

Pre- and postnatal growth of the Cape porcupine *Hystrix africaeaustralis*

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(With 1 figure in the text)

Pre- and postnatal growth of the Cape porcupine *Hystrix africaeaustralis* is evaluated by means of the Huggett & Widdas equation, a modification thereof, and the von Bertalanffy equation. Specific foetal growth velocity for the Cape porcupine is higher than that recorded for most other hystricomorph rodents, but similar to that recorded for large-bodied rodents of the same group. Relatively high foetal growth velocity in porcupines is ascribed to their relatively short gestation period, the latter being longer than expected for mammals of equal size, but shorter than expected for a hystricomorph rodent.

Postnatal growth is nearly linear up to the age of 20 weeks and asymptotic body weight is attained at an age of 52 weeks, this coinciding with the observed age at sexual maturity. Growth rates of males and females are similar. Their high rate of postnatal growth and development results in an extended reproductive period, thereby enhancing individual reproductive values by counteracting the effects of seasonal breeding and small litter size.

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Introduction

The Cape porcupine *Hystrix africaeaustralis* occurs throughout the Southern African sub-region (Smithers, 1983) and has been recorded as far north as Kilimanjaro (south-eastern Kenya) where they become sympatric with the Crested porcupine *H. cristata* (Kingdon, 1974). Although common and widespread, no comprehensive study has been undertaken as yet on the biology of *H. africaeaustralis*.

A study of the growth of porcupines is of importance since growth rate, age at weaning, period of parental dependence, age at sexual maturity and productivity are all important in determining the successful survival of the species (Case, 1978). The confusion existing about the relationship(s) between the New and Old World Hystricomorpha (see Lavocat, 1974; Wood, 1974) may furthermore be elucidated by providing information on aspects of growth in the Cape porcupine (an Old World hystricomorph of the family Hystricidae).

Prenatal growth and development of hystricomorph rodents have been the subject of an intensive study by Roberts & Perry (1974) who concluded that hystricomorph foetal growth rates are extremely slow when compared with those of other animals of similar birth weight. This argument was used by them as well as Frazer & Huggett (1974) to reject the use of the well-known Huggett & Widdas (1951) equation for describing foetal growth rates in this group of rodents.

This paper describes pre- and postnatal growth of the porcupine and re-evaluates the applicability of the Huggett & Widdas equation to hystricomorph rodents.

Materials and methods

Body weight, body length (curvilinear from the tip of the nose along the spine to the tip of the tail), total length (straight line length taken from the tip of the nose to the tip of the tail along the side of the body), shoulder height (straightened leg) and thoracic girth were recorded for 118 porcupines culled in the Tussen-die-Riviere (TdR) Game Farm (South Africa) as part of a cropping operation of the Conservation Management Subdivision of the Orange Free State Provincial Administration.

Each specimen was assigned to a 'dental age class' based on the criteria established and described by van Aarde (1985a), where age classes I and II represented porcupines < 5 months of age, class III animals 5.1–8 months of age, class IV those 8.1–18 months old, class V those 18.1–23 months old, class VI those 23.1–30 months of age, and classes VII to IX those older than 30 months of age. This age determination system involves the sequence of eruption and replacement of the molars and premolars and the pattern of wear of the occlusal surface of the molar toothrow as recorded in known-age captive porcupines.

Foetuses removed from the uteri of culled pregnant females were weighed and their crown-rump lengths measured following van Zyl & Skinner (1970). Foetal age and specific foetal growth velocity were determined using the formula $\sqrt[3]{W} = a(t - t_0)$, where W = foetal weight, a = specific foetal growth velocity, t = gestation age in days, and t_0 = the calculated intercept on the age axis (Huggett & Widdas, 1951). The theoretical value for a was calculated using a birth weight of 351 g, where $t = 93.5$ days (van Aarde, 1984) and $t_0 = t \times 0.3$ (see Huggett & Widdas, 1951). Birth weight for captive porcupines varied from 300–400 g ($\bar{x} = 351 \pm 47.4$ g; $n = 19$) and pregnancy lasted 93–94 days (93.5 ± 0.6 days; $n = 4$) (see van Aarde, 1985c).

