	192·00	175·29	165·19	387·51	357·33	273·59	182·03
		7·86		5·93‡	21·93	13·26*	25·10	17·26‡	29·69	15·77‡
112	45	219·80	29	196·93	184·00	168·90	404·39	365·76	307·46	199·33
		8·83		5·89‡	22·52	13·79†	25·76	17·61‡	33·05	17·81‡
126	44	223·75	28	199·54	190·74	170·88	415·12	370·41	329·07	207·88
		8·54		5·35‡	25·20	13·67‡	28·13	17·02‡	32·72	17·89‡
140	41	226·33	27	201·43	194·50	172·19	421·54	373·61	344·94	211·64
		7·14		5·95‡	25·16	13·87‡	27·76	17·52‡	34·38	18·38‡
154	40	227·76	26	203·08	195·76	173·75	424·25	376·85	357·90	217·71
		6·55		5·98‡	25·63	13·92‡	27·54	17·68‡	35·86	18·25‡
168	39	228·86	26	203·71	196·34	174·15	425·97	377·87	366·63	220·81
		6·84		5·89‡	26·21	13·96‡	28·21	17·53‡	38·77	18·26‡
182	38	230·38	25	205·12	197·65	175·20	428·78	380·32	375·71	232·28
		6·57		6·22‡	26·42	14·29‡	27·81	17·60‡	42·21	18·19‡
196	37	230·93	25	205·88	197·97	175·36	429·71	381·24	366·21	223·26
		6·68		6·07‡	26·75	14·42‡	28·24	17·60‡	40·84	16·44‡
210	38	231·11	24	206·04	199·17	176·04	431·22	382·08	366·50	230·25
		6·69		6·23‡	26·76	14·41‡	28·43	17·67‡	79·02	16·90‡

Female mean significantly different from male mean at: * 5%; † 1%; ‡ 0·1% level.

Table 2. *The mean and* S.D. *of the velocity of physical measurements at each age in days post-copulation*

	Nose-rump length (mm day)				Tail length (mm day)		Total length (mm day)		Weight (g day)	
Age	N	Male	N	Female	Male	Female	Male	Female	Male	Female
23–26	65	2·46	44	2·52	2·77	2·44	5·22	4·49	1·11	0·98
		0·69		0·80	0·87	0·83	1·37	1·43	0·44	0·40
26–29	68	2·72	45	2·63	2·49	2·65	5·21	5·39	1·32	1·30
		0·83		0·68	0·67	0·66	1·30	1·21	0·37	0·37
29–32	65	2·75	42	2·88	2·71	2·79	5·45	5·59	1·44	1·41
		0·61		0·53	0·65	0·69	1·08	1·07	0·36	0·38
32–35	62	2·65	38	2·78	2·47	2·61	5·14	5·38	1·49	1·50
		0·66		0·59	0·60	0·55	1·12	0·88	0·40	0·38
35–42	60	2·61	36	2·46	2·45	2·54	5·07	5·00	1·67	1·57
		0·41		0·37	0·48	0·38	0·70	0·57	0·39	0·29*
42–49	56	3·24	36	3·19	2·75	2·81	6·00	5·99	3·24	3·03
		0·57		0·48	0·60	0·67	0·95	0·83	0·68	0·50*
49–56	53	2·69	36	2·41	3·26	3·29	5·95	5·71	4·57	3·85
		0·55		0·38†	0·58	0·38	0·88	0·60	1·01	0·78‡
56–63	51	2·52	35	2·18	2·04	2·45	5·20	4·63	5·39	4·19
		0·50		0·67†	0·41	0·48‡	0·68	0·90†	1·03	1·09‡
63–70	47	2·51	33	2·00	1·93	1·60	4·40	3·60	4·75	2·62
		0·52		0·55‡	0·47	0·30‡	0·76	0·55‡	1·26	0·77‡
70–77	46	2·04	32	1·19	1·94	1·39	4·01	2·58	5·54	2·36
		0·66		0·42‡	0·66	0·34‡	0·92	0·62‡	0·91	1·11‡
77–84	45	1·18	31	0·93	1·37	1·12	2·55	2·00	4·21	2·06
		0·51		0·42*	0·35	0·31†	0·61	0·63‡	0·84	0·86‡
84–98	45	0·74	29	0·52	0·69	0·37	1·42	0·91	3·18	1·40
		0·30		0·25†	0·34	0·15‡	0·38	0·38‡	0·77	0·50‡
98–112	45	0·54	29	0·35	0·58	0·27	1·13	0·61	2·42	1·24
		0·36		0·17†	0·34	0·12‡	0·41	0·24‡	0·76	0·60‡
112–126	44	0·28	28	0·20	0·46	0·18	0·75	0·39	1·51	0·62
		0·29		0·17	0·47	0·10†	0·49	0·18‡	0·73	0·49‡
126–140	41	0·11	27	0·13	0·33	0·09	0·44	0·22	0·99	0·25
		0·14		0·13	0·29	0·08‡	0·31	0·12‡	0·45	0·30‡
140–154	40	0·12	26	0·11	0·17	0·06	0·28	0·17	0·95	0·38
		0·14		0·13	0·26	0·07*	0·27	0·13*	0·51	0·37‡
154–168	39	0·08	26	0·05	0·06	0·03	0·14	0·07	0·65	0·22
		0·08		0·05	0·07	0·03*	0·12	0·06†	0·66	0·72*
168–182	38	0·11	25	0·09	0·05	0·04	0·16	0·13	0·69	0·76
		0·12		0·11	0·07	0·06	0·15	0·14	0·73	0·87
182–196	37	0·04	25	0·05	0·05	0·01	0·09	0·07	0·06	−0·64
		0·07		0·09	0·10	0·03	0·12	0·11	0·68	0·68
196–210	38	0·01	24	0·01	0·06	0·01	0·09	0·01	−0·69	0·49
		0·03		0·02	0·10	0·02*	0·14	0·03	4·01	0·36

Female mean significantly different from male mean at: * 5%; † 1%; ‡ 0·1% level.

