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Post-natal growth of elephants *Loxodonta africana* in Etosha National Park, Namibia

M. LINDEQUE*

Etosha Ecological Institute, P.O. Okaukuejo, Via Outjo, Namibia

AND A. S. VAN JAARSVELD

Mammal Research Institute, University of Pretoria, Pretoria 0002, South Africa

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(With 4 figures in the text)

Post-natal growth in the African elephant (*Loxodonta africana*) was described using three alternative mathematical models, and two age estimation schedules. Von Bertalanffy, Gompertz and Logistic equations all provided adequate models of post-natal growth in a species for which age estimation methods are largely unsubstantiated. Gompertz and Logistic models overestimated pre-weaning growth and underestimated adult size. Self-accelerating growth is of short duration (one and three years in females and males, respectively), and we found no evidence of a secondary growth spurt in males. Males, nevertheless, continue to grow throughout their lifespan, while females reach asymptotic size at the age of 35–40 years. We found no evidence of differences in growth rate of males and females up to 10 years, and there does not seem to be differential investment in male and female offspring. Growth rates of captive elephants differ substantially from all wild populations studied and may not serve as adequate references for the revision of existing age estimation schedules.

Contents

Introduction

The formal description of growth in African elephants has always been hampered by the lack of confidence in age estimation techniques for this species. There is, however, little hope of acquiring data for a sufficient number of known-age individuals in the next few decades to achieve an acceptable revision of presently used age schedules. As the largest land mammal, the growth of African elephants has formerly aroused some interest, as several unusual features related to age,

* To whom correspondence should be addressed

size and growth are apparent in this species. The myth of the pygmy elephant (Hanks, 1972; Western, 1986), the reportedly greater body size of 'desert' elephants of the Kaokoveld, Namibia (Bosman & Hall-Martin, 1986), inter-population differences in growth rates due to variable environmental and social stresses (Laws, Parker & Johnstone, 1975) and the secondary growth spurt described in adult males (Laws, 1966; Laws & Parker, 1968; Laws *et al.*, 1975) are examples of growth-related phenomena which might implicate sampling bias and age estimation inaccuracies.

Irregularities in age frequencies in some populations (e.g. Hanks, 1972; Smuts, 1975) were attributed to biases in Laws' (1966) age schedule (Fatti *et al.*, 1980), but could also result from biased use of this schedule (Lindeque, 1991*a*). The only other evidence warranting a re-examination of the widely used age schedule of Laws (1966) comes from a series of captive elephants (Lang, 1965, 1980), and was used to derive a new growth model and age schedule (Croze, Hillman & Lang, 1981; Jachmann, 1988).

Models of growth in African elephants are, however, of practical value despite the lack of confidence in age estimation procedures. Estimates of individual age or population age structures based on the relative size of individuals, skeletal material, tusks, footprints and even faecal boli (Croze, 1972; Western, Moss & Georgiadis, 1983; Jachmann & Bell, 1984; Pilgram & Western, 1986) are widely used in studies of almost all aspects of elephant biology in Africa. The variety of growth models (and age estimation methods) available were derived from different analytical methods, and it is not possible to use published data to investigate inter-population variance in some key demographical and morphometrical parameters. Models suitable for estimating the age of elephants in the Etosha National Park (= Etosha N.P.) are presented in this paper, as well as a comparison of different types of models and age schedules, and their life-history implications.

Materials and methods

A range of body measurements previously described by Laws (1966) were recorded from elephants culled and found dead from other causes in Etosha N.P., north-western Namibia from 1983 to 1987.

Body measurements and age estimation

Shoulder height (SHS) (M: 242, F: 315) was measured on laterally recumbent elephants with the front leg extended and locked in position, as the linear distance between the edge of the sole to the distal edge of the scapula (representing the kind of height measurement possible to record from a lateral view of an elephant). Head-body length (HBL) (M: 236, F: 224) was measured between the base of the trunk (= first transverse fold) to the base of the tail over the body curves. The standard distance measured on vertical aerial photographs of elephants (Croze, 1972) was measured on recumbent elephants from midway between the ear: head junctions, over the curves to the apex of the anal flap (EBL) (M: 187, F: 250). Hind foot lengths (HFL) (M: 154, F: 192) were measured from the posterior edge of the sole to the anterior edge of the sole. Where hooves curved under the sole, the measurement was taken to approximate the typical sole length. The relative ages of individuals were estimated following Laws (1966) and Jachmann (1988) as described in Lindeque (1991*a*, *b*).