Body weight for porcupines ($n = 18$) born in captivity at the Experimental Farm of the University of Pretoria was recorded at weekly intervals over the first 92 weeks of life. Husbandry of these animals has been described by van Aarde (1985b). Growth was described by fitting the theoretical von Bertalanffy curve to the data using the programme of Abramson (1965) as developed by Tomlinson & Abramson (1961). Age-specific body weight was transformed to the third power and individual estimates for the curve were obtained through retransformation. The theoretical curve was derived from mean values of body weight for each age in weeks using the growth equation of Beverton & Holt (1957): $W_t = W_\infty [1 - e^{-k(t-t_0)}]^3$ where W_t = weight at age t in weeks, W_∞ = asymptotic body weight, k = a coefficient of catabolism, t = age in weeks, and t_0 = the theoretical age at which the animal would have a zero body weight. All values are expressed as means \pm one standard deviation of the mean.

Results

Prenatal growth

Using the equation of Huggett & Widdas (1951) and their approximation for t_0 ($t \times 0.3$), specific foetal growth velocity (a) was calculated at 0.1047 and the intercept at the age axis (t_0) at 28.1 days. The correction factor used to estimate t_0 from t (gestation period) is, however,

arbitrary and may introduce errors of up to 10% in specific foetal growth rates (a) of mammals with a gestation period longer than 50 days (Huggett & Widdas, 1951). An analysis of the t_0 values observed by Roberts & Perry (1974) for seven different New World hystricomorph rodent species indicated that they differed from +19.9 to -36.6% from the theoretical values; these differences arising from t_0 being under- or overestimated, using the approximations of Huggett & Widdas (1951). An evaluation of the data provided by Roberts & Perry (1974) showed that these differences increase linearly and significantly ($r = 0.93$; $P < 0.01$) with an increase in gestation length.

By calculating t_0 for hystricomorph rodents with a gestation period longer than 100 days as $t \times 0.3$ (instead of $t \times 0.2$; Huggett & Widdas, 1951), for those with a gestation period of 63–100 days as $t \times 0.4$ (instead of $t \times 0.3$), and for those with a gestation period less than 63 days as $t \times 0.25$, the theoretical t_0 and a values approximated those observed by Roberts & Perry (1974) (see Table I). This procedure resulted in the specific foetal growth velocity for the porcupine

TABLE I
Comparison between the observed and theoretical specific foetal growth velocities (a) for hystricomorph rodents based on various approximations of t_0

Species	$\sqrt[3]{W^*}$	Observed values*		Theoretical values*		Theoretical values**		Mean gestation length (days)
		t_0	a	t_0	a	t_0	a	
<i>Galea musteloides</i>	3.405	12	0.0718	16	0.0896	13	0.0873	52.0
<i>Proechimys guairo</i>	2.466	22	0.0765	19	0.0560	26	0.0636	64.8
<i>Octodon degus</i>	2.422	38	0.0483	27	0.0384	36	0.0449	90.0
<i>Chinchilla laniger</i>	2.503	30	0.0436	22	0.0407	35	0.3070	116.5
<i>Myocastor coypus</i>	6.400	40	0.0595	26	0.0603	39	0.0711	129.0
<i>Cavia porcellus</i>	4.500	16	0.0900	19	0.0978	16	0.0970	62.4
<i>Hystrix africae australis</i>	6.891	-	-	28	0.1047	38	0.1813	93.5

* From Roberts & Perry (1974)

** Values calculated using $t \times 0.25$, $t \times 0.4$ and $t \times 0.3$ for animals with gestation periods 63 days, > 63, < 100 and > 100 days, respectively

