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PRE- AND POSTNATAL GROWTH PHENOMENA OF BURCHELL'S ZEBRA *EQUUS BURCHELLI ANTIQUORUM*

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Abstract – Between 1969 and 1972 growth data were collected from 175 zebra *Equus burchelli antiquorum* and 138 zebra embryos and foetuses from the Central District of the Kruger National Park, Republic of South Africa. Statistical analysis of data indicated no significant difference between body mass of adult stallions (range = 267,3 to 373,3 kg; mean = 318,5 kg; n = 57) and adult non-pregnant mares (range = 272,6 to 386,9 kg; mean = 321,6 kg; n = 51) (t = 0,587). The heaviest zebra had a body mass of 429,4 kilogram. This was a pregnant mare carrying a 35,2 kg foetus. Von Bertalanffy growth curves indicated that shoulder heights in young zebra may reach the adult range by one year of age, the adult body mass range is, however, only attained after three years of age. These curves also showed that age classification of free roaming zebra is only reliable up to the age of about two years, after which individual variation is too great. Stallions were significantly taller at the shoulder than mares (mean = 1,8 cm) (t = 2,032) and neck thickness was the only body dimension showing visible sexual dimorphism in adults. Here the stallion had a neck girth on average 8,1 cm greater than the mare. Regression equations for estimating body mass from body dimensions were calculated by using a standard logarithmic transformation and fitting a linear regression by the method of least squares and also by undertaking standard straight line linear regression analyses. Exponential curves obtained by the first method indicated that growth was not isometric (not linear) and that the ratios of any of the dimensions of length to body mass were constantly changing, i.e. growth is allometric. Marked allometric growth differences existed between the two sexes except in the case of the heart girth-body mass relationship. Comparison of growth data from *E. b. antiquorum* with that of *E. b. boehmi* from Tanzania (Sachs 1967), indicates that *E. b. antiquorum* is considerably larger. Body masses differ by an average of 70 kg and 102 kg for stallions and mares respectively. Average birth mass for zebra was 33,7 kg (n = 2♂ + 2♀). The largest foetus had a body mass of 39,0 kilogram. Foetal growth curves are provided. The first signs of body stripes occur at between 250 and 270 days of pregnancy (gestation period = 375 days).

Introduction

Although organic growth is defined as "the measurable increase of an organic system produced by its assimilation of materials obtained from its environment" (von Bertalanffy 1938) or even more simply as "the normal process of increase in size" (Dorland 1965), it nevertheless varies considerably between species and within a species. Within a species growth variation reflects the climatic and imposed management factors of the environment (Thornton 1960).

Data on growth characteristics of zebra in the Kruger National Park (K.N.P.), Republic of South Africa, were collected for the following purposes:

(1) To derive mathematical relationships between body dimensions and body mass. These can be used to replace less accurate visual mass estimation methods.
(2) To examine the use of von Bertalanffy growth curves and equations as an objective method of studying organic growth.
(3) To establish recognisable age specific body dimensions for use in the field during assessments of population age structure.
(4) To determine whether any sex specific growth differences exist.
(5) To collect a representative series of standard body measurements for comparison of present growth phenomena with those collected over the same area and different areas in the future.
(6) To determine the average mass of animals of as many age classes as possible so that reliable zebra biomass figures can be computed.
(7) To compare growth phenomena of K.N.P. zebra with those of the same species in other natural areas.
(8) To establish the age of maximum productivity. This has a bearing on the commercial exploition of zebra on game farms.

Foetal growth data were collected so that they could be correlated with conception age (see Hugget and Widdas 1951). Where the ages of embryos and foetuses can be determined, important events such as mating and foaling can be predicted.

Material and Methods

Between 1969 and 1972 growth data were collected from 175 zebra and 138 zebra embryos and foetuses from the Central District of the K. N. P. (Table 1). In animals from two years upwards cropping was random with respect to age. The sexes, however, had to be selected since stallions are susceptible to hunter selection. Immatures and foals were selectively destroyed while some young foals were captured alive and then released.

Table 1

Specimens used to study pre- and postnatal growth phenomena in Burchell's zebra

AGE GROUP	MALES	FEMALES
Embryos and foetuses	72	66
Foals (0–12 months)	9	16
Immatures (1–2 years)	5	6
Two to 4½ year olds	11	20
Five to 17 year olds	57	51
Totals	154	159

In the present study a zebra conceptus under three months of age is regarded as being an embryo, while terms such as "foetal growth" are used interchangeably with "prenatal growth" and in particular when discussing foetal growth curves.

Body dimensions

Zebra were measured before bloat or rigor mortis had set in. All measurements of length were taken "over the curves" (along the contours of the body) (Ansell 1965) using a flexible steel tape.

The following body dimensions were routinely recorded (Fig. 1):

(a) Total length – from the grinding surface of the first upper incisors to the fleshy tip of the tail.
(b) Tail length – from the sacro-coccygeal joint to the fleshy tip of the tail.
(c) Vertebral column – from the anterior atlas joint (Fig. 1) to the fleshy tip of the tail.
(d) Head length – from the grinding surface of the first upper incisors to the anterior atlas joint.
(e) Ear length – from the notch to the tip of the ear excluding the hairs.
(f) Shoulder height – taken from the top of the withers (middle of the the backbone) to the tip of the hoof.
(g) Heart girth – the circumference of the chest measured immediately behind the fore legs.
(h) Hind foot – from the centre of the heel (hock) to the tip of the hoof.
(i) Neck thickness – smallest circumference of the neck just posterior to the lower jaw.

Embryonic and foetal measurements were similar to those recorded on adults except when mass was less than four grams. In these instances only mass and crown-rump length were recorded. All specimens were measured in the fresh state.

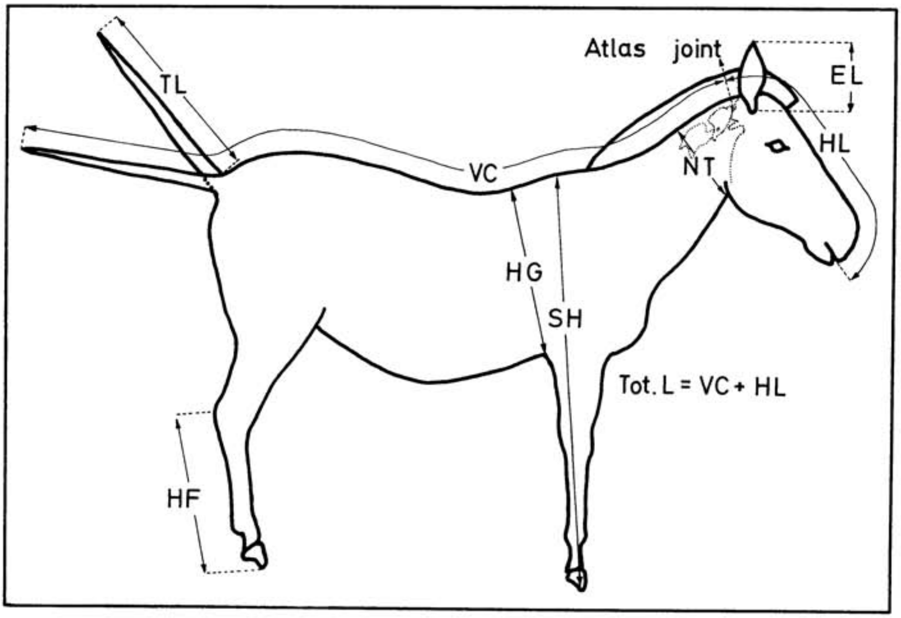


Fig. 1. Routine body dimensions recorded from Kruger Park zebra (including foetuses). Tot. L. = total length; TL = tail length; VC = vertebral column; HL = head length; EL = ear length; SH = shoulder height; HG = heart girth; HF = hind foot; NT = neck thickness. All measurements taken "over curves"

Body mass

Body mass of each zebra was recorded whole in the field using either a 0-200 lb or 0-1 120 lb Salter spring balance. All measurements of mass were later converted to kilograms.

Since the jugular vein was severed when the animal went down, blood loss had to be compensated for. The speed of the coagulation process, however, reduced blood loss to a minimum. This is a phenomenon peculiar to zebra. A "Hiab" hydraulic hoist fitted onto the back of the transport vehicle (Fig. 2) greatly facilitated measurement of mass.

To gain a better knowledge of the true body mass of pregnant mares the mass of the uterus plus its contents was also determined and later subtracted from the total body mass.

Eye-fitted growth curves

For comparison with the more sophisticated von Bertalanffy growth curves, eye-fitted growth curves were plotted by calculating mean body dimensions for 16 different age classes. Here, except for neck thickness, data for stallions and mares were pooled and means calculated.

Fig. 2. The "Hiab" hydraulic hoist and the attached heavy duty "Salter" spring scale (0–510 kg) used for measuring body mass.

Von Bertalanffy growth curves

Based on the work of von Bertalanffy (1938), equations of use in analytical studies on growth phenomena have been described by Beverton and Holt (1957). The formula for growth in mass given by Beverton and Holt (1957) is as follows (*vide* Hanks 1972a). (In the following examples mass has been substituted for weight as used by the above authors):

$$m_t = M_\infty \left(1-e^{-K(t-t_0)}\right)^3$$

Here m_t = mass at age t;
M_∞ = asymptotic mass; the maximum mass that an animal can attain under given conditions;

e = base of the natural (Naperian) logarithm;

K = coefficient of catabolism, a constant representing the catabolism of body materials per unit mass and time;

t = age of animal;

t_0 = theoretical age at which the animal would have zero mass with the same growth pattern as that observed in later life.