Post-natal growth

Post-natal growth was described by fitting 3 alternative curves to the data as in Zullinger *et al.* (1984) and van Jaarsveld, Skinner & Lindeque (1988). Von Bertalanffy, Gompertz and Logistic equations were fitted following Du Toit & Herbst (1981). Actual growth increments were determined over approximately 3 years in 5 male elephants fitted with radio-collars in Etosha N.P., where age estimates at initial measurement were derived from molar progression (Laws, 1966).

Results

Post-natal growth

Tables I and II present the equations fitted to elephant growth parameters and the calculated growth parameters based on the age schedules of Laws (1966) and Jachmann (1988), respectively. All curve-fittings using the three models were significant ($F > 0{\cdot}01$), and the correlation coefficients (R^2) were generally similar. All three models could thus be used to describe post-natal growth in elephants, but Von Bertalanffy equations provide a marginally better fit to the data over the first few age groups. Asymptotic values derived for the parameters in Tables I and II were highest using Von Bertalanffy equations, intermediate with Gompertz and lowest with Logistic equations in both males and females. These differences are slight. Gompertz and Logistic models generally fitted the data better than Von Bertalanffy models when using the age schedule of Jachmann (1988).

Figures 1 and 2 illustrate the three curves, observed data as well as the calculated growth rates for shoulder height (SHS) in females and males, respectively. Similar trends were apparent from age-specific increases in body length (HBL, EBL), tusk diameter and lengths of hind feet. No indication of a secondary growth spurt in males was evident from Fig. 2 or the other parameters.

TABLE I

*Calculated parameters of equations fitted to elephant growth parameters using the age schedule of Laws (1966). (**n** denotes sample size, correlation coefficients (R^2) are given in parentheses)*

	Equation		
Growth parameter	Von Bertalanffy $L_t = L[1 - e^{-K(t-t_0)}]$	Gompertz $y = ab^{r^t}$	Logistic $y = a/(1 + br^t)$
SHS Males	$L_t = 344{\cdot}86\,[1 - e^{-0{\cdot}05\,(t+8{\cdot}86)}]$	$y = (336{\cdot}76^*0{\cdot}40)^{0{\cdot}93^t}$	$y = 331{\cdot}88\,[1 + (1{\cdot}39^*0{\cdot}91)^t]$
$n = 242$	(0·95)	(0·94)	(0·94)
SHS Females	$L_t = 262{\cdot}25\,[1 - e^{-0{\cdot}11\,(t+4{\cdot}99)}]$	$y = (260{\cdot}52^*0{\cdot}45)^{0{\cdot}87^t}$	$y = 259{\cdot}22\,[1 + (1{\cdot}15^*0{\cdot}85)^t]$
$n = 315$	(0·94)	(0·94)	(0·93)
HBL Males	$L_t = 495{\cdot}82\,[1 - e^{-0{\cdot}04\,(t+12{\cdot}51)}]$	$y = (472{\cdot}66^*0{\cdot}40)^{0{\cdot}95^t}$	$y = 459{\cdot}89\,[1 + (1{\cdot}38^*0{\cdot}93)^t]$
$n = 236$	(0·94)	(0·94)	(0·93)
HBL Females	$L_t = 368{\cdot}14\,[1 - e^{-0{\cdot}08\,(t+8{\cdot}44)}]$	$y = (365{\cdot}40^*0{\cdot}50)^{0{\cdot}91^t}$	$y = 363{\cdot}36\,[1 + (0{\cdot}93^*0{\cdot}90)^t]$
$n = 224$	(0·91)	(0·90)	(0·90)
EBL Males	$L_t = 395{\cdot}05\,[1 - e^{-0{\cdot}04\,(t+11{\cdot}43)}]$	$y = (378{\cdot}93^*0{\cdot}38)^{0{\cdot}95^t}$	$y = 370{\cdot}20\,[1 + (1{\cdot}49^*0{\cdot}93)^t]$
$n = 187$	(0·95)	(0·95)	(0·94)
EBL Females	$L_t = 288{\cdot}24\,[1 - e^{-0{\cdot}08\,(t+7{\cdot}12)}]$	$y = (285{\cdot}50^*0{\cdot}46)^{0{\cdot}90^t}$	$y = 283{\cdot}51\,[1 + (1{\cdot}10^*0{\cdot}88)^t]$
$n = 250$	(0·92)	(0·92)	(0·91)
HFL Males	$L_t = 58{\cdot}94\,[1 - e^{-0{\cdot}06\,(t+8{\cdot}38)}]$	$y = (58{\cdot}00^*0{\cdot}43)^{0{\cdot}92^t}$	$y = 57{\cdot}40\,[1 + (1{\cdot}23^*0{\cdot}90)^t]$
$n = 154$	(0·91)	(0·91)	(0·91)
HFL Females	$L_t = 47{\cdot}52\,[1 - e^{-0{\cdot}12\,(t+5{\cdot}35)}]$	$y = (47{\cdot}37^*0{\cdot}50)^{0{\cdot}87^t}$	$y = 47{\cdot}25\,[1 + (0{\cdot}97^*0{\cdot}85)^t]$
$n = 192$	(0·86)	(0·86)	(0·86)