Tail length (Figs. 7, 8; Tables 1, 2)

There is no appreciable sex difference in tail length till about 75 d PC, after which time the males become progressively longer, the difference being about 10% at completion of growth.

The velocity curve for both sexes closely resembles that of nose-rump length. There is a rise to 30 d PC, a fall to 40, a marked rise to 55 and then a gradual deceleration. In the male this deceleration is diminished from 65 to 75 d PC, when the velocity becomes constant. In the female no such diminution of deceleration occurs. This 'relative spurt' in tail length in the male therefore occurs some 10–15 d after the 'relative spurt' in nose-rump length. It is a phenomenon of late puberty. From 60 to 160 d PC the males have a significantly greater velocity than females.

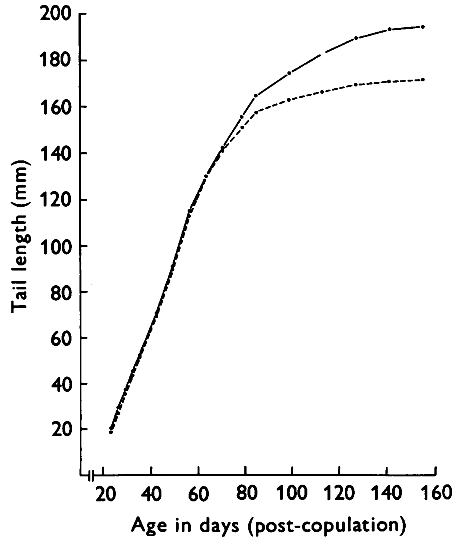

Fig. 7

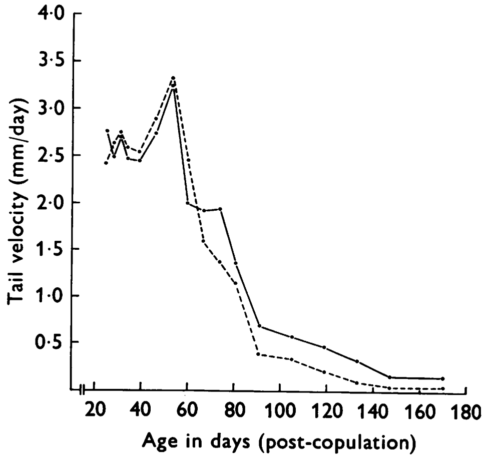

Fig. 8

Fig. 7. Tail length of male and female animals. Male, ———; Female, – – – –.

Fig. 8. Tail length velocity of male and female animals. Male, ———; Female, – – – –.

Total length (Figs. 9, 10; Tables 1, 2)

Total length is simply the sum of nose-rump and tail lengths. A sex difference first appears at about 60 d, both in length attained and in velocity of length. The velocity curves resemble those of the component measurements; the relative spurt in males is at about 75 d PC, and the male velocity is significantly larger than the female from 60 d PC to completion of growth.

Body weight (Figs. 11, 12; Tables 1, 2)

Body weight is included here for comparison with the length measurements. The weight-attained curves are S-shaped. Males are heavier than females at all ages, the difference becoming statistically significant at 55 d PC and increasing so that by 150 d males are 35% heavier.

The velocity curves are somewhat different from those of length. The velocity in both sexes increases gradually till about 40 d PC (corresponding more or less to the time at which the pups begin to supplement their diet with increasing amounts of non-milk food) when a much larger increase occurs, reaching a peak at 60 d PC.

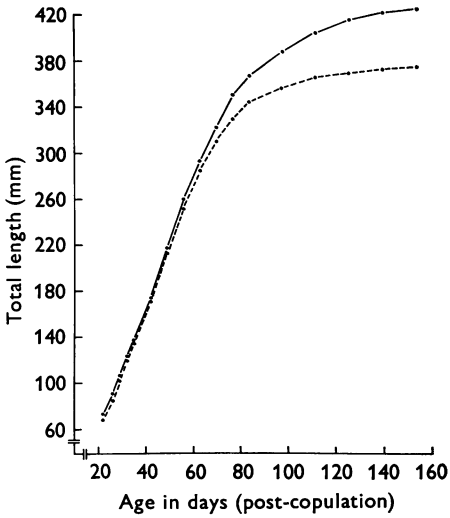

Fig. 9

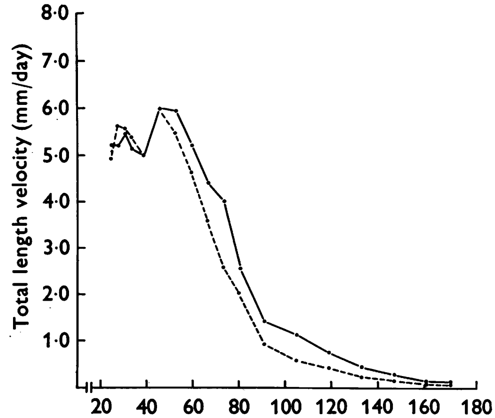

Fig. 10

Fig. 9. Total length of male and female animals. Male, ———; Female, – – – –.

Fig. 10. Total length velocity of male and female animals. Male, ———; Female, – – – –.