A similar formula can also be derived to describe growth in length of any body dimension (see Table 4).

Since growth in mass and growth in height are important parameters for assessing age in the field, they were selected, together with total length and heart girth, for the computation of theoretical von Bertalanffy growth curves. Measurements for stallions and mares were pooled.

Computer facilities at the University of Rhodesia (Hanks *in litt.)* and the University of Pretoria (Robinson *pers. comm.*) were used to fit von Bertalanffy functions to the experimental age specific mass and body dimension data respectively. An outline of the program used to describe growth in mass is given by Hanks (1972a) while that used for the three body dimensions is described by Abramson (1965).

Mass-length relationships (linear regression analysis using logarithmic transformations)

Mass-length relationships were derived using the standard logarithmic transformation and fitting a linear regression by the method of least squares (Ricker 1958, 1968; Pienaar and Thomson 1969). A computer program (Robinson 1966) and computer facilities of the National Parks Board of Trustees (Robinson *pers. comm.*) were used for these computations. Data from stallions and mares were treated both separately and together. In the case of pregnant mares the mass of the uterus plus its contents was subtracted from the total body mass.

Mass-length relationships (straight line regression analysis)

Standard linear regression analyses described by Dunn (1964) and Snedecor (1965) were used to derive regression equations for body mass on shoulder height and body mass on heart girth. Since these measurements showed the highest correlations ($r = 0,95$ and $0,97$ respectively), only they were selected for comparison with the more sophisticated logarithmic transformations previously mentioned. In contrast to the logarithmic tranformations, data on the sexes were always pooled. The mass of pregnant mares was also corrected by subtracting the mass of the uterus plus its contents.

Correlation coefficients were calculated and significance tests (t – tests) carried out as described by the above-mentioned authors.

The ages of all zebra were estimated as described by Smuts (1974a). Foetal and embryonic ages were estimated by the method of Huggett and Widdas (1951). This method is based on the linear relationship between foetal mass and conception age (Fig. 3). Here body mass and conception age of one foetus must be known and therefore birth mass and gestation time are most frequently used. For zebra the following data were used; gestation time (t_g) = 375 days (Kenneth and Ritchie 1953; Wackernagel 1965; Klingel 1969; and one personal observation in the K.N.P. of 396 days); birth mass (m) = 34,0 kg (n = 4, range 30,2 kg to 35,5 kg) and thus $m^{1/3} = 32{,}4$ g; $t_0 \sim 0{,}15 \times t_g = 0{,}15 \times 375 = 56$ days (*vide* Huggett and Widdas 1951). By plotting "t_0" of 56 days the first point is fixed, the "t_g" of 375 days and its ordinate $m^{1/3}$ of 32,4 g fixes the second point (Fig. 3). By calculating $m^{1/3}$ for each foetus it is possible to estimate conception age using the graph in Fig. 3. Alternatively the formula $m^{1/3} = a\,(t - t_0)$ of Huggett and Widdas (1951) can be used. Here "t" = time from conception (days) and "a" = the specific foetal growth velocity, a constant for each species. Using these data, the specific foetal growth velocity of zebra = 0,1016. Time of conception (t) can thus be estimated from

$$t = \frac{m^{1/3} + at_0}{a}$$

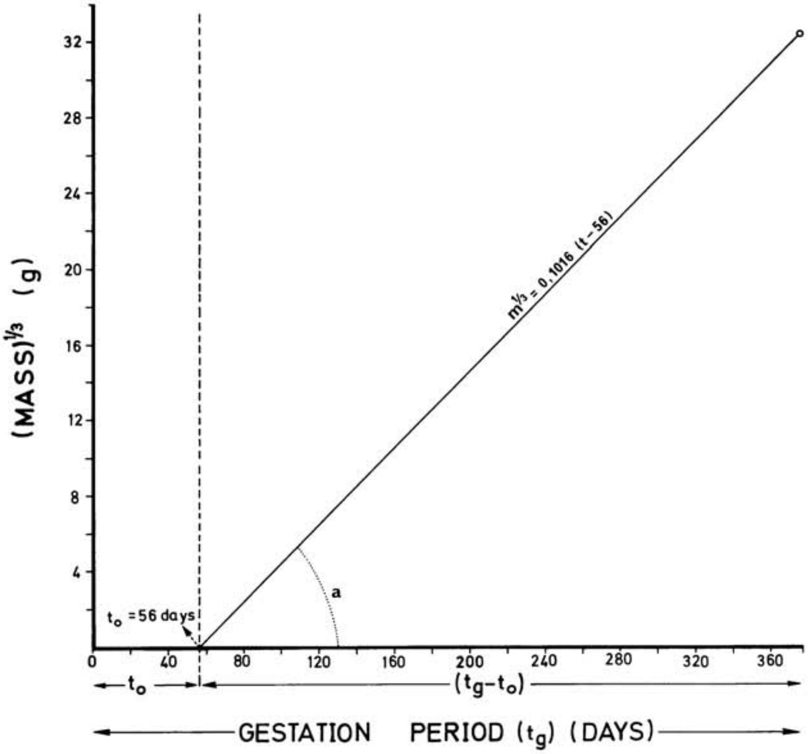


Fig. 3. Graphical method employed to determine "a", the specific foetal growth constant for Burchell's zebra (modified after Huggett and Widdas 1951). The linear relationship: $m^{1/3} = 0{,}1016\ (t - 56)$, can be used to determine "t", the time from conception in days for any zebra embryo or foetus of known mass (m). The standard form for the linear relationship is: $y = 0{,}1016x - 5{,}69$.

In very small embryos (± 100 mg), ages are best estimated by comparison with data on the domestic horse. Here ages were estimated by comparison with data given by Ewart (1915) and van Niekerk (1965).

Results

Curves depicting growth with age phenomena for nine selected body dimensions are illustrated in Fig. 4 and 5.

Since the mean mass of non-pregnant adult mares (5-17-year olds) is 321,6 kg (n = 20) and that of pregnant mares, in which the mass of the uterus plus its contents has been subtracted, is 321,2 kg (n = 31) their masses can be regarded as being identical i.e. excess mass in pregnant mares is due to the stage of pregnancy. With this in mind, comparisons of body mass between adult stallions and adult mares were made using non-pregnant mares together with mares from which the mass of the uterus plus its contents had been subtracted. These comparisons are shown in Table 2.

Table 2

Comparison between body masses of adult Burchell's zebra stallions and mares (5–17 years old). Both non-pregnant mares and pregnant ones from which the mass of the uterus plus its contents were subtracted, were used

PARAMETER	MASS (kg)	
	Stallions	Mares
Maximum	373,3	386,9*
Minimum	267,3	272,6
Mean	318,5	321,6**
Diff. between means	– 3,1 ns	+ 3,1 ns
No. in sample	57	51
t - value	t = 0,587	

* Maximum mass for a pregnant mare (heaviest zebra) = 429,4 kg (945,0 *lbs)*. This was a 14-year old mare carrying a full term 35,2 kg foetus.

** Modal mass for adult stallions plus adult mares = 311–320 kg (Fig. 7).

ns Non-significant at 5% level.

Fig. 6 shows a curve and an equation for estimating the mass of the uterus plus its contents from the conception age of the foetus.

Fig. 7 illustrates continuous variation in a sample of 108 adult zebra (57♂♂ + 51♀♀) and clearly indicates that in the small sample body mass approaches a normal type distribution. Here measurements of mass in pregnant mares were again corrected by subtracting the mass of the uterus plus its contents.

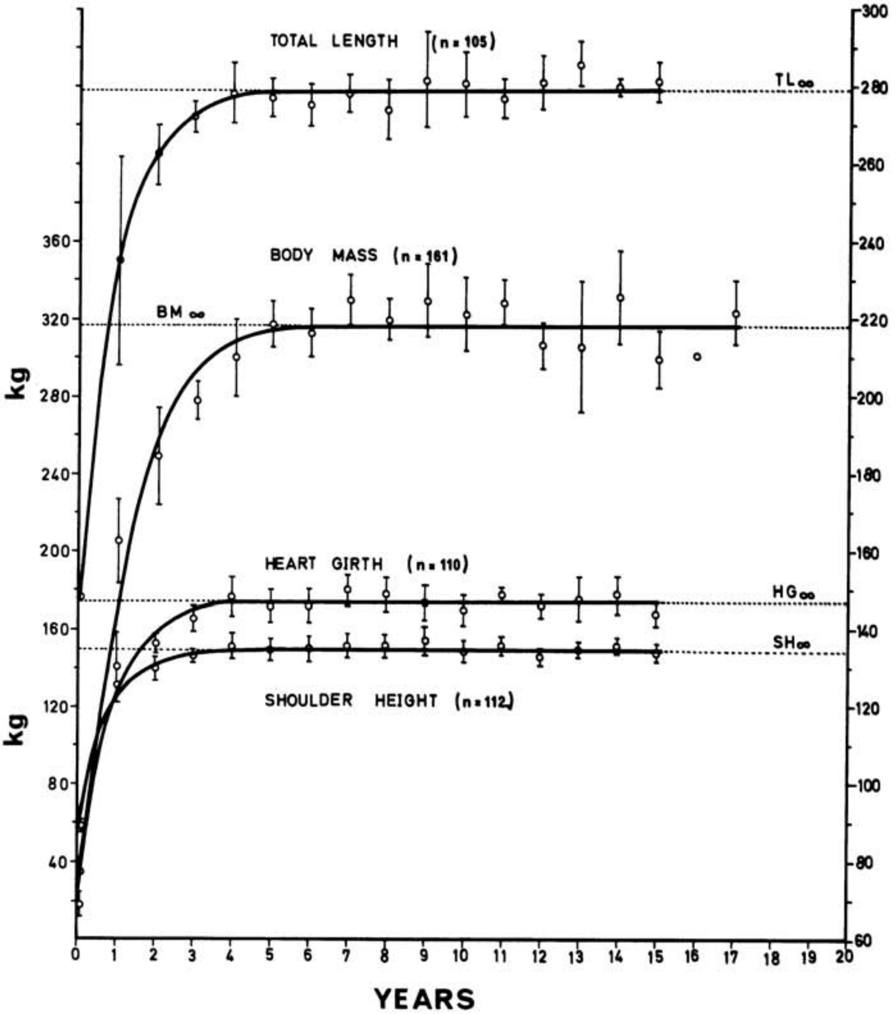


Fig. 4. Curves depicting growth with age phenomena for eight selected body dimensions routinely collected from zebra. In all cases data for stallions and mares were pooled and means calculated. The circles indicate means for each age class. The figures in brackets give approximate age at which the mean dimension for adults is attained and the sample size. All curves were fitted by eye. (y = years; m = months).