* See text

TABLE II

*Calculated parameters of equations fitted to elephant growth parameters using the age schedule of Jachmann (1988). (**n** denotes sample size, correlation coefficients (R^2) are given in parentheses)*

	Equation		
Growth parameter*	Von Bertalanffy $L_t = L\,[1 - e^{-K(t - t_0)}]$	Gompertz $y = ab^{c^t}$	Logistic $y = a/(1 + br^t)$
SHS Males $n = 242$	$L_t = 336{\cdot}89\,[1 - e^{-0{\cdot}07\,(t + 6{\cdot}67)}]$ (0·90)	$y = (331{\cdot}02*0{\cdot}39)^{0{\cdot}94^t}$ (0·96)	$y = 327{\cdot}25/[1 + (1{\cdot}47*0{\cdot}88)^t]$ (0·97)
SHS Females $n = 315$	$L_t = 262{\cdot}84\,[1 - e^{-0{\cdot}13\,(t + 4{\cdot}05)}]$ (0·88)	$y = (261{\cdot}41*0{\cdot}43)^{0{\cdot}85^t}$ (0·93)	$y = 260{\cdot}30/[1 + (1{\cdot}24*0{\cdot}82)^t]$ (0·93)
HBL Males $n = 236$	$L_t = 470{\cdot}49\,[1 - e^{-0{\cdot}05\,(t + 8{\cdot}86)}]$ (0·92)	$y = (456{\cdot}91*0{\cdot}40)^{0{\cdot}93^t}$ (0·93)	$y = 449{\cdot}24/[1 + (1{\cdot}41*0{\cdot}90)^t]$ (0·93)
HBL Females $n = 224$	$L_t = 363{\cdot}78\,[1 - e^{-0{\cdot}10\,(t + 6{\cdot}16)}]$ (0·93)	$y = (361{\cdot}51*0{\cdot}48)^{0{\cdot}89^t}$ (0·86)	$y = 359{\cdot}74/[1 + (1{\cdot}02*0{\cdot}87)^t]$ (0·86)
EBL Males $n = 187$	$L_t = 376{\cdot}18\,[1 - e^{-0{\cdot}05\,(t + 8{\cdot}36)}]$ (0·91)	$y = (366{\cdot}02*0{\cdot}38)^{0{\cdot}93^t}$ (0·95)	$y = 360{\cdot}13/[1 + (1{\cdot}51*0{\cdot}91)^t]$ (0·95)
EBL Females $n = 250$	$L_t = 286{\cdot}60\,[1 - e^{-0{\cdot}10\,(t + 5{\cdot}48)}]$ (0·90)	$y = (284{\cdot}35*0{\cdot}44)^{0{\cdot}88^t}$ (0·92)	$y = 282{\cdot}65/[1 + (1{\cdot}19*0{\cdot}86)^t]$ (0·91)
HFL Males $n = 154$	$L_t = 58{\cdot}04\,[1 - e^{-0{\cdot}08\,(t + 6{\cdot}46)}]$ (0·90)	$y = (57{\cdot}36*0{\cdot}42)^{0{\cdot}90^t}$ (0·90)	$y = 56{\cdot}92/[1 + (1{\cdot}31*0{\cdot}87)^t]$ (0·90)
HFL Females $n = 192$	$L_t = 47{\cdot}52\,[1 - e^{-0{\cdot}14\,(t + 4{\cdot}27)}]$ (0·85)	$y = (47{\cdot}42*0{\cdot}43)^{0{\cdot}89^t}$ (0·85)	$y = 47{\cdot}33/[1 + (1{\cdot}05*0{\cdot}82)^t]$ (0·85)