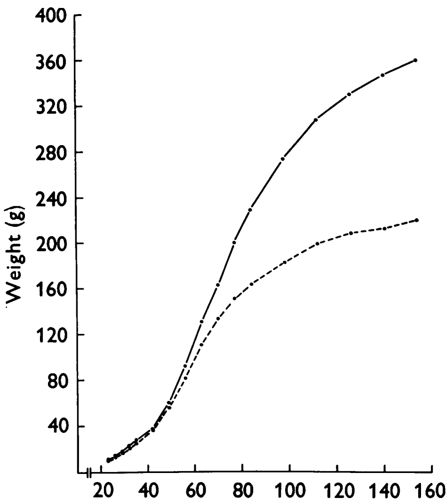

Fig. 11

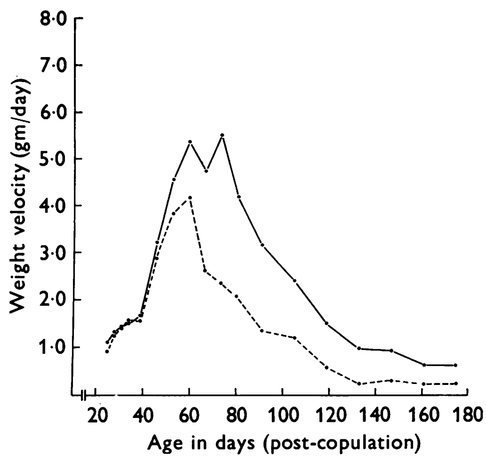

Fig. 12

Fig. 11. Weight of male and female animals. Male, ———; Female, – – – –.

Fig. 12. Weight velocity of male and female animals. Male,———; Female,– – – –.

Thereafter the female velocity declines, rapidly at first and then more slowly. The male velocity, unlike the female, has a double peak which is not due to sampling error, since it is present also in the pure longitudinal series followed from 23 to 140 d PC. This peak is considerably higher than the female one and from 40 to 140 d the male velocity is significantly greater than the female.

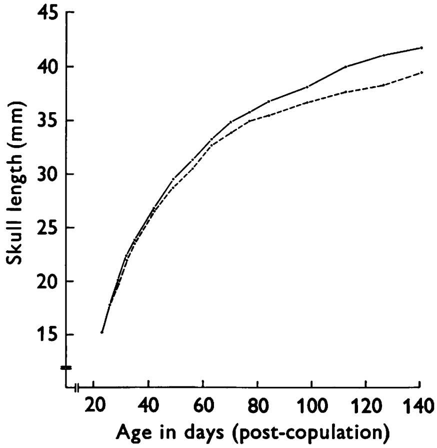

Fig. 13

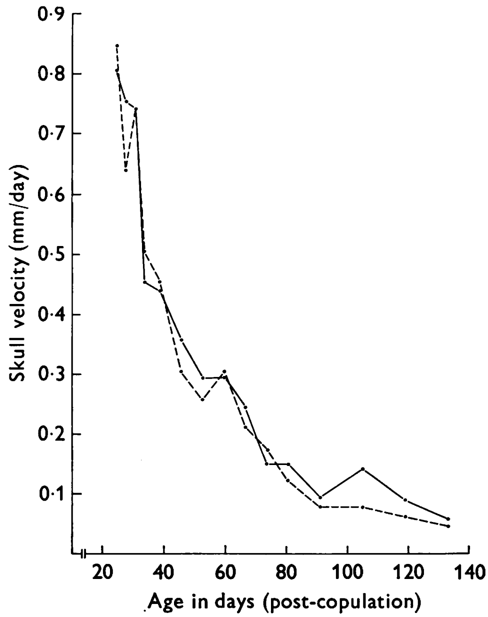

Fig. 14

Fig. 13. Skull length of male and female animals. Male, ———; Female, – – – –.

Fig. 14. Skull length velocity of male and female animals. Male, ———; Female, – – – –.

Skull length (Figs. 13, 14; Tables 3, 4)

The curve for skull length is parabolic from birth onwards. Males have longer skulls than females from about 30 d PC, the difference increasing steadily, becoming statistically significant at 60 d PC and reaching 7% at 140 d PC, the last age at which this measurement was taken.

The velocity curves show a fairly steady decrease from 23 d PC onwards. There is a definite diminution of this decrease, however, at 60 d PC which is as well, or better, shown by the females as by the males. Significant growth is still taking place in both sexes at 130 d PC, beyond which our records cease. There is apparently an increase of male velocity at 105 d PC, but this may be sampling artefact.

Pelvis length (Figs. 15, 16; Tables 3, 4)

Males are larger at all ages, and significantly so from 70 d PC onwards. The difference steadily increases until the males are 11% larger at 140 d PC.

The velocity increases steadily from 23 d PC to a peak at 50 d PC, then falls steadily till 140 d. In the males, but not the females, there is a slight decline in deceleration at 65 d PC.

Arm length (Figs. 17, 18; Tables 3, 4)

Males have longer forelimbs than females at all ages, the difference becoming significant at about 60 d PC and thereafter increasing to 10% at 140 d PC.