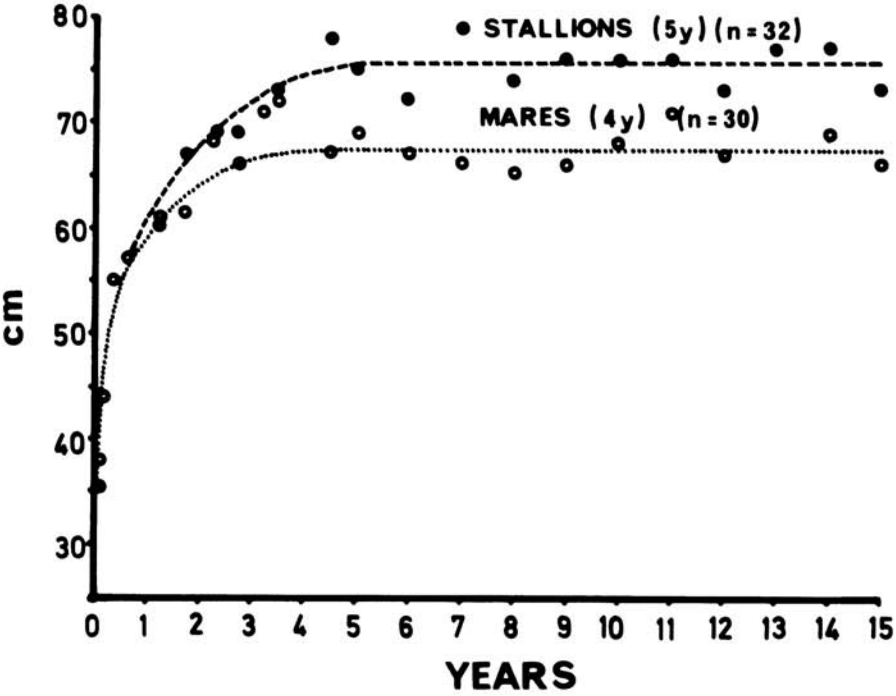


Fig. 5. Curves depicting sex-specific neck thickness growth rates for Burchell's zebra. The circles represent means for each age class while the figures in brackets indicate the approximate age at which the mean dimension for adults is attained. Both curves were fitted by eye. (y = years; n = sample size).

Table 3 gives the comparison of a few relevant body dimensions of adult stallions and mares and the statistical significance of the differences.

Table 4 lists the parameters used in deriving the von Bertalanffy growth relationships with regard to body mass, total length, heart girth and shoulder height by age, for stallions plus mares. The theoretical or fitted growth curves for each of these are illustrated in Fig. 8. Sample means ± two standard errors are also illustrated. Von Bertalanffy growth formuli, for measurements of mass and length, together with their associated parameters are given below Table 4.

Table 5 gives the computer print-out data used to plot the exponential curves (body mass-length relationships) illustrated in Fig 9. Correlation coefficients (r), sample sizes (n) and the equations for estimating body mass from either shoulder height, heart girth, neck thickness or total length are given below each section of Table 5.

Linear regression equations (straight line regressions) for body mass on heart girth and body mass on shoulder height are given in Table 6.

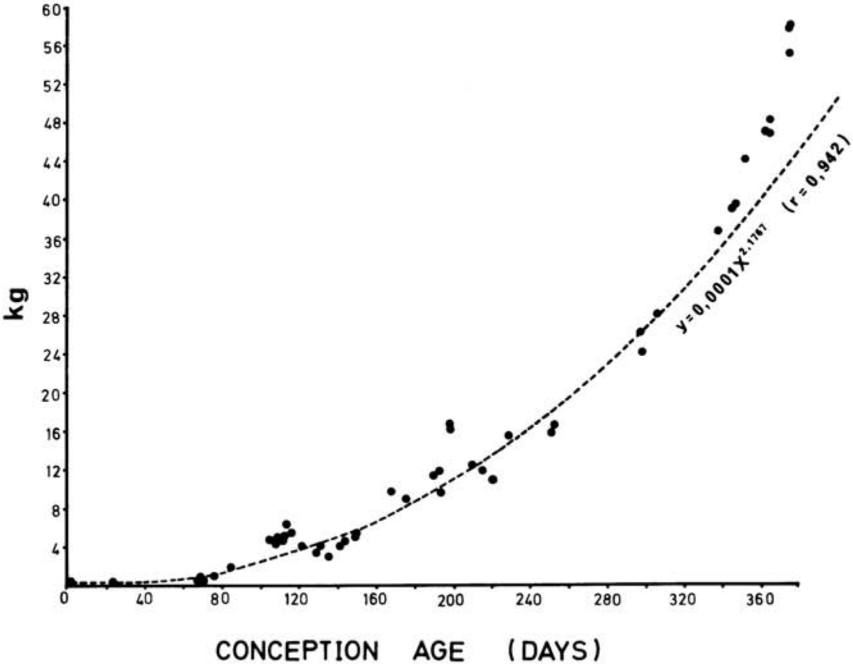


Fig. 6. Curve illustrating growth in mass of the pregnant mare's uterus plus its contents for Burchell's zebra. The curve was fitted by undertaking a logarithmic transformation and fitting a linear regression by the method of least squares. The standard equation $y = ax^b$ was used to describe the regression. This equation and the correlation coefficient (r) are also given. (n = 48).

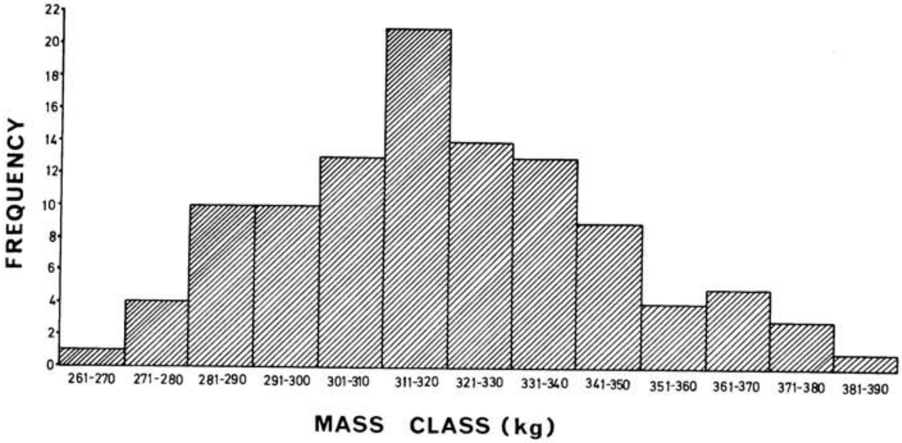


Fig. 7. Variation in body mass shown by a sample of 108 adult Burchell's zebra (5–17 years old) (n = 57♂♂+51♀♀). In the case of pregnant mares, body mass was corrected by subtracting the mass of the uterus plus its contents.

Table 3

Comparison between body dimensions of adult Burchell's zebra stallions and mares and pregnant and non-pregnant mares (5–17 years old)

Parameter	Vertebral column (cm)		Head length (cm)	
	Stallions	Mares	Stallions	Mares
Maximum	236,7	250,4	70,8	69,2
Minimum	194,0	196,5	63,4	63,0
Mean	212,3	215,2	67,7	66,8
Diff. between means	− 2,9 ns	+ 2,9 ns	+ 0,9 ns	− 0,9 ns
No. in sample	42	45	32	32
t - value	t = 1,451		t = 1,938	

Parameter	Heart girth (cm)		Heart girth (cm)	
	Pregnant Mares	Non-pregnant Mares	Stallions	Mares (Pregnant and Non-pregnant)
Maximum	159,5	156,1	159,3	159,5
Minimum	139,8	138,9	137,3	138,9
Mean	149,2	146,5	146,9	148,1
Diff. between means	+ 2,7 ns	− 2,7 ns	− 1,2 ns	+ 1,2 ns
No. in sample	28	18	46	46
t - value	t = 1,845		t = 0,649	

Parameter	Shoulder height (cm)		Neck Thickness (cm)	
	Stallions	Mares	Stallions	Mares
Maximum	146,8	140,8	80,5	73,1
Minimum	126,8	129,4	68,7	61,4
Mean	136,3	134,5	75,6	67,5
Diff. between means	+ 1,8 *	− 1,8 *	+ 8,1 **	− 8,1 **
No. in sample	32	32	32	30
t - value	t = 2,032		t = 10,220	