TABLE II
Age (weeks) and sex-specific mean body weight (\pm S.D.) for porcupines born in captivity. Sample sizes are given in brackets and subscripts denote degrees of freedom

Age (weeks)	Mean (\pm S.D.) body weight (kg)		t_{df} = value
	Males	Females	
5	1.80 \pm 0.50 (8)	1.58 \pm 0.50 (8)	$t_{14} = -1.11$
10	3.90 \pm 1.11 (6)	3.37 \pm 0.56 (8)	$t_{12} = 0.98$
15	4.98 \pm 0.34 (6)	5.18 \pm 1.08 (6)	$t_{10} = 0.37$
20	6.40 \pm 0.61 (6)	6.06 \pm 0.86 (8)	$t_{12} = -0.72$
25	7.26 \pm 0.73 (6)	7.84 \pm 1.25 (8)	$t_{12} = 0.81$
30	7.28 \pm 1.11 (6)	8.12 \pm 0.08 (6)	$t_{10} = 1.67$
35	8.75 \pm 0.49 (6)	8.73 \pm 0.64 (6)	$t_{10} = -0.05$
40	9.50 \pm 0.69 (5)	10.22 \pm 0.86 (5)	$t_8 = 1.22$
45	9.65 \pm 0.64 (5)	10.05 \pm 0.60 (5)	$t_8 = 0.76$
50	10.87 \pm 1.02 (5)	10.90 \pm 0.90 (5)	$t_8 = 0.05$
60	11.15 \pm 1.77 (5)	11.68 \pm 1.09 (5)	$t_8 = 0.51$

TABLE III

Age (dental age class) and sex-specific mean (\pm S.D.) body weights for porcupines culled on the Tussen-die-Riviere Game Farm between February 1977 and July 1982. Sample sizes are given in brackets and subscripts denote degrees of freedom

Dental age class	Mean (\pm S.D.) body weight (kg)			$t_{d.f.}$ = value
	Males	Females		
II	4.0 \pm 1.43 (8)	4.1 \pm 1.55 (9)		t_{15} = 0.89
III	6.9 \pm 1.38 (19)	6.2 \pm 2.06 (15)		t_{32} = 1.18
IV	9.1 \pm 1.50 (22)	11.0 \pm 1.94 (12)		t_{32} = -3.12*
V	10.8 \pm 2.01 (6)	12.4 \pm 2.05 (7)		t_{11} = -1.42
VI	11.5 \pm 1.89 (15)	12.1 \pm 1.19 (6)		t_{19} = -1.23
VII	11.9 \pm 2.10 (18)	12.9 \pm 2.22 (25)		t_{41} = -0.91
VIII	11.7 \pm 1.42 (23)	13.2 \pm 1.24 (11)		t_{32} = -2.85*
IX	11.0 \pm 1.16 (3)	12.3 \pm 2.25 (6)		t_7 = -1.85

* Differences significant ($P < 0.05$)