The velocity curve lies between those of skull and pelvis lengths. The peak is reached

Table 3. *The mean and* S.D. *of physical measurements at each age in days post-copulation*

	Skull length (mm)				Pelvis length (mm)		Forelimb (arm) length (mm)		Hind-limb (leg) length (mm)	
Age	N	Male	N	Female	Male	Female	Male	Female	Male	Female
23	34	15·20	28	15·21	5·86	5·78	16·28	15·83	18·61	18·12
		0·81		0·85	0·44	0·48	0·85	0·97	1·49	1·92
26	42	17·84	33	17·81	7·46	7·27	20·25	19·98	24·57	22·92
		0·95		1·11	0·63	0·59	1·25	1·38	1·65	1·82
29	39	20·19	36	19·67	8·99	8·69	24·11	23·47	29·81	28·38
		1·25		1·20	0·75	0·74	1·63	1·79	2·34	2·36
32	44	22·43	36	21·97	10·78	10·39	27·84	27·38	34·82	34·48
		1·24		1·14	0·81	0·84	1·71	1·96	2·41	3·08
35	43	23·87	32	23·53	12·59	12·31	31·65	31·15	41·31	40·33
		1·12		1·17	0·89	0·91	1·80	1·68	2·91	3·05
42	41	26·95	30	26·69	16·88	16·58	37·67	37·54	53·56	52·74
		1·19		1·08	1·08	0·98	1·83	1·87	3·28	2·87
49	36	29·61	24	28·74	21·58	20·94	43·70	42·48	64·26	62·04
		1·06		1·01	1·31	1·07	1·71	1·28	2·96	2·78†
56	31	31·45	28	30·65	26·16	25·44	48·68	47·35	72·45	70·26
		0·77		0·80	1·30	1·15	1·51	1·31	2·35	2·53‡
63	28	33·43	20	32·76	29·98	29·01	52·47	50·61	78·69	75·64
		0·93		1·05*	1·27	1·32	1·30	1·31‡	2·47	2·73‡
70	27	35·09	27	33·95	33·30	31·91	55·52	52·87	83·56	79·81
		1·05		1·05‡	1·15	1·25‡	1·30	1·29‡	2·36	2·79‡
77	20	35·93	25	35·10	36·09	34·15	58·45	55·27	88·76	83·59
		1·13		0·90†	1·16	1·15‡	1·54	1·39‡	2·32	2·26‡
84	27	36·84	25	35·74	38·35	35·61	60·06	56·64	91·71	85·68
		0·99		0·89‡	1·14	1·09‡	2·05	1·25‡	1·70	1·81‡
98	24	38·28	20	36·76	40·88	37·25	63·22	58·06	93·90	87·29
		1·02		1·08‡	1·26	1·42‡	1·42	1·32‡	2·54	1·81‡
112	22	40·25	17	37·75	42·28	38·28	64·14	58·48	95·60	88·37
		1·20		0·95‡	1·46	1·22‡	1·90	1·31‡	3·28	1·89‡
126	18	41·25	17	38·52	43·85	39·39	64·97	59·23	94·25	89·06
		1·12		0·85‡	1·67	1·35‡	1·45	1·32‡	2·13	2·31‡
140	20	41·98	18	39·03	44·63	39·88	66·56	59·80	96·62	89·85
		1·14		0·91‡	1·49	1·30‡	1·46	1·26‡	2·51	1·79‡

Female mean significantly different from male mean at: * 5%; † 1%; ‡ 0·1% level.

in both sexes at about 30 d PC (corresponding to the first nose-rump and tail peak). There are possibly small declines in the deceleration in both sexes at 75 d and in males only at 45 d, but it is not certain that these are significant.

Leg lengths (Figs. 19, 20; Tables 3, 4)

Males have longer hind limbs than females at all ages, the difference becoming statistically significant at 50 d PC and increasing to 8% at 140 d PC.

The velocity increases from 23 d PC to reach a peak at 33 d in both sexes (3 d after

Table 4. *The mean and* S.D. *of the velocity of physical measurements at each age in days post-copulation*

Age	Skull length (mm day)				Pelvis length (mm day)		Arm length (mm day)		Leg length (mm day)	
	N	Male	N	Female	Male	Female	Male	Female	Male	Female
23–26	34	0·81	24	0·85	0·47	0·43	1·18	1·19	1·72	1·55
		0·33		0·36	0·15	0·15	0·22	0·27	0·37	0·69
26–29	37	0·76	35	0·64	0·50	0·47	1·30	1·21	1·76	1·72
		0·31		0·30	0·15	0·14	0·29	0·28	0·41	0·33
29–32	43	0·74	36	0·74	0·59	0·56	1·22	1·23	1·83	2·00
		0·24		0·29	0·10	0·10	0·30	0·27	0·33	0·44
32–35	43	0·46	32	0·51	0·59	0·62	1·25	1·21	2·05	2·01
		0·15		0·16	0·13	0·14	0·30	0·21	0·40	0·38
35–42	41	0·44	30	0·46	0·62	0·61	0·85	0·91	1·74	1·75
		0·09		0·10	0·08	0·08	0·16	0·14	0·19	0·17
42–49	36	0·36	24	0·31	0·65	0·64	0·84	0·73	1·49	1·40
		0·12		0·12	0·08	0·05	0·19	0·17*	0·18	0·13
49–56	31	0·30	28	0·26	0·65	0·63	0·70	0·66	1·17	1·16
		0·12		0·09	0·05	0·07	0·14	0·13	0·17	0·20
56–63	28	0·30	20	0·31	0·55	0·52	0·53	0·48	0·89	0·78
		0·13		0·10	0·07	0·08	0·17	0·13	0·18	0·16
63–70	27	0·25	27	0·21	0·50	0·41	0·44	0·34	0·74	0·60
		0·10		0·09	0·07	0·08‡	0·13	0·14†	0·20	0·21*
70–77	20	0·15	25	0·18	0·40	0·31	0·42	0·34	0·76	0·54
		0·14		0·11	0·07	0·10‡	0·12	0·13†	0·19	0·21‡
77–84	27	0·15	25	0·12	0·32	0·22	0·28	0·21	0·38	0·31
		0·09		0·12	0·06	0·07‡	0·11	0·09*	0·17	0·16
84–98	24	0·10	20	0·08	0·18	0·12	0·19	0·11	0·18	0·13
		0·05		0·07	0·04	0·04‡	0·05	0·04‡	0·07	0·07*
98–112	22	0·14	17	0·08	0·10	0·08	0·10	0·05	0·13	0·08
		0·06		0·04‡	0·05	0·04	0·04	0·03‡	0·11	0·05
112–126	18	0·09	17	0·06	0·11	0·08	0·06	0·05	0·04	0·04
		0·05		0·05	0·04	0·05†	0·04	0·03	0·04	0·04
126–140	20	0·06	18	0·05	0·05	0·04	0·08	0·05	0·10	0·08
		0·04		0·04	0·03	0·03	0·05	0·03	0·06	0·06

Female mean significantly different from male mean at: * 5%; † 1%; ‡ 0·1% level.

the arm length). It then falls, but with a clear interruption at 75 d which is present in both sexes, though greater in males. This corresponds in age to the questionable interruption in arm length deceleration.