Parameter	Hind foot (cm)		Ear length (cm)	
	Stallions	Mares	Stallions	Mares
Maximum	57,7	55,4	18,0	19,5
Minimum	48,2	49,4	15,0	16,3
Mean	53,5	52,2	16,7	17,4
Diff. between means	+ 1,3 **	− 1,3 **	− 0,7 **	+ 0,7 **
No. in sample	32	32	32	32
t - value	t = 2,950		t = 2,968	

ns Non-significant at 5% level
* Significant at 5% level
** Significant at 1% level

Table 4

Data used to plot the von Bertalanffy growth curves (Fig. 8) for Burchell's zebra. Computer calculated components of the respective growth equations are given below the table, as are the growth equations

AGE (YEARS)	BODY MASS				TOTAL LENGTH				HEART GIRTH				SHOULDER HEIGHT			
	Fitted Mass (kg)	Sample Mean (kg)	SE of Sample Mean (kg)	n	Fitted Length (cm)	Sample Mean (cm)	SE of Sample Mean (cm)	n	Fitted Heart Girth (cm)	Sample Mean (cm)	SE of Sample Mean (cm)	n	Fitted Shoulder Height (cm)	Sample Mean (cm)	SE of Sample Mean (cm)	n
0 (birth)	34,2	33,7	1,39	4	149,2	148,2	1,90	2	71,2	69,0	1,80	2	89,7	88,9	0,85	2
1	165,5	205,0	10,75	6	233,3	235,5	13,68	4	126,6	130,3	4,52	4	122,3	125,3	2,74	4
2	253,0	249,2	12,44	11	262,9	262,6	3,95	10	139,8	136,4	2,09	10	131,4	129,6	1,30	10
3	292,0	278,4	5,14	17	273,4	272,2	1,95	13	144,7	142,7	1,38	13	133,9	132,9	0,91	13
4	307,5	300,2	10,11	10	277,0	277,9	4,21	6	146,3	148,5	2,37	6	134,6	136,0	1,71	6
5	313,4	318,2	5,84	23	278,3	277,4	2,58	10	146,7	146,1	2,12	11	134,8	134,6	1,26	11
6	315,6	313,0	5,76	8	278,8	275,1	2,73	6	146,9	146,0	2,20	6	134,8	134,8	1,75	6
7	316,4	330,3	6,61	14	278,9	277,8	2,68	7	146,9	150,2	2,10	8	134,8	135,7	1,34	8
8	316,7	319,9	5,54	6	279,0	273,6	4,17	4	146,9	149,2	2,10	5	134,8	135,0	1,38	4
9	316,8	330,0	9,50	9	279,0	281,7	5,98	5	147,0	147,1	2,22	6	134,8	137,0	2,09	6
10	316,8	322,6	9,40	11	279,0	281,2	3,95	7	147,0	144,7	1,72	7	134,8	134,4	1,45	7
11	316,9	329,1	6,22	9	279,0	276,9	2,34	10	147,0	148,9	0,94	10	134,8	135,7	0,99	10
12	316,9	307,1	6,01	11	279,0	281,1	3,44	7	147,0	146,1	1,55	7	134,8	132,7	1,29	7
13	316,9	306,4	17,20	5	279,0	285,7	3,09	4	147,0	148,1	2,77	4	134,8	135,3	1,02	4
14	316,9	332,2	11,95	6	279,0	280,2	1,11	4	147,0	149,3	2,24	5	134,8	136,0	0,98	4
15	316,9	300,3	7,62	8	279,0	281,5	2,67	6	147,0	144,1	1,25	6	134,8	134,0	1,36	6
16	316,9	304,4	—	1	—	—	—	—	—	—	—	—	—	—	—	—
17	316,9	323,6	13,50	2	—	—	—	—	—	—	—	—	—	—	—	—
	M_∞ = 316,8643 (SD = 2,1010) K = 0,9910 (SD = 0,0514) t_0 = 0,6509 (SD = 0,0377)				L_∞ = 279,0200 (SE = 1,1100) K = 1,0440 (SE = 0,0804) t_0 = 0,2672 (SE = 0,0883) SE of estimate = 9,6191 cm				L_∞ = 146,9500 (SE = 0,6200) K = 1,1784 (SE = 0,0983) t_0 = 0,5623 (SE = 0,0752) SE of estimate = 5,6668 cm				L_∞ = 134,8300 (SE = 0,4000) K = 1,2829 (SE = 0,1249) t_0 = 0,8535 (SE = 0,1061) SE of estimate = 3,7004 cm			

$$m_t = M_\infty \left(1-e^{-K(t-t_0)}\right)^3 \quad \text{or} \quad l_t = L_\infty \left(1-e^{-K(t-t_0)}\right)$$

Legend: m_t = mass in kg at age t; l_t = length in cm at age t; e = 2,7183 (base of Naperian logarithm); t = age of animal; M_∞ = asymptotic mass; L_∞ = asymptotic length; K = coefficient of catabolism; t_0 = theoretical age at which the animal would have zero mass.

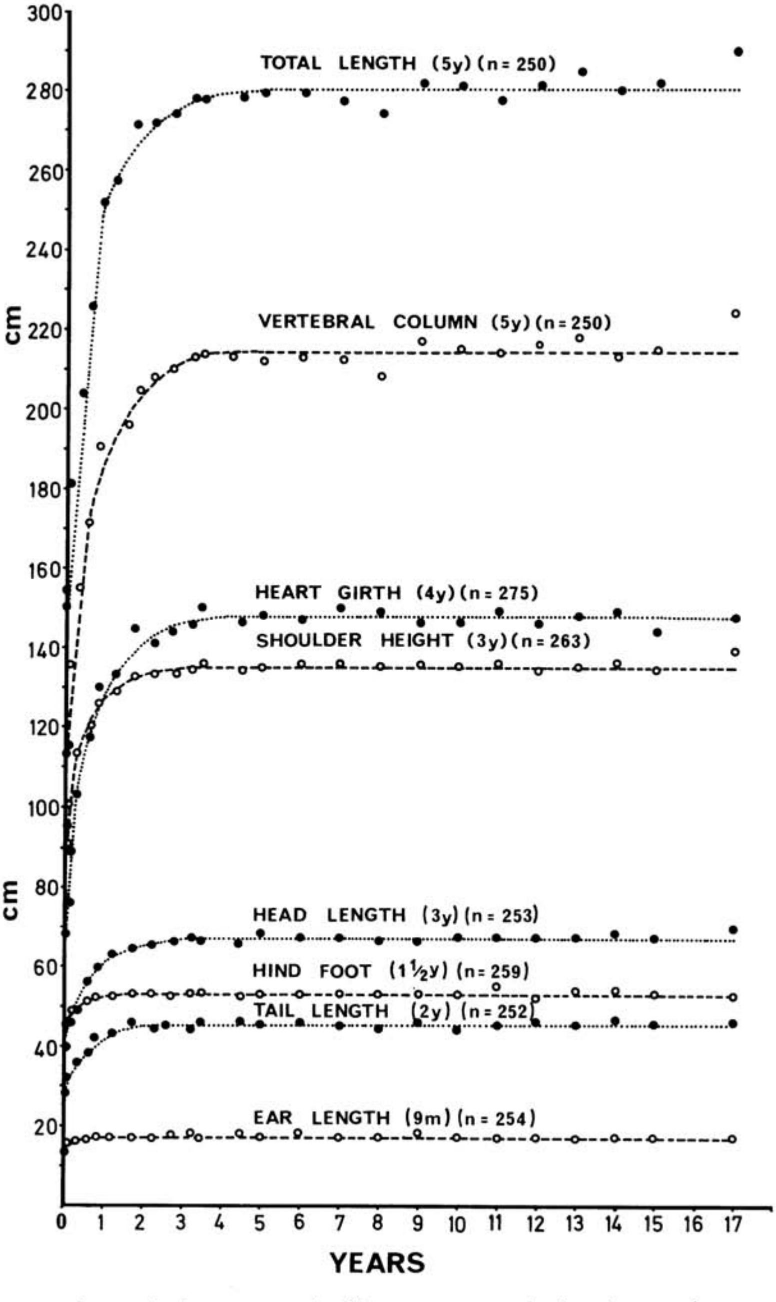


Fig. 8. Theoretical von Bertalanffy computer calculated growth curves for Burchell's zebra. The curves illustrate average growth characteristics for the sexes together. Sample means plus and minus two standard errors are given by the open circles and vertical lines respectively. TL, BM, HG and SH, the asymptotes of each particular curve, are indicated by the broken lines. The figures in brackets are the sample sizes (n).