* See text

The three growth models used in Figs 1 and 2 describe the data equally well and are for all practical purposes equally useful. Apart from a slightly earlier onset of growth plateaus when using the age estimation schedule of Jachmann (1988), the shapes of growth curves resulting from either schedule are virtually identical. Male growth in the parameters used differ from female growth in not reaching a clear plateau before the terminal age group, except when using the age schedule of Jachmann (1988).

Growth rates

Table III presents growth increments measured in five males over approximately three years. The average annual increment in at least shoulder height and body length approximate the growth curves presented. This limited data set could be biased due to individual variation in growth rate, and potential bias in repeating measurements affected by posture. Calculated growth rates derived from logistic curves in the parameters measured in the larger sample are illustrated in Figs 1 and 2. The self-accelerating phase is exceptionally short in elephants (1 year in females, 3 years in males using either age schedule), while the self-retarding phase is expressed from the age of 1–40 years in females (Batt, 1980). Male elephants grow throughout their life-span, but females reach a growth plateau at approximately 35–40 years.

Discussion

Previous descriptions of elephant growth have relied on the Von Bertalanffy equation (Laws,

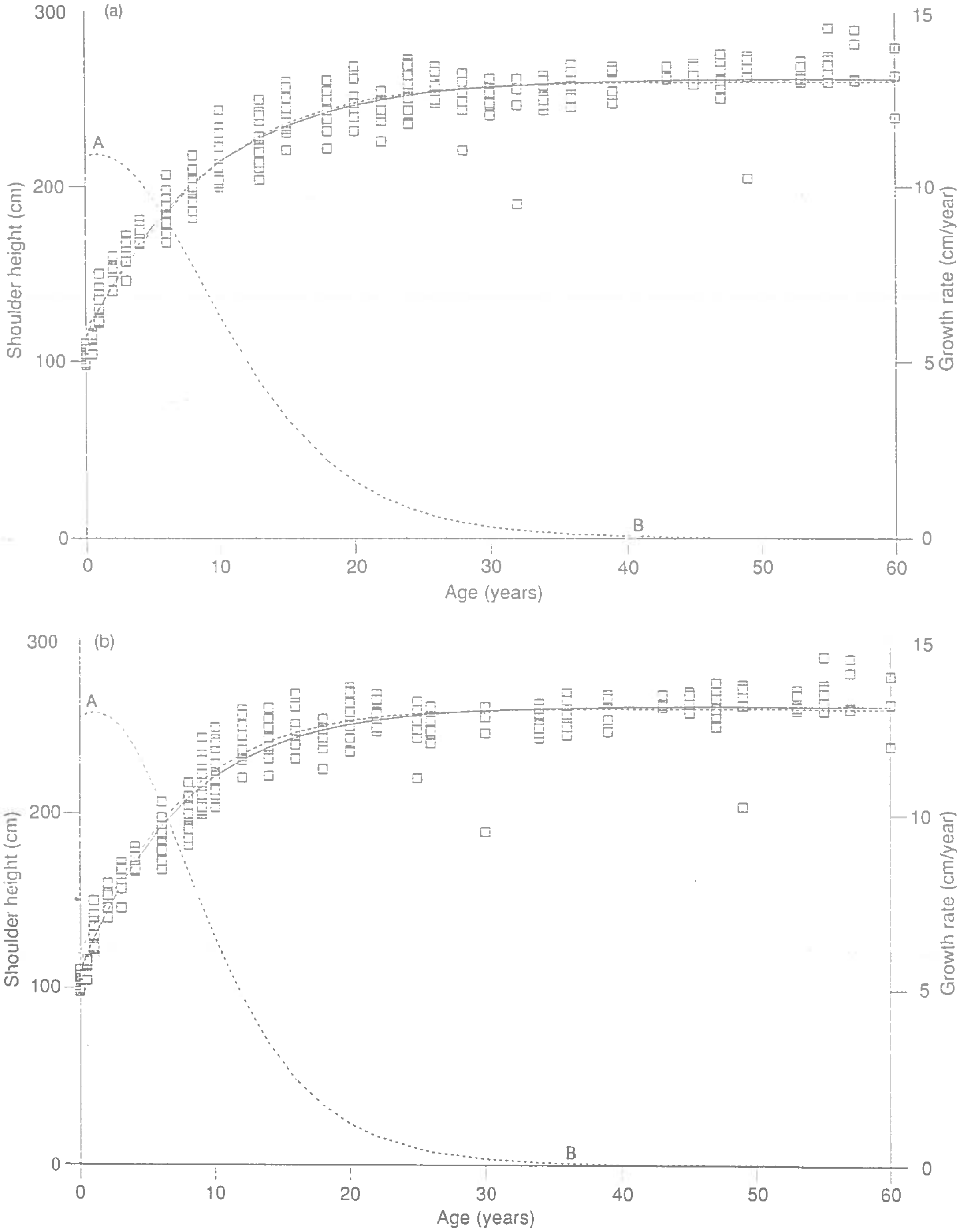

FIG. 1. Von Bertalanffy (——), Gompertz (- - -) and Logistic (. . . . .) plots for post-natal growth in shoulder height against age estimated according to Laws (1966) in (a) and Jachmann (1988) in (b), for female African elephants. Actual data points are represented by □: $n = 315$. Calculated growth rates (-·-·-) derived from Logistic curves illustrate the inflection point A and the growth plateau point B.