Shape changes

In Figs. 21–23 the means of one dimension at each age are plotted against the corresponding means of another. Such plots may reveal shape changes during growth, and the genesis of sex dimorphism in shape (see Hiernaux, 1968 for discussion).

Figure 21 shows tail length plotted against nose-rump length. The lines are fairly

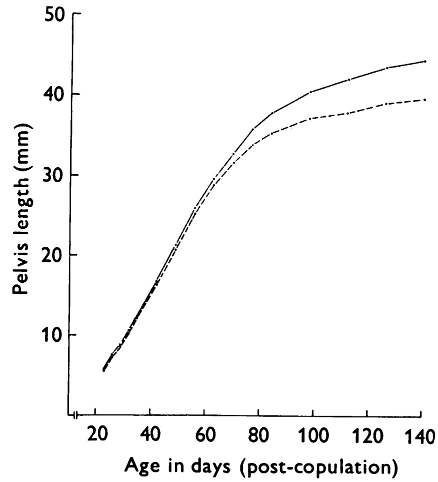

Fig. 15

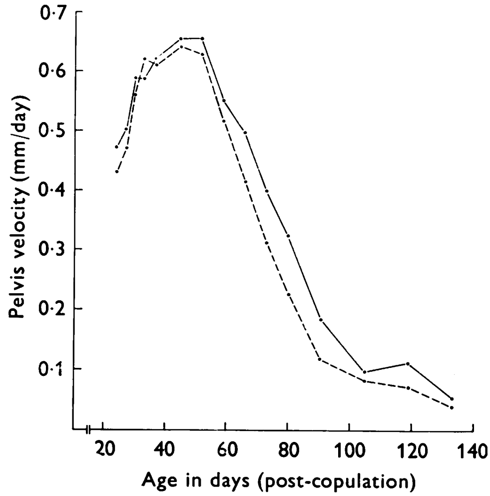

Fig. 16

Fig. 15. Pelvis length of male and female animals. Male, ———; Female, - - - -.

Fig. 16. Pelvis length velocity of male and female animals. Male, ———; Female, - - - -.

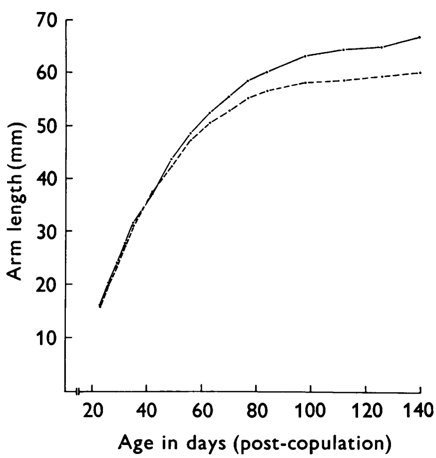

Fig. 17

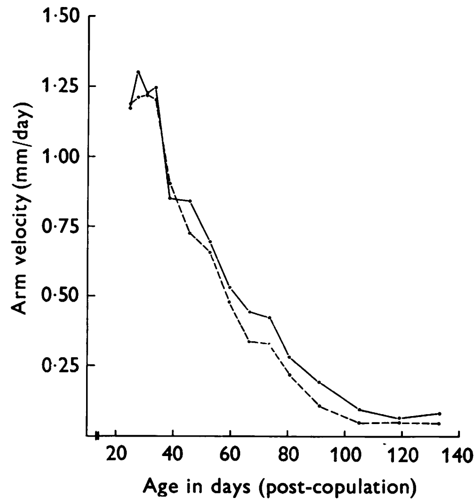

Fig. 18

Fig. 17. Forelimb (arm) length of male and female animals. Male, ———; Female, - - - -.

Fig. 18. Forelimb velocity of male and female animals. Male, ———; Female, - - - -.

straight, and on the assumption of linearity the females have a significantly higher regression ($P < 0{\cdot}05$). When the females have stopped growing (or very nearly), they have longer tails than males of the same body length. But towards the end of their growth the males increase in tail length rather more than in body length (the line