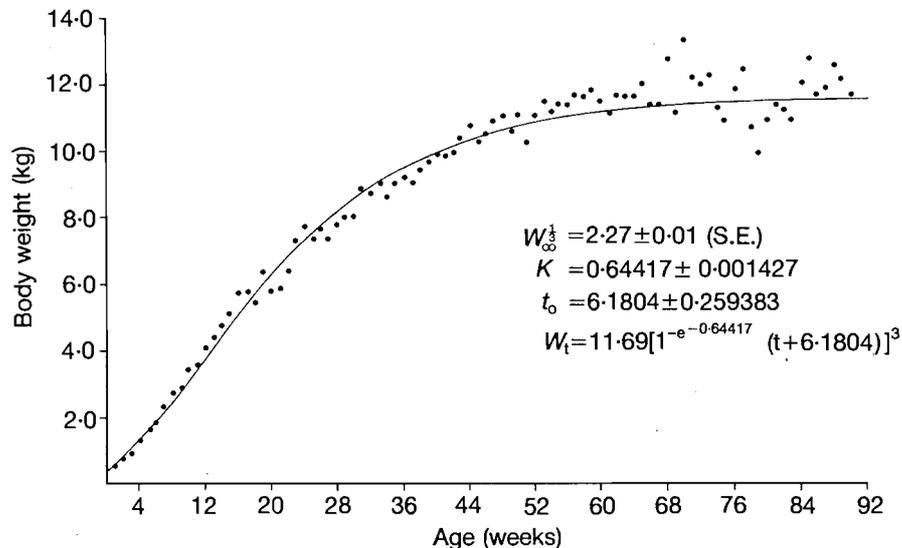


FIG. 1. The von Bertalanffy growth curve for porcupines (both sexes combined) born in captivity and weighed at weekly intervals over the first 92 weeks of life. The curve is described by the equation $W_t = W_\infty [1 - e^{-K(t-t_0)}]^3$, where W_∞ = asymptotic body weight, K = coefficient of catabolism, t = age in weeks and t_0 = theoretical age at which body weight equals zero.

being calculated at 0.1813 cf. 0.1047 using the approximation ($t \times 0.3$) suggested by Huggett & Widdas (1951).

Postnatal growth

Age-specific body weights for captive male and female porcupines did not differ significantly (Table II) and the von Bertalanffy growth curve presented in Fig. 1, with its associated constant and coefficients, describes growth in body weight for both sexes. Growth in body weight during the first 20 weeks of life was approximately linear, and asymptotic weight (11.7 ± 0.01 kg), given

by the growth equation, was attained at the age of approximately 52 weeks (Fig. 1). Age-specific body weights for free-ranging porcupine males and females did not differ significantly for most classes (II, III, V, VII, IX; Table III). Differences in mean body weights of age classes IV and VIII ($t = 3.12$ and 2.85 , respectively, $d.f. = 32$) is ascribed to the presence of pregnant females within these classes, resulting in females being heavier than males.

The frequency distribution of males and females in specific weight classes, however, did differ significantly ($\chi^2 = 12.67$; $P < 0.01$), with more females than males occurring in the heavier weight classes. Age-specific body measurements for males and females confirm the lack of sexual dimorphism in body sizes (Table IV).

Discussion

Prenatal growth

Based on differences between calculated and observed values of specific foetal growth velocities for seven New World hystricomorph species, Roberts & Perry (1974) stated that the Huggett & Widdas equation is not applicable to hystricomorph rodents. They ascribed the observed differences to the fact that 'foetal growth rates of the hystricomorphs are extremely slow compared with those of other animals of similar birth weight'.

Huggett & Widdas (1951) clearly stated that t_0 (intercept of the growth curve on the age axis) has no clear biological significance in foetal development, but Roberts & Perry (1974) gave biological meaning to it by suggesting that the value of t_0 is in good agreement with the time at which embryo development accelerates. Considering that calculated specific foetal growth velocities are affected by t_0 values, and that the correction factors used to estimate t_0 from gestation length are arbitrary and may introduce considerable error (Huggett & Widdas, 1951), it would appear that the correction factors used in the present study to estimate t_0 resulted in more realistic estimates of foetal growth velocities for some hystricomorph rodents (Table I).

Frazer & Huggett (1974) used slow early development as an argument for rejecting the use of the Huggett & Widdas equation in describing prenatal growth rates in hystricomorph rodents. They based their argument on differences between observed and theoretical specific growth velocities for the chinchilla *Chinchilla laniger*, but did not consider that these differences actually resulted from totally different values (51 cf. 110 days) for gestation lengths being used to estimate t_0 for the same species!

Therefore, it is suggested that the equation of Huggett & Widdas (1951) may, in a modified form, be used to estimate specific foetal growth velocities for hystricomorph rodents, with the approximations used to estimate t_0 being $t \times 0.25$ for hystricomorphs with a gestation period less than 63 days, $t \times 0.4$ for those with a gestation period between 63 and 100 days, and $t \times 0.3$ for those with a gestation period longer than 100 days.