Table 5

Computer calculated mass-length relationships for Burchell's zebra derived by using the standard logarithmic transformation and fitting a linear regression by the method of least squares. The standard equation $y = ax^b$ describes the relationships. Regression equations for estimating body mass from each body dimension are given at the end of each section of the table. Here, however, y-values have been replaced by "Mass" and x-values by "SH", "HG", "NT" or "TL" respectively

Shoulder height (cm)	BODY MASS (kg)			Heart girth (cm)	BODY MASS (kg)		
	Males	Females	Combined		Males	Females	Combined
10	0,04	0,00	0,00	10	0,17	0,15	0,18
20	0,42	0,02	0,07	20	1,19	1,06	1,22
30	1,70	0,15	0,43	30	3,70	3,37	3,78
40	4,58	0,66	1,51	40	8,28	7,65	8,40
50	9,89	2,06	4,02	50	15,46	14,44	15,62
60	18,56	5,20	8,93	60	25,76	24,26	25,93
70	31,60	11,39	17,53	70	39,65	37,62	39,80
80	50,10	22,46	31,45	80	57,60	55,02	57,68
90	75,23	40,88	52,66	90	80,09	79,94	80,02
100	108,20	69,87	83,52	100	107,50	103,90	107,20
110	150,40	113,50	126,70	110	140,40	136,20	139,80
120	203,00	176,60	185,50	120	179,10	174,50	178,00
130	267,60	265,40	263,30	130	224,10	219,20	222,40
140	345,70	386,90	364,20	140	275,70	270,70	273,20
150	438,60	549,50	492,60	150	334,40	329,40	331,00
				160	400,60	395,90	396,00
n	50	59	109	n	52	59	111
r	0,779	0,965	0,907	r	0,898	0,982	0,966
Males	$\text{Mass}=0{,}00001354(\text{SH})^{3{,}4514}$			Males	$\text{Mass}=0{,}0002727(\text{HG})^{2{,}7980}$		
Females*	$\text{Mass}=0{,}000000004687(\text{SH})^{5{,}0867}$			Females*	$\text{Mass}=0{,}0002102(\text{HG})^{2{,}8469}$		
Combined	$\text{Mass}=0{,}0000001473(\text{SH})^{4{,}3767}$			Combined	$\text{Mass}=0{,}0002962(\text{HG})^{2{,}7794}$		

Here individual mass estimation equations have been derived for two age classes, (i) adults plus sub-adults and (ii) immatures plus foals. The second pair of equations in Table 6 are the ones for immatures and foals

Table 5 (continued)

Neck thick-Ness (cm)	BODY MASS (kg) Males	Females	Com-bined	Total length (cm)	Males	Females	Com-bined
10	14,51	0,84	2,40	10	0,50	0,01	0,02
20	42,17	7,19	13,46	30	4,17	0,19	0,41
30	78,71	25,23	36,91	50	11,19	1,05	1,89
40	122,50	61,48	75,50	70	21,47	3,21	5,14
50	172,80	122,70	131,50	90	34,91	7,40	10,85
60	228,70	215,80	207,00	110	51,48	14,40	19,71
70	290,00	347,70	303,80	130	71,13	25,08	32,40
80	356,10	525,80	423,50	150	93,82	40,33	49,61
				170	119,50	61,10	71,99
				190	148,20	88,39	100,20
				210	179,90	123,20	135,00
				230	214,60	166,70	177,00
				250	252,10	219,80	226,80
				270	292,60	283,80	285,20
				290	336,00	359,80	352,80
				310	382,30	449,00	430,20
n	34	39	73	n	48	58	106
r	0,844	0,969	0,914	r	0,773	0,958	0,918
Males	$\text{Mass}=0{,}4194(\text{NT})^{1{,}5391}$			Males	$\text{Mass}=0{,}005768(\text{TL})^{1{,}9353}$		
Females*	$\text{Mass}=0{,}0006736(\text{NT})^{3{,}0962}$			Females*	$\text{Mass}=0{,}000002407(\text{TL})^{3{,}3198}$		
Combined	$\text{Mass}=0{,}007805(\text{NT})^{2{,}4878}$			Combined	$\text{Mass}=0{,}00001660(\text{TL})^{2{,}9757}$		

* These equations do not give reliable estimations in the case of heavily pregnant mares and appropriate corrections should be made (see Fig. 6).

Legend: SH = shoulder height; HG = heart girth; NT = neck thickness;
TL = total body length.

(or specimens having shoulder height or heart girth measurements less than 120 cm). Scatter diagrams showing the relationship between body mass and heart girth and body mass and shoulder height are illustrated in Fig. 10.

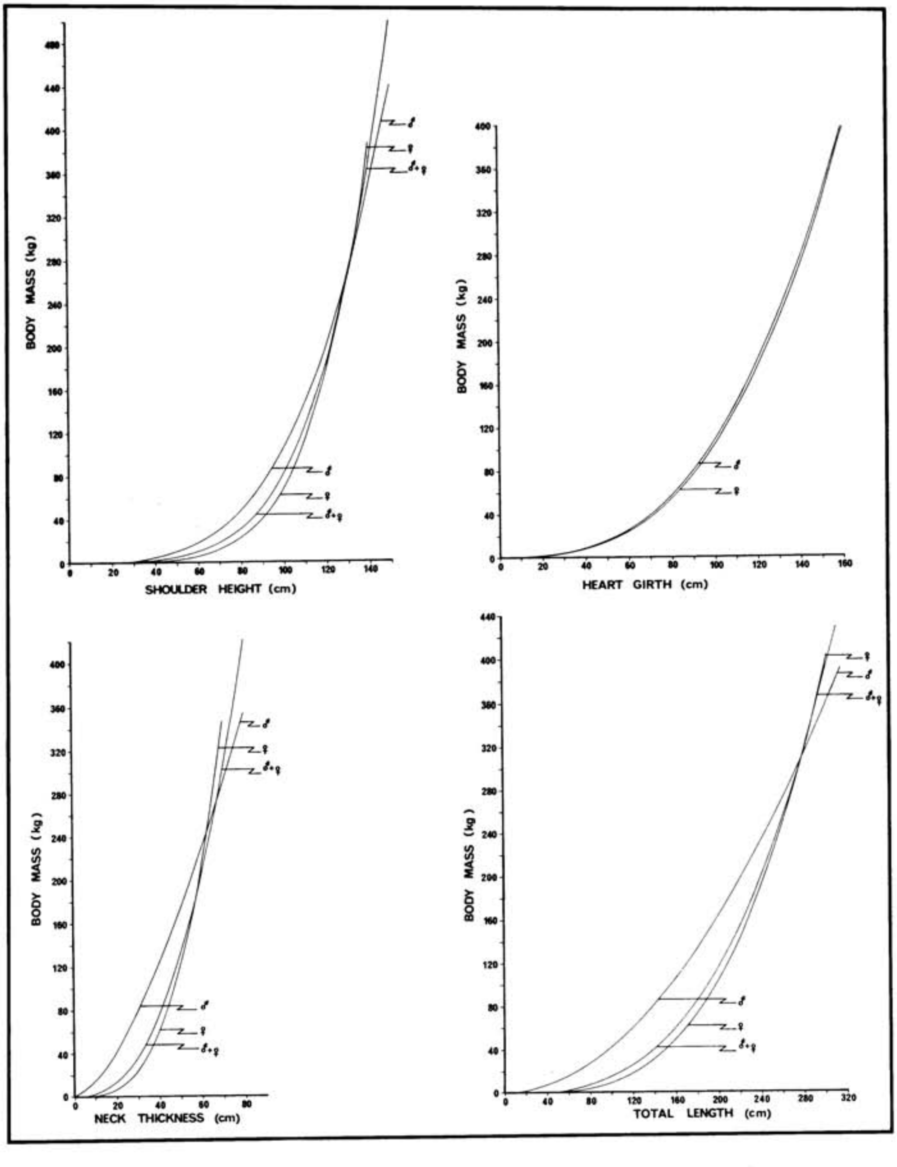


Fig. 9. Exponential curves (mass-length relationships) for Burchell's zebra. The curves were plotted using data given in Table 5 and illustrate sex specific growth differences. In the case of the body mass-heart girth relationship, the curve for males plus females has not been illustrated since it also runs between that for the two sexes which, in this instance, are very close together.

Table 6

Linear regression equations for estimating body mass of (i) adult and sub-adult Burchell's zebra and (ii) immatures and foals. The sexes are treated together. Equations were derived as described by Dunn (1964) and Snedecor (1965). The standard equation $y = ax + b$ *describes the relationship except that mass (M) replaces the y-values and "HG" or "SH" replace the x-values*

(i) ADULTS* AND SUB-ADULTS (HG OR SH $>$ 120cm)

Linear Relationship*	n	r	t-value	SD (kg)	CV (%)
$M = 3{,}93HG - 267{,}96$	56	0,974	21,885**	27	11,3
$M = 6{,}9SH - 625{,}60$	50	0,951	21,308**	33	13,2

(ii) IMMATURES AND FOALS (HG OR SH $<$ 120cm)

Linear Relationship	n	r	t-value	SD (kg)	CV (%)
$M = 2{,}56HG - 150{,}11$	17	0,971	15,722**	11	12,9
$M = 4{,}05SH - 338{,}19$	12	0,953	9,935**	15	18,0

Legend: M = body mass (kg); HG = heart girth (cm); SH = shoulder height (cm); r = correlation coefficient; SD = standard deviation; CV = coefficient of variation.

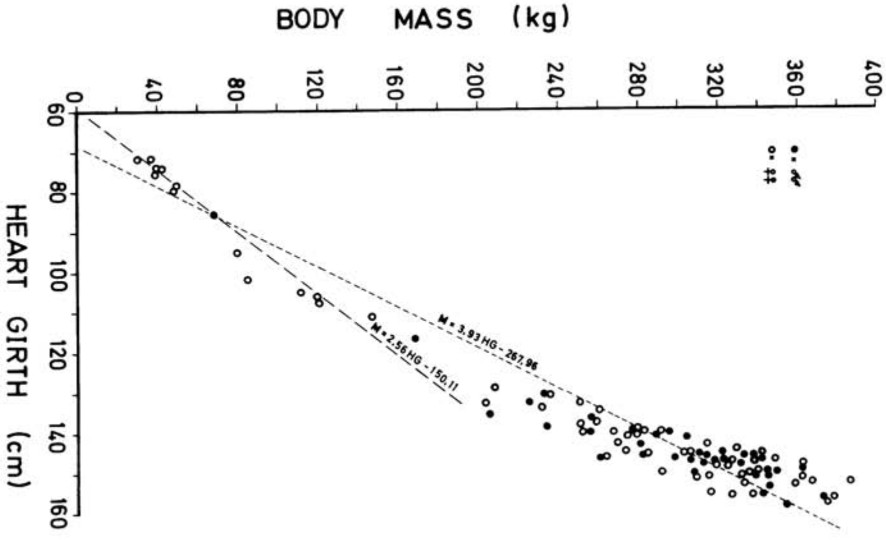
* These equations do not give reliable predictions in the case of heavily pregnant mares and appropriate corrections should be made (see Fig. 6).