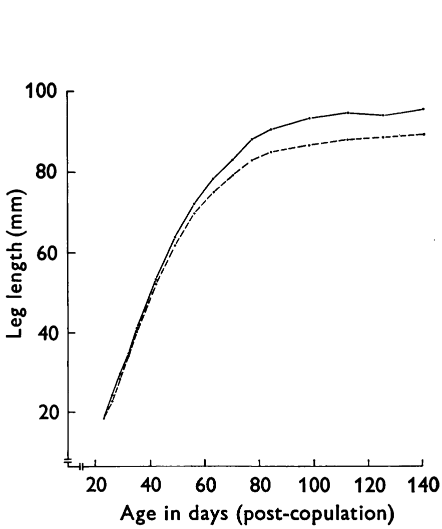

Fig. 19

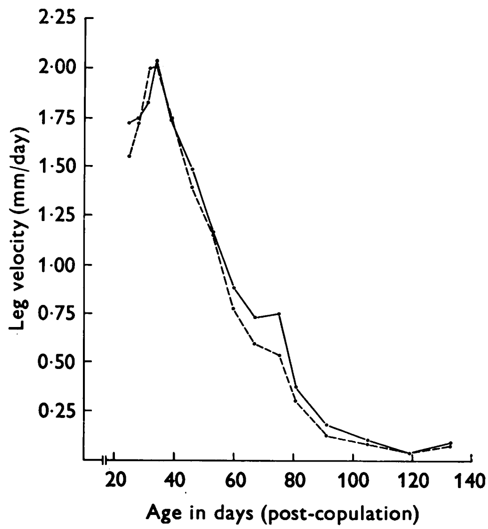

Fig. 20

Fig. 19. Hind-limb (leg) length of male and female animals. Male, ———; Female, – – – –.

Fig. 20. Hind-limb velocity of male and female animals. Male, ———; Female, – – – –.

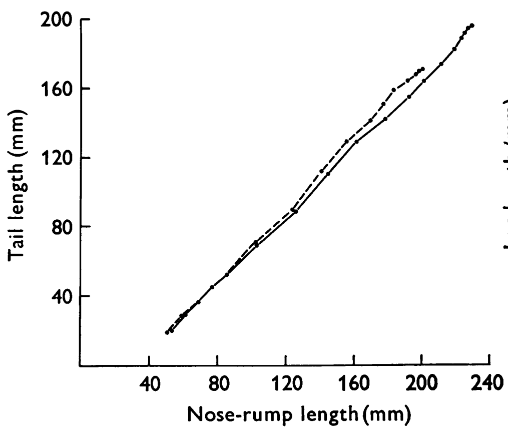

Fig. 21

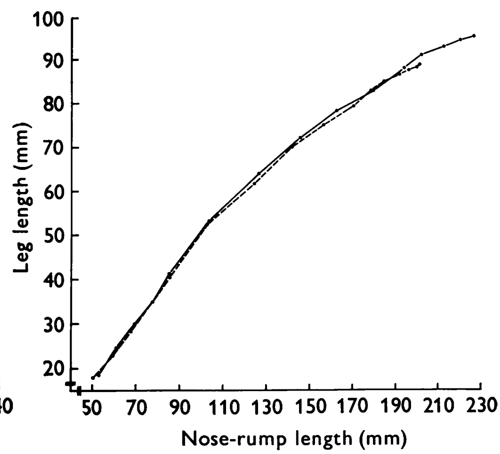

Fig. 22

Fig. 21. Tail length plotted against nose-rump length for male and female animals. Male, ———; Female, – – – –.

Fig. 22. Hind-limb (leg) length plotted against nose-rump length for male and female animals. Male, ———; Female, – – – –.

curves upwards a bit) so that finally the proportions are the same in both sexes, despite the males' larger size.

In Fig. 22 leg length is plotted against nose-rump length and in Fig. 23 arm length against leg length. In neither instance is there much shape difference between the sexes, despite the males' greater size. Pelvis length plotted against skull length gives the same result. Evidently in this strain of rat sex differences in skeletal lengths are almost entirely of size and not of shape.

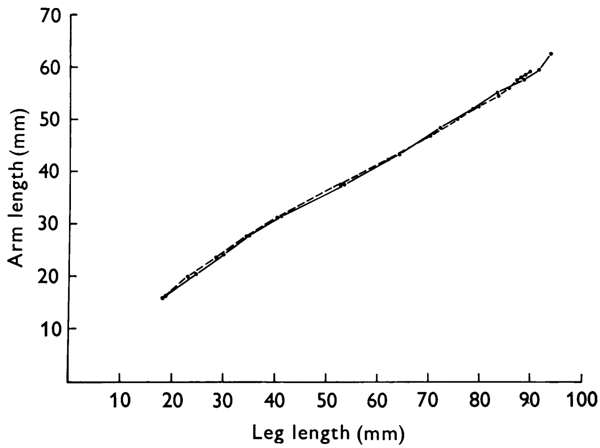

Fig. 23. Forelimb (arm) length plotted against hind-limb (leg) length for male and female animals. Male, ———; Female, – – – –.

DISCUSSION

Methods

The chief novelties that we have introduced are (*a*) the use of age reckoned from copulation, not birth (*b*) the anaesthetization of animals before measurement (*c*) a new and accurate method for measuring body and tail length and (*d*) standardized radiography for the measurement of a considerable range of body dimensions.

Length of gestation varies in rats (from 19 to 23 d PC in our strain) and weight and length at birth are dependent upon it to a considerable degree. The use of post-copulatory (PC) age instead of post-birth age reduces the variability between rats and between litter means in weight and other measurements throughout the growing period. We reduced all litters to a standard number of animals at birth (eight), a prerequisite for studies of normative growth in these animals.

The results obtained on anaesthetized animals were in our hands much more reliable than those on conscious ones. This is probably due to the degree of relaxation in conscious animals varying from occasion to occasion. Measurements of nose-rump and tail length taken by the same observer some 20 min apart varied by as much as 5% in conscious animals compared with only 1% in anaesthetized animals. Differences between duplicate measurements made by different, but experienced observers using the present technique also approximated 1%.

The apparatus and technique we use for nose-rump and tail length differs from that of Acheson & MacIntyre (1959) not only in our using anaesthetized animals but also in our taking both measurements without moving the animal in between. Our read-out system also has considerable advantages.