Calculated specific foetal growth velocities (0.1047 and 0.1813) for the porcupine are higher than those reported for most other hystricomorph rodents (Asibey, 1974; Frazer & Huggett, 1974; Roberts & Perry, 1974) but similar to the values estimated for the Capybara *Hydrochoerus hydrochaeris* (Trapido, 1949 in Frazer & Huggett, 1974), Paca *Agouti paca* (0.103; Collett, 1981) and *Hystrix indica* (0.1021–0.1191; Tohmé & Tohmé, 1980). Relatively high values were all recorded in larger (in terms of body size) species when compared to other hystricomorph rodents. The lack of a definite positive relationship between body size and gestation length in hystricomorph rodents (van Aarde, 1984), however, suggests that gestation length in large

Age (dental age class) and sex-specific mean (\pm S.D.) body weight, shoulder height, body length, curvilinear body length and thoracic girth for porcupines killed on the Tussen-die-Riviere Game Farm between September 1981 and July 1982. Sample sizes are given in brackets

Age class	Body weight (kg)		Shoulder height (cm)		Body length (cm) (Straight nose-tail)		Curvilinear body length (cm)		Thoracic girth (cm)	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
II	4.4 \pm 1.11 (7)	4.2 \pm 1.33 (5)	18.9 \pm 2.23	20.8 \pm 2.78	51.2 \pm 4.73	51.6 \pm 7.32	57.8 \pm 5.63	56.6 \pm 8.25	35.2 \pm 4.25	33.0 \pm 3.44
III	7.7 \pm 1.36 (14)	6.9 \pm 1.38 (13)	23.8 \pm 1.49	22.8 \pm 2.03	62.2 \pm 4.08	61.8 \pm 6.87	70.1 \pm 4.29	68.1 \pm 5.18	42.8 \pm 3.22	42.1 \pm 4.53
IV	9.4 \pm 1.40 (9)	10.7 \pm 2.08 (4)	25.6 \pm 1.53	26.7 \pm 1.91	68.3 \pm 3.60	71.5 \pm 3.09	76.9 \pm 4.28	76.5 \pm 1.99	47.2 \pm 4.27	44.4 \pm 4.95
V	9.5 \pm 0.85 (2)	12.0 \pm 2.06 (4)	25.8 \pm 0.35	26.4 \pm 1.61	66.5 \pm 2.12	72.9 \pm 4.80	73.8 \pm 2.47	80.1 \pm 5.06	45.0 \pm 0.00	47.7 \pm 2.30
VI	11.5 \pm 0.75 (6)	13.7 \pm 0.93 (5)	27.0 \pm 0.98	29.0 \pm 1.41	72.5 \pm 2.26	78.0 \pm 3.39	78.6 \pm 1.50	83.6 \pm 4.62	49.5 \pm 3.38	52.4 \pm 2.96
VII	11.7 \pm 0.91 (7)	12.6 \pm 1.45 (11)	27.9 \pm 1.90	27.3 \pm 1.49	72.4 \pm 3.20	74.4 \pm 2.76	80.7 \pm 4.41	81.6 \pm 1.95	50.9 \pm 3.50	48.9 \pm 5.78
VIII	12.4 \pm 1.24 (17)	13.5 \pm 0.93 (5)	28.4 \pm 1.64	27.3 \pm 1.24	75.1 \pm 2.92	78.6 \pm 1.07	82.6 \pm 3.35	85.7 \pm 3.96	49.2 \pm 3.70	51.1 \pm 3.86
IX	11.0 \pm 1.16 (3)	12.3 \pm 2.25 (6)	29.7 \pm 1.15	28.1 \pm 2.07	77.0 \pm 3.61	74.1 \pm 3.82	85.0 \pm 5.00	81.1 \pm 3.45	47.0 \pm 4.58	48.4 \pm 3.83

hystricomorph rodent species is shorter than expected for the group, thereby possibly explaining the relatively high rate of foetal growth observed for them.