** Significant at 1% level.

Crown-rump measurements, ages and body masses of six embryos are given in Table 7. The growth curves illustrated in Fig. 11 were plotted using data in Table 8.

Discussion

All measurements of length were taken "over the curves" since this is the easiest to employ under field conditions and gives the best assess-



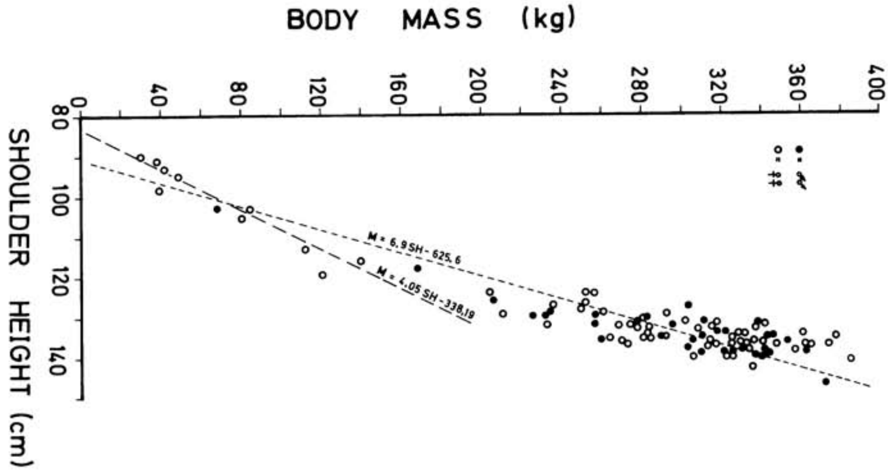


Fig. 10. Scatter diagrams of the body masses of 96 Burchell's zebra plotted as functions of heart girth and shoulder height. Broken lines = linear regression with their appropriate regression equation (see Table 6).

Table 7

Crown-rump measurement, body mass and conception age for six Burchell's zebra embryos

Conception age (days)	Mass (g)	Crown-rump length (cm)
15	—	0,40
68	1,93	2,71
69	2,04	2,65
70	2,87	3,25
72	4,15	3,89
72	4,03	3,79

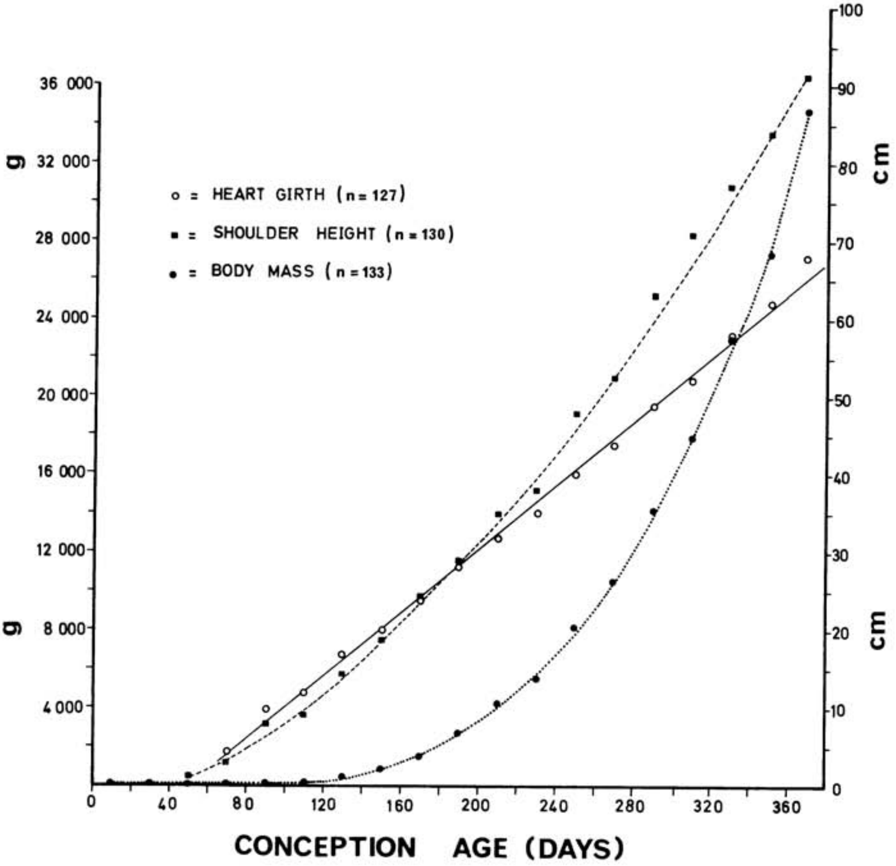


Fig. 11. Growth curves for three selected measurements taken from Burchell's zebra embryos and foetuses. Conception ages were estimated by the method of Huggett and Widdas (1951). The curves were fitted by eye.

Table 8

Data on maxima, minima, means and confidence limits for three selected Burchell's zebra embryonic and foetal measurements and 19 corresponding age classes. Data for males and females have been pooled

AGE CLASS (DAYS AFTER CONCEPTION)	MASS (g)					SHOULDER HEIGHT (cm)					HEART GIRTH (cm)				
	n	Max.	Min.	Mean	CL*	n	Max.	Min.	Mean	CL*	n	Max.	Min.	Mean	CL*
0 – 20	2	0,01	0,01	0,01	—	0	—	—	—	—	0	—	—	—	—
21 – 40	1	—	—	0,01	—	0	—	—	—	—	0	—	—	—	—
41 – 60	1	—	—	1,9	—	1	—	—	1,4	—	0	—	—	—	—
61 – 80	6	13,8	4,0	8,5	3,4	6	3,9	1,9	3,0	0,7	4	5,0	4,0	4,7	0,5
81 – 100	1	—	—	87,3	—	1	—	—	7,9	—	1	—	—	9,6	—
101 – 120	5	234,5	105,9	150,9	53,8	5	10,4	8,1	9,1	0,8	5	13,0	10,5	11,6	1,1
121 – 140	6	533,4	325,8	467,8	59,5	6	16,3	12,2	14,4	1,1	6	17,8	15,0	16,5	0,8
141 – 160	10	1 239,4	691,8	918,1	135,6	10	22,5	15,3	18,6	1,5	10	21,9	16,2	19,7	1,1
161 – 180	3	1 861,4	1 180,4	1 483,1	392,3	3	27,7	21,1	24,1	3,8	3	24,9	23,2	23,9	1,0
181 – 200	11	3 178,0	2 350,0	2 691,8	537,2	11	31,5	26,5	28,9	1,1	11	30,5	25,4	27,8	0,8
201 – 220	12	4 676,2	3 350,0	4 176,4	201,7	12	38,8	31,6	35,0	1,3	12	34,2	28,9	32,1	1,1
221 – 240	7	6 310,6	4 903,2	5 512,6	414,4	7	43,4	33,0	38,2	2,7	7	37,5	33,0	34,7	1,2
241 – 260	9	8 950,0	6 810,0	8 061,7	467,5	9	52,1	45,4	47,7	1,6	9	44,7	31,1	39,5	2,7
261 – 280	4	11 804,0	9 715,6	10 430,7	919,2	4	56,1	49,0	52,3	3,3	4	48,7	41,3	44,0	3,2
281 – 300	10	15 890,0	12 485,0	14 187,5	854,4	10	72,7	54,3	63,4	3,7	10	52,2	44,4	48,7	1,4
301 – 320	6	19 158,8	17 252,0	17 926,0	517,1	6	74,1	67,7	71,3	1,8	6	55,5	50,4	52,3	1,4
321 – 340	9	24 970,0	20 430,0	23 043,0	965,2	9	83,2	65,5	77,2	3,5	9	59,9	54,5	57,5	1,6
341 – 360	17	29 737,0	23 608,0	27 293,4	651,8	17	89,5	78,1	84,2	1,2	17	65,8	58,8	61,7	0,8
361 – 375	13	39 044,0	31 780,0	34 818,3	1 487,9	13	98,5	85,8	91,4	2,0	13	71,9	63,7	67,7	1,6

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* CL = Confidence limits at the 5% level.

Table 9

Comparison of body masses between zebra (Equus burchelli) *from the Kruger National Park, eastern Zambia and those from Tanzania. In all instances only adults have been included, while the masses of mares have been corrected in the case of pregnant individuals*

AREA AND SUBSPECIES	BODY MASS (kg)							
	Adult Stallions				Adult Mares			
	n	Max.	Min.	Mean	n	Max.	Min.	Mean
Kruger Park *(antiquorum)*	57	373,3	267,3	318,5	51	386,9	272,6	321,6
Eastern Zambia *(boehmi)*	10	357,3	277,3	323,3	7	341,4	281,0	322,7
Tanzania (Serengeti) *(boehmi)*	13	284,0	220,4	247,8	8	241,5	175,5	219,1

Table 10

Comparison between mean body dimensions of adult Kruger Park zebra (E. b. antiquorum) *and adult zebra from Tanzania* (E. b. boehmi)

BODY DIMENSION (cm)	KRUGER NATIONAL PARK		SERENGETI (TANZANIA)		PERCENTAGE BY WHICH THE KRUGER PARK MEAN EXCEEDS THE TANZANIA MEAN	
	Mean ♂♂	Mean ♀♀	Mean ♂♂	Mean ♀♀	♂♂	♀♀
Total length	280,0	279,4	252,1	251,3	10,0	10,1
Vertebral column (excluding tail)	167,2	170,1	146,1	146,8	12,6	13,7
Shoulder height	136,3	134,5	127,7	122,7	6,3	8,8
Heart girth	146,9	148,1	135,6	130,6	7,7	11,8
Hind foot	53,5	52,2	50,8	49,2	5,1	5,8
				Average	8,3	10,0

Tables 9 and 10 give comparative growth data for three zebra subspecies.

ment of the animal's condition, i.e. since muscle growth or subcutaneous fat deposition does not take place evenly over the animal's body, a measurement over the curves will provide the best correlation between an increase in mass and a particular body measurement. "Between the peg" measurements taken from one protruberant bone to another would, for example, consistently fail to register changes in condition or muscular development.