Some previous workers say they had difficulty in measuring the radiographic image in young rats (e.g. Scow *et al.* 1949). The sites of measurement we have chosen were

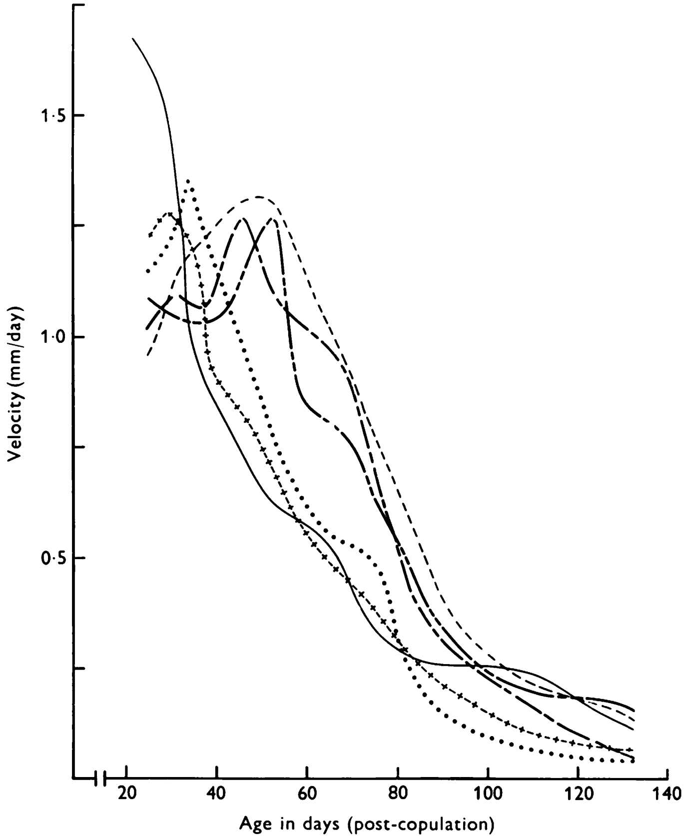

Fig. 24. The velocity of male skull, pelvis, forelimb, hind limb, nose-rump and tail lengths. ———, skull (× 2·0); – – – –, Arm (× 1·0); · · · ·, Leg (× 0·66); —·—·—, Nose-rump (× 0·4); —··——··—, Tail (× 0·4); - - - - -, Pelvis (× 2·0).

those that could be reliably located throughout the whole of the growth period by our technique. The difference between duplicate measurements on the same film by the same observer was under one per cent 95% of the time, and between different observers was only around 1·5%.

Results

The rat growth curve. Figure 24 shows velocity curves in males for skull, pelvis, arm, leg, nose-rump and tail length, obtained by smoothing the curves of Figs. 6, 8, 14, 16, 18 and 20 above. Though there are some complications, the basic curve consists of an increase in growth velocity from some time before birth until a peak is reached, followed by a gradual decline or deceleration. The decline is checked temporarily at an age corresponding to puberty. In man and some other primates this second wave of growth occurs later, when the general velocity is relatively lower, and results in a marked actual acceleration (the adolescent spurt, see Tanner, 1962) rather than a mere diminution of deceleration.

The peak of the basic velocity curve in the rat is reached at different ages by different parts of the body. As in other animals there is a general cephalocaudal maturity gradient; the skull is ahead of the body and the forelimbs ahead of the hind limbs. In these rats the skull length has its peak at or before birth; at 23 d PC there is a higher velocity than at any subsequent age. The arm length peaks next, at 30 d PC, and then the leg length at 33 d PC. The major peak of nose-rump length is at 45 d, of pelvis length at 50 d and of tail length at 55 d. There are no sex differences in these timings. Body weight has its major peak at about 60–70 d, with males perhaps a little later than females, probably because the peak in this measurement is confounded with the puberty 'relative spurt'.

Nose-rump and tail length show a curious earlier feature. Both increase in velocity from 23 d to a small peak at 30 d, fall to 40 d and then increase to their major peak. This occurs in both sexes. It is unlikely to be due to sampling error. It may be related to food intake, the amount of milk available becoming relatively smaller as the pups get bigger, and failing to sustain a high velocity from 30 to 40 d, after which time the pups begin to supplement their diet with solid food. Neither Acheson & MacIntyre (1959), Swanson & Werff ten Bosch (1963) nor Ostadaleva & Parisek (1968) measured their animals this young, so no previous data on this age period are available.

Most measurements show a secondary feature in the velocity curve. The decline after the peak is checked for a few days at a period corresponding to or somewhat later than vaginal opening (54 d on average in this strain) or testicular descent (50 d). There is no actual acceleration (i.e. increase in absolute velocity) in most measurements, but the rate of deceleration gets less, producing the appearance of a 'shoulder' on the declining velocity curve. This 'relative spurt' as we may call it, is distinctly greater in males than females, just as the true adolescent acceleration is greater in males in primates.

The age of the maxima of the 'relative spurt' are harder to determine than those of the basic curve velocity peaks, since they are much less marked. They seem to be at about 50–55 d in nose-rump length, 65–75 d in tail length (males only; none visible in females) 60–65 d in skull length (both sexes) and pelvis length (males only) and about 75 d in leg length (both sexes) and, perhaps, arm length. In weight it is impossible to disentangle this relative spurt from the basic curve peak; the two overlap, particularly in the male. The limb relative spurts occur sufficiently later than the others to make one wonder whether they are not under some quite different influence, unconnected with sexual maturation.

Swanson & Werff ten Bosch (1963) noted a similar 'halt in the deceleration of growth rate' in their Wistar albino rats. These had vaginal opening about a week later than ours (about 63 d PC). There was a spurt in tail length, more marked in males than females, at about 90 d PC, coinciding with a secondary spurt in body weight, also more marked in males. The secondary relative spurt in male tail length can also be seen in the data of Acheson & MacIntyre (1959).