The relatively long gestation periods listed for hystricomorph rodents (Weir, 1974) result, according to Roberts & Perry (1974), from very slow early growth of the embryo. The range of foetal growth velocities observed for hystricomorph rodents (0.04–0.18) is, nevertheless, similar to those observed for most mammalian orders (see Frazer & Huggett, 1974), thus indicating that rate of foetal development in hystricomorph rodents is not exceptional.

Postnatal growth

The von Bertalanffy equation has been applied to a large number of vertebrates and observed growth curves are sufficiently close to the empirical relationships to make the use of the equation an acceptable descriptive method for growth. Figure 1 indicates that the von Bertalanffy growth curve describes postnatal growth in body weight of porcupines extremely well. Growth in captive porcupines was nearly linear up to the age of 20 weeks and asymptotic body weight was attained at the age of 52 weeks, the latter coinciding with the observed age at sexual maturity (van Aarde, 1984).

The extended lactation period observed in porcupines (100.6 ± 37.8 days; $n = 9$; van Aarde, 1985c) and the protection and care afforded through intensive parental care (van Aarde, 1984) conceivably contribute to the relatively high rate of growth maintained during the first year of life. With sexual maturity attained during the second year of life and a life expectancy of approximately 20 years (Kingdon, 1974), it is apparent that the relatively high rate of postnatal growth and development result in an extended reproductive period, thereby probably enhancing individual reproductive values by counteracting the slow reproductive rate due to seasonal breeding and a small litter size ($\bar{x} = 1.5 \pm 0.66$; $n = 165$; see van Aarde, 1985c). Furthermore, it is suggested that this high rate of growth compensates for the small neonatal size of porcupines ($< 3.0\%$ of maternal body weight; $n = 16$), which in turn may be ascribed to the relatively short gestation period (see van Aarde, 1985c).

Asymptotic body weight predicted by the von Bertalanffy equation was slightly lower than the mean adult body weight attained by adult animals. However, the relatively short span for which data were included in the analysis may have been a confounding factor. The calculated coefficient of catabolism ($k = 0.65$) was higher than those recorded for the hyrax *Procavia capensis* (Fairall, 1980; Steyn & Hanks, 1983) and eland *Taurotragus oryx* (Jeffery & Hanks, 1981), but lower than that recorded for other ungulates (see Steyn & Hanks, 1983 for references). This constant, however, has no biological or physiological significance (Roff, 1980), and a comparison with other hystricomorph rodents, for which data are presently not available, would thus not have had any phylogenetic or biological meaning.

Variability in age-specific body measurements of free-ranging porcupines (see Table IV) precluded a more complete analysis, but suggests limited changes in body size after the age of 23 months has been attained. Case (1978) reported in a lengthy analysis on the adaptive significance of postnatal growth that growth rate is adapted to certain features of an animal's environment. He regarded feeding requirements, infant mortality rate and the availability of food to parents of particular importance in explaining interspecific differences in postnatal growth rates. The information available on hystricomorph rodents does not provide a basis for such an analysis. Case (1978), however, concluded that life-history attributes such as growth rate, precociality and relatively high birth weight are in these rodents similar to those in ungulates. The three

rodent subgroups (myomorphs, sciuriforms & hystricomorphs), furthermore, have very similar growth rates but differ markedly in other respects. Hystricomorphs in general, have long gestation periods, a small litter size and relatively high birth weights (Weir, 1974).

The growth rates of male and female porcupines and resulting asymptotic body weights are similar. The form of paternal investment afforded by a pair-bond system in porcupines (van Aarde, 1984) limits the degree of sexual selection imposed on males, which favours a lack of sexual dimorphism, thus partly explaining the similarity in body size of the sexes.

This is confirmed by a lack in sexual dimorphism of other size-related parameters (see Table IV).

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