In young zebra there were insufficient data available to validate separation of the sexes. Under the age of two years it is unlikely that sex-specific growth rate differences exist, and the limited data tend to support this. In the case of domestic horses, Joubert and Bosman (1971) proved no disparity between growth in mass for male and female foals from birth to 13 months of age. In adults, however, stallions were found to have a mass six per cent greater than that of mares.

By referring to Fig. 4 and Fig. 5 the following deductions can be made with regard to growth with age phenomena of K. N. P. zebra:

(1) During progression from the neonatal to the adult stage the greatest degree of growth is displayed by the vertebral column. Excluding the tail, the length of which increases by 59,9 per cent within the first two years of life, the vertebral column doubles in length by the time the adult dimension is attained (5 years of age). By contrast, shoulder height increases by a mere 48,1 per cent. In the newly born zebra foal these two dimensions are significant, as it has frequently been noted that young zebra appear to be disproportionately tall at the shoulder (King 1965). Between birth and adulthood, the increase of 84,4 cm in vertebral column length and the relatively small increase of 44,0 cm in shoulder height soon produce the balance which exists between vertical and horizontal dimensions.

(2) Ear length reaches the adult mean at the early age of nine months. The vertebral column, which also shows the greatest percentage increase in length, only reaches the adult mean at five years of age.

(3) Shoulder height reaches the adult mean just after three years of age. The range of heights displayed by adult animals may, however, be reached by one year of age (Fig. 8; Table 4). This means that animals slightly shorter than adults would in most cases be between one and three years of age. After approximately two years of age it would, however, be almost impossible to estimate a zebra's age by judging its height since the height difference between this age class and adults is, on an average, only five cm (Fig. 8; Table 4). When body mass is used for visual age estimation purposes, it becomes quite obvious that a two-year old zebra is less bulky than an adult. This is borne out by a mean mass difference of 64 kg between two-year olds and adults (5+ years old) (Fig. 8; Table 4). The greatest proportion of this bulk is carried in the hindquarters, so that adults and sub-adults, when

viewed laterally, all appear to be adult. Rear viewing, however, illustrates the difference quite clearly as the hindquarters of adults are noticeably broader than those of sub-adults.

(4) Excluding behavioural attributes and the location of the external genitals, the only sex-specific characteristic that can be relied upon to some extent, is neck thickness. This, however, applies only to adult animals (Fig. 5; Table 3). Here the neck of the adult stallion has an average girth 8,1 cm greater than that of the mare. Although this method of sexing is relatively difficult it can be used to pick out the adult stallion(s) on a good photograph of a group of zebra viewed laterally.

Table 2 and Table 3 show that although there is no significant difference between the average mass of adult stallions and adult mares (t = 0,587), stallions are on an average 1,8 cm taller at the shoulder than mares. These heights differ significantly at the five per cent level (t = 2,032). A similar difference is displayed by the hind foot measurement which differs significantly at the one per cent level (t = 2,950). None of these small differences are, however, discernable in the field.

At the one per cent level, ear length in mares is significantly greater than that of stallions (t = 2,968) while heart girth defeats expectations in showing no significant difference between the two sexes (t = 0,649). This result is borne out by the non-significant difference observed between the means of heart girth in pregnant and non-pregnant mares (t = 1,845) (Table 3).

Von Bertalanffy growth curves

During recent years a number of growth studies on large mammals have been undertaken using functions of the type described by von Bertalanffy in 1938. The perfecting and practical application of these functions, however, originated in studies of fish populations where the work of Beverton and Holt (1957) merits particular mention. According to these authors the functions derived by von Bertalanffy satisfy the essential requirements for describing growth in fish and have now been applied with equal success to large land mammals. One such detailed study was done by Hanks (1972a) on the Zambian elephant *Loxodonta africana* while Laws (1968) and Laws and Parker (1968) calculated theoretical growth equations for Hippopotami *Hippopotamus amphibius* and elephants respectively, from Uganda. A comparable study using a non-linear least squares computer program to describe the shape of growth curves in cottontail rabbits *Sylvilagus floridanus* has been described by Bothma, Tear and Gates (1972). Other than these, growth curves for game animals have generally been fitted by eye (Child 1964, Roth 1965; Pienaar 1969; and Blood, Flook and Wishart 1970).

The underlying concepts and mathematical derivations of the von Bertalanffy growth equations are discussed in detail by Beverton and

Holt (1957) and Gulland (1969). The basis of these theoretical growth curves and equations is:

(1) They provide an objective method of fitting curves to growth data.

(2) They provide a means of comparing theoretical growth rates of animals in different populations and can thus be of value in taxonomic studies. In addition to being used to relate body measurements with age, von Bertalanffy curves can also be used to illustrate the relationship between two measurements (e.g. mass and height). In the present study theoretical growth curves (Fig. 8) were fitted to age specific measurements of body mass, shoulder height, heart girth and total length. These measurements are of value in visual age classification of live field specimens. Von Bertalanffy equations, on the other hand, can be used to calculate theoretical mass or body lengths when age is known. The appropriate equations are given below Table 4. In addition, the values of M_∞, SH_∞, TL_∞, K and t_0 are important since they can be used in objective comparisons of present growth data with those collected in the future. These comparisons can be done in the same or different parts of the species' range and should indicate whether any growth rate changes of possible genetic or density dependent origin, are taking place.

The eye-fitted growth curves for shoulder height, heart girth and total length (Fig. 4) compare well with the corresponding theoretical von Bertalanffy curves in Fig. 8. It is clear that large quantities of age-specific body measurements would be sufficient to plot adequate eye-fitted growth curves of practical value. Von Bertalanffy computations, however, eliminate the subjectivity which frequently limits the comparative value of growth data.

Mass -length relationships (linear regression analyses)

The relationships existing between body mass and body dimensions have long been known. In the case of domestic livestock (especially cattle) these relationships have been employed extensively to derive formulae of use in objective body mass estimations (Brody, Davis and Ragsdale 1937; Manning and Williams 1950; Ross 1958). In wild game animals, however, body measurements were not always easy to obtain since animals either had to be immobilized or destroyed. With the initiation of various game cropping schemes in Africa measurements have, however, gradually become available in the quantities required for suitable statistical analyses. Mass estimation methods for numerous small- and medium-sized herbivores have subsequently been dealt with by McCulloch and Talbot (1965) and Talbot and McCulloch (1965) while similar techniques have been applied to large herbivores such as the black rhinoceros *Diceros bicornis* and the elephant by Freeman and King (1969) and Krumrey and Buss (1968) respectively.

In the case of the zebra it is extremely difficult to make reliable visual estimations of body mass. This is due to the disruptive effect of the body stripes (Cott 1957). Field determination of mass, on the other hand, is a cumbersome procedure requiring special apparatus.

Since scatter diagrams (Fig. 10) indicated that body mass-length relationships were curvilinear, it was decided to employ appropriate logarithmic transformations to all body mass-length data and to fit linear regressions by the method of least squares (Table 5). For comparative purposes straight line regression analyses were also carried out on untransformed data. In these cases, however, data for the two sexes were pooled and individual regression equations computed for shoulder height and heart girth measurements (Table 6).

Linear regression analyses using logarithmic transformations

From the data in Table 5 it can be seen that heart girth-body mass relationships have the highest correlation coefficients. Surprisingly neck thickness-mass relationships provide the next highest "r" values, followed by shoulder height and then total length. In all instances relationships involving only females have the highest correlations.

When viewing the exponential curves in Fig. 9, a number of deductions can be made with respect to body mass-length relationships in the zebra. Firstly the curves indicate that relative growth of each pair of measurements is not isometric, i.e. the relationships are not linear. Instead the dimensions illustrated may be said to grow allometrically, i.e. the ratios of any of the dimensions of length to body mass are constantly changing. The scatter diagrams in Fig. 10 similarly indicate allometric growth in the zebra. The exponential curves are, however, of additional value since they illustrate that although body mass for adult stallions and adult mares does not differ significantly (Table 2), marked allometric growth differences exist between the sexes. In this respect only the heart girth-body mass relationship shows similar allometric growth in the sexes. In the others males show an initial greater rate of increase in body mass relative to shoulder height, neck thickness or total length. These rates, are, however, eventually all surpassed by female animals.

Since allometric growth rates differ between the sexes, one must conclude that sex specific regression equations will give more reliable estimations of body mass than combined data. In the case of heart girth, however, there is very little difference between estimations obtained by any one of the three equations.

Linear regression analyses using untransformed data

Considering the data in Table 6, it may seem surprising that with a correlation coefficient of 0,974 for the regression of mass on heart girth, one still obtains a standard deviation as high as 27 kilogram. This contrasts markedly with the results of McCulloch and Talbot (1965) derived from data on *Equus burchelli boehmi*. They obtained a residual standard deviation of 11,8 kg (26 lbs), and a coefficient of variation of 4,7 per cent while the correlation coefficient was only 0,648. These results could be due to their small sample size of 16 zebra.