Clegg (1966) in Wistar albinos found that the peak velocity of growth of accessory reproductive organs in the male was at *c.* 70 d PC and that the number of Leydig cells reached its maximum at that time also. As peak weight velocity in his rats occurred at the same age as it did in ours, it seems likely that in our strain too the age of maximum pubertal growth of reproductive organs was 70 d PC, a considerable time after the descent of the testes.

Sex differences. The males of this strain of rats are from birth very slightly larger than the females, but the difference only becomes appreciable, and statistically significant in our data, at about 60 d PC (50 d for nose-rump and 75 for tail). The males' mean velocity is significantly greater from 60 d PC (nose-rump and tail) or

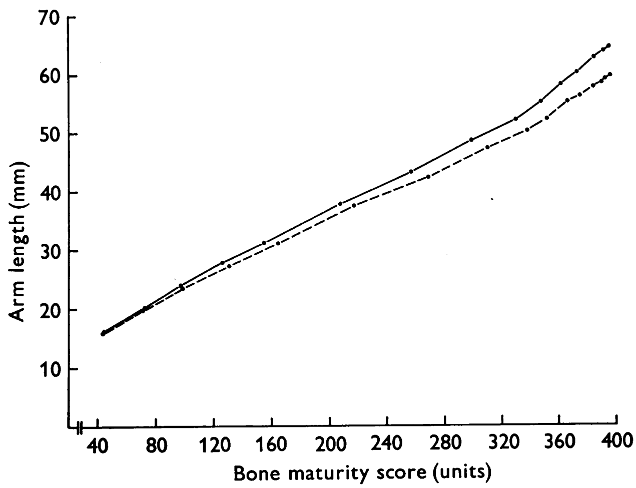

Fig. 25. Forelimb (arm) length plotted against total bone maturity score for male and female animals. Male, ———; Female, – – – –.

65 d PC (arm, leg and pelvis) until growth is nearly complete. Hence the sex difference in most measurements gets gradually larger from the time of puberty onwards until at full growth males are from 7% (skull length) to 12% (nose-rump) larger and some 35% heavier.

The sex difference in size from 30 to 80 d is somewhat masked by the fact that females mature a little faster than males; from 32 until 80 d females are significantly advanced over males in bone maturity (Hughes & Tanner, 1970). Thus at equal bone maturity, or equal percentage of adult size, the male–female difference is rather greater than at a given chronological age. It seems as if the greater size of the male comes about through a rather steadily increasing gradient throughout the whole of growth, rather than any sudden development at or around puberty. Figure 25 demonstrates this for arm length, plotted against bone maturity score. In tail length, however, and to a lesser extent in nose-rump length, the sex difference is specifically further increased at puberty by the greater relative spurt of the male.

The sex difference is chiefly one of size and not shape. Our measurements show little sign of sex dimorphism in shape, but they are all measurements of length.

Shape differences might be shown, for example in the pelvis, by inclusion of measurements of breadth (see Harrison, 1968, Bernstein & Crelin, 1967).

Strain differences. There are evidently differences in rates of growth between different strains of rat. The Sprague–Dawley strain studied by Acheson & MacIntyre (1959) was greater than ours in length and weight from at least 30 d onwards and probably grew up a little faster. The shape of the growth curves and the manner in which the sex differences appear, however, are very similar in our strain, Acheson's Sprague–Dawley rats and Swanson's Wistar albinos.

SUMMARY

An apparatus is described with which reliable measurements of nose-rump and tail length may be made on anaesthetized rats from birth to maturity. A radiographic technique for measurement of skull, limb and pelvis lengths is also described.

The growth of black-hooded rats has been studied longitudinally. Age is better reckoned from day of copulation than days after birth, for reasons given. Litters were reduced to 8 rats each at birth. Nose-rump, tail, skull, pelvis, forelimb (arm) and hind limb (leg) lengths and body weight were measured at 3 d intervals from 23 d post-copulatory (PC) (approximating birth) to 35 d PC, weekly to 84 d PC and fortnightly to 140 or 210 d PC.

Means and S.DS. of these measurements at each age are given, and means and S.DS. of individual increments from one period to the next. Males are slightly larger than females from 23 d PC onwards, but the difference becomes significant only at about 60 d PC for most measurements and increases thereafter, to reach between 7% (skull length) and 12% (nose-rump) for length measurements and 35% for body weight when growth is practically complete. The sex difference is essentially one of size; the present length measurements show no dimorphism in shape or proportion.

The basic curve of growth rate consists of a rise from early in life to a peak, followed by a gradual decline. The peak is reached at or before 23 d PC by skull length, at 30 d PC by arm length, 33 d by leg length, 45 d by nose-rump length, 50 d by pelvis length and 55 d by tail length. There are no sex differences in this basic curve. Nose-rump and tail length show a smaller rise in velocity from 23 to 30 d followed by a fall to 40 d then a larger rise.

The decline in velocity shows a check ('relative spurt') in most measurements, more marked in males, at about 55 d for nose-rump length, 60 d in skull and pelvis length and 65 to 75 d for tail, arm and leg lengths. This occurs at or a little after puberty (testis descent 50 d vaginal opening 54 d) and may correspond to the pubertal acceleration seen in many primates. In the rat there is no actual acceleration, but only a lessened deceleration.

We wish to thank the Nuffield Foundation for the support which made this work possible, Mr W. Bell and Mr L. A. Cox for measuring the test series of radiographs, Mr H. Goldstein and Miss M. T. Manning for help with the data processing and Dr W. A. Marshall and Mr R. H. Whitehouse for helpful comments on the manuscript. Some technical parts of the paper are based on a thesis by P.C.R.H. submitted for F.I.S.T.

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