The high standard deviation quoted in Table 6 may also be accounted for by the fact that shoulder height and heart girth measurements do not take into account the mass of the contents of the viscera, i.e. experimental animals were taken at different times of the year and additionally they may or may not have been drinking before they were destroyed. In domestic cattle kept under normal ranching conditions in East Africa, Hutchinson (1959), for example, found that daily water intake amounted to approximately seven per cent of the live mass. Talbot and McCulloch (1965), found that variations in stomach contents between wild animals of the same species and size amounted to 10 per cent of live mass. Supporting their finding is the fact that in a small sample of six adult zebra destroyed in the K. N. P. on the same day and all within a period of about two hours the masses of caecal plus stomach contents varied by as much as 24,2 kg in animals of the same sex and age. This represents a difference of 7,6 per cent of the mean adult mass. Additionally it has been determined that zebra in the K.N.P. drink an average of 21,1 litres of water at a time (standard deviation = 5,4 litres) (Young 1970). This volume of water would account for a possible mean mass variation of 21,3 kg or a 6,7 per cent increase in mass.

Bearing in mind these possible natural daily mass fluctuations it is not surprising that one obtains standard deviations of between 27 kg and 33 kg in adult animals. Additionally the computed regression equations all exhibit a certain amount of inaccuracy since a straight line has been fitted to what is basically a curvilinear relationship (Fig. 10). An even greater source of variation probably stems from the type of measurements used for mass estimation, i.e. heart girth and shoulder height. These two dimensions do not take into account the greatest source of mass, namely the rump and buttocks. It is in their hind quarters that zebra display the most marked mass increase due to muscle growth or the deposition of thick layers of yellow fat, or both. In contrast to wild ungulates in East Africa (McCulloch and Talbot 1965) zebra in the K. N. P. definitely respond to changes in food or other environmental factors by depositing and mobilizing quantities of subcutaneous body fat. Huntley (1971), who studied seasonal variation in the physical condition of mature male blesbok *Damaliscus dorcas phillipsi* and koedoe *Tragelaphus strepsiceros*, found that although there were significant changes in the fat reserves, these changes took place without expressing themselves in the external appearance of the animals. They also had a very small effect on the total body mass of the animal, e.g. a change of 50 per cent in the fat content of a koedoe accounted for a change of only 0,75 per cent of its body mass. In zebra subcutaneous fat deposition is particularly noticeable along the dorsal part of the neck, the sternal region and over the rump buttocks, where the layer may be more than three centimetres thick. This type of subcutaneous fat deposition may also explain why heart girth measurements give better results than shoulder height. At this stage one might also have assumed that some measurement taken over the curves of the buttocks and rump would have produced slightly better results. Here a basic rule may be suggested, namely, that to derive the most reliable mass estimation equations one must incorporate those measurements which are most likely to portray changes in the animal's mass. These measurements could of course vary considerably from species to species. The same consideration applies to heavily pregnant mares. Here the equations in Table 6 do not give reliable predictions since the required measurements again do not take mass of the uterus plus its contents into account. In these instances predictions will be similar to those obtained for non-pregnant animals and allowance will have to be made for the stage of pregnancy by adding the mass of the uterus plus its contents. This mass can be estimated as shown in Fig. 6 and the validity of the prediction considerably increased. Foetal mass is, however, required for this correction.

Whatever the measurement(s) taken, it should be obvious that unless the mass of the visceral contents can be measured, no estimation equation can be expected to account for all possible variations and although the equations in Tables 5 and 6 will not always give the preferred degree of accuracy they are nevertheless far more accurate than visual estimation methods. They also have a wide range of application, since data were collected from a variety of age and mass classes, taken during all seasons of the year.

In conclusion it may be said that regression equations computed using logarithmic transformations (Table 5) will provide the most reliable estimations of body mass. This is particularly so in the case of foals and immatures where growth is markedly curvilinear. When adults only are considered, untransformed data can be used to compute suitable equations. In addition to these considerations, the sexes should be treated separately whenever possible.

In future studies on zebra it would be valuable to collect measurements across the hindquarters together with belly girth and then to compute regression equations incorporating these and other variables such as heart girth, shoulder height and body length.

Relative sizes of zebra subspecies

A number of points emanate from a comparison of the average masses of K.N.P. zebra with those of zebra from eastern Zambia (Wilson 1968) and Tanzania (Sachs 1967). According to Ansell (1967) all the zebra sampled by these authors belong to the species *E. b. boehmi.* Comparing average masses, however, there appear to be some differences within the subspecies *boehmi,* and between this subspecies and the subspecies found in the K. N. P. (Table 9).

Table 9 indicates that there are no obvious differences in mass between K. N. P. zebra and those from eastern Zambia. The means for stallions and mares differ by only 5,2 kg and 1,6 kg respectively. In the case of the Serengeti zebra, however, there are very marked differences from the other two areas. Here the mean masses of stallions and mares differ by about 70 kg and 102 kg respectively from those of the K. N. P. Alternatively one may say that adult stallions from the K. N. P. are on an average 22 per cent heavier than those from Tanzania and mares 32 per cent heavier. Comparing body dimensions between adult animals from Tanzania and the K.N.P. provides similar results (Table 10).

In contrast to these differences the tails of East African zebra appear to be between one and two centimetres longer than those of zebra found in the K.N.P. while ear lengths are the same.

This significance of the differences illustrated in Tables 9 and 10 lies in the following:

(1) There is more likely to be a taxonomic difference between East African zebra and zebra from eastern Zambia than between the eastern Zambian zebra and those of the K.N.P. This conflicts with the present classification of the Equidae (Ansell 1967).
(2) The large mean mass differences will have to be taken into account when comparing kill frequencies of large predators from the three regions.
(3) Data to be used in biomass calculations will differ considerably.

Like the K. N. P. zebra, the local wildebeest *Connochaetes taurinus taurinus* show a similar set of differences to the East African sub-species *Connochaetes taurinus albojubatus*. Here, average body mass of adult animals of both sexes from the K. N. P. exceeds that of animals from East Africa by over 50 kg (Braack 1973).

Commercial exploitation of zebra

With regard to the commercial exploitation of zebra on game farms, the optimal age for cropping would be when animals are between one and four years of age. The specific age, however, would have to be decided with regard to the animal's sex and the market for zebra meat and hides. Animals over two years of age generally have the best skin since in young specimens the adult pelage is not yet fully grown. In adult stallions (over four years of age), however, intraspecific fighting takes place and skins may be scarred and so loose some of their commercial value.

In terms of meat production approximately one year would be the optimal age at which to harvest zebra, since after this age the rate of increase in body mass starts to decline (Fig. 8). Table 4 indicates that average body mass for males and females increases by 131,3 kg, 87,5 kg and 39,0 kg during the first, second and third years of life respectively. Productivity is thus highest during the first year of life after which it tapers off rapidly.

Prenatal development

According to Geddie (1968) an embryo is a young animal in its earliest stages of development. A foetus, on the other hand (Abercrombie Hickman and Johnson 1963), is the mammalian embryo after recognisable appearance of the main features of the fully developed adult. From these definitions it is obvious that the use of each word to describe a particular growth phase of the conceptus depends on their interpretation by the writer, as well as the particular animal concerned. Additionally when terminology such as "foetal membranes" and "foetal growth" are used in the biological field, they are generally meant to cover any phase of prenatal development.

Foetal growth data illustrated in Fig. 11 are relatively typical for most mammals. It should, however, be noted that at about mid-term (± 190 days) foetal shoulder height starts exceeding heart girth. This phenomenon has a functional basis and can be explained by the fact that parts essential to life processes and body functions appear relatively well developed at birth (McMeekan 1940). In this context the long legs of the zebra foal could be of considerable survival (escape) value. This differential growth rate is reversed again in the postnatal stage, when, at about one year of age, heart girth exceeds shoulder height (Fig. 8).

Although morphological characteristics can be used for deriving foetal ages (Cloete 1939), , these have not been collected to any extent for zebra. One obvious characteristic, the appearance of body stripes was, however, noted. In foetal zebra the first signs of striping occur at between 250 and 270 days. In all cases striping commences antero-dorsally (forehead region) and then proceeds towards the postero-ventral regions. This conforms in general to the law of developmental direction which states that growth in body proportions exhibits a well-defined anterior-posterior gradient from earlier to later developing regions (Jackson 1941, here quoted from McMeekan 1940). The abdomen and the lower parts of the legs are the last regions to receive their stripes.

The pelege at full term varies considerably from foetus to foetus and may be relatively smooth and short or long and fluffy. Although many young foals have a mantle of long upright hairs on the back, especially over the croup (Ansell 1960), this is by no means the rule.

Whatever the possible causes of foetal growth variations (Smuts 1974b) and birth masses, the value and practicality of the foetal growth with age relationships described by Hugget and Widdas (1951) can no longer be doubted. The method has been used extensively in animals such as the African elephant (Hanks 1972b; Laws 1969; Perry 1953), the wildebeest (Watson 1969), the impala *Aepyceros melampus* (Fairall 1969) and Grant's zebra (King 1965). In most of these instances the relationship was used so that predictions could be made with respect to calving and mating seasons. King *(op cit.),* however, related foetal measurements to foetal mass and then used measurements to obtain rough indications of conception age. In the present study the conception age of all embryos and foetuses was determined and used to study foetal growth, and will later be used to predict mating and foaling seasons.

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