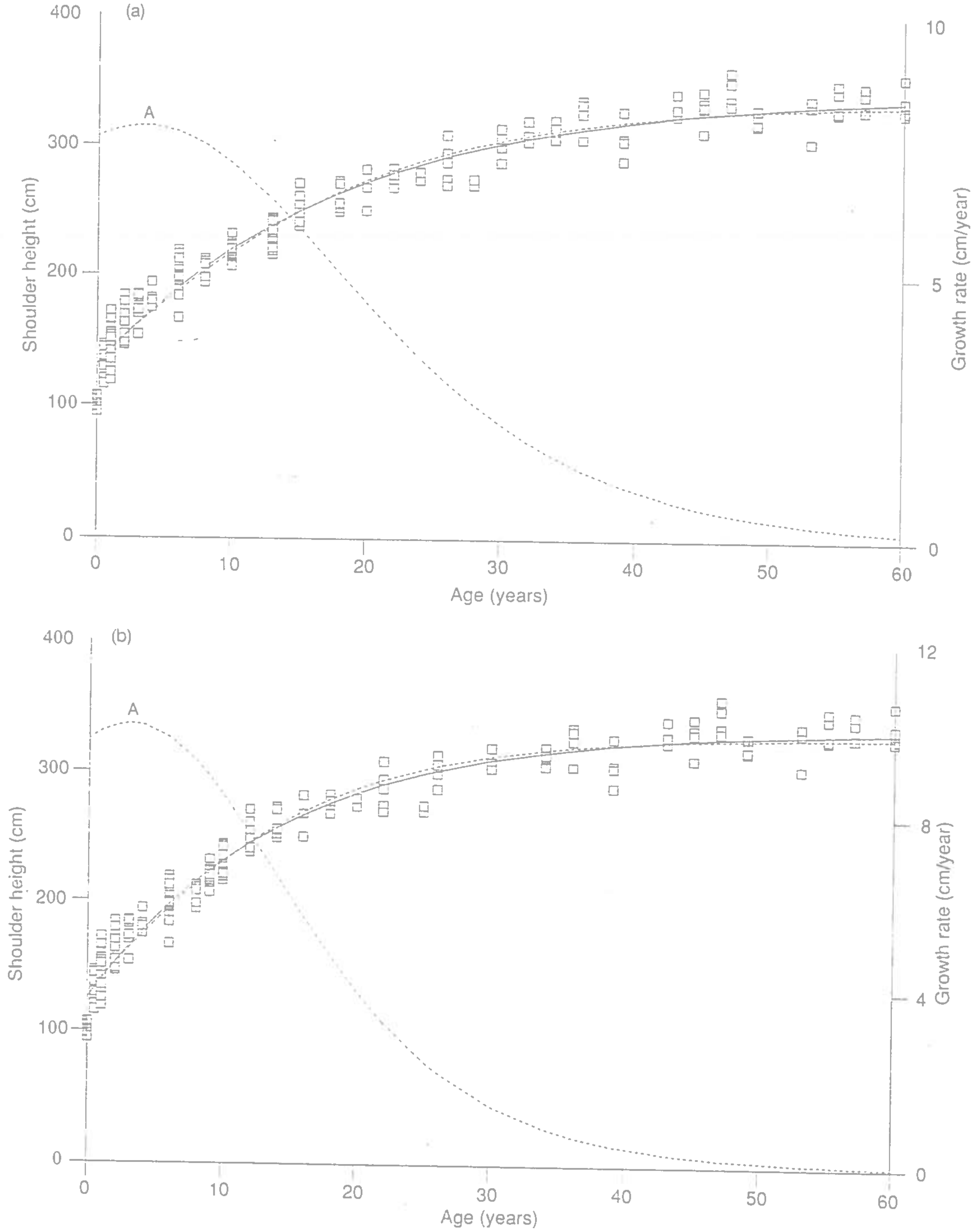

FIG. 2. Von Bertalanffy (——), Gompertz (– – –) and Logistic (· · · · ·) plots for post-natal growth in shoulder height against age estimated according to Laws (1966) in (a) and Jachmann (1988) in (b), for male African elephants. Actual data points are represented by □; $n = 242$. Calculated growth rates (-·-·-) derived from Logistic curves illustrate the inflection point A.

TABLE III

Recorded growth in cm of male elephants in Etosha National Park

Age at first measuring (years)	Months between measurements	Growth parameter	
		SHS	EBL
26 ± 2	35	298	320
		310	322
		* 4·1	0·7
32 ± 2	37	304	324
		309	343
		* 1·6	6·2
34 ± 2	39	321	335
		330	367
		*2·8	9·9
47 ± 2	36	351	369
		358	378
		* 2·3	3·0
53 ± 2	34	358	358
		360	365
		* 0·7	2·5

* Approximate annual increments

1966; Laws & Parker, 1968; Hanks, 1972; Laws, Parker & Johnstone, 1975; Sherry, 1978; Jachmann & Bell, 1984; Jachmann, 1988) and a variety of log linear and polynomial expressions (Laws, 1967; Hanks, 1972; Brownlee & Hanks, 1977; Malpas, 1977; Sherry, 1978; Lee & Moss, 1986; Viljoen, 1990; Lindeque, 1991*b*). Von Bertalanffy growth curves seem to provide adequate models of post-natal growth in elephants and possibly a better description of growth over the first few years than both the Logistic and Gompertz models which generally overestimate pre-weaning growth and underestimate asymptotic size, as in the majority of mammals (Zullinger *et al.*, 1984).

No evidence of a secondary or post-pubertal growth spurt could be detected in males as based on our data and calculated growth rates illustrated in Figs 1 and 2, and we support Hanks (1972) in that the additional growth acceleration described by Laws *et al.* (1975) is probably due to age estimation bias. African elephants are markedly sexually dimorphic, as is also evident from Figs 1 & 2, but most of the difference in mature size of males and females is due to continuous growth in males compared to the early onset of growth plateaus in females, as generally applies to sexually dimorphic terrestrial mammals (Bennett & Harvey, 1985; Georgiadis, 1985). Lee & Moss (1986) postulated that marginally greater maternal investment in male offspring results in faster growth in males than in females from the age of five years. Calves are generally independent after two to three years and, if still suckling beyond this period, no differences were apparent between males and females (Lee & Moss, 1986) and it is thus difficult to reconcile differential maternal investment with differential growth rates at age five. According to our data, male and female growth curves only diverge after the onset of puberty between 10 and 20 years of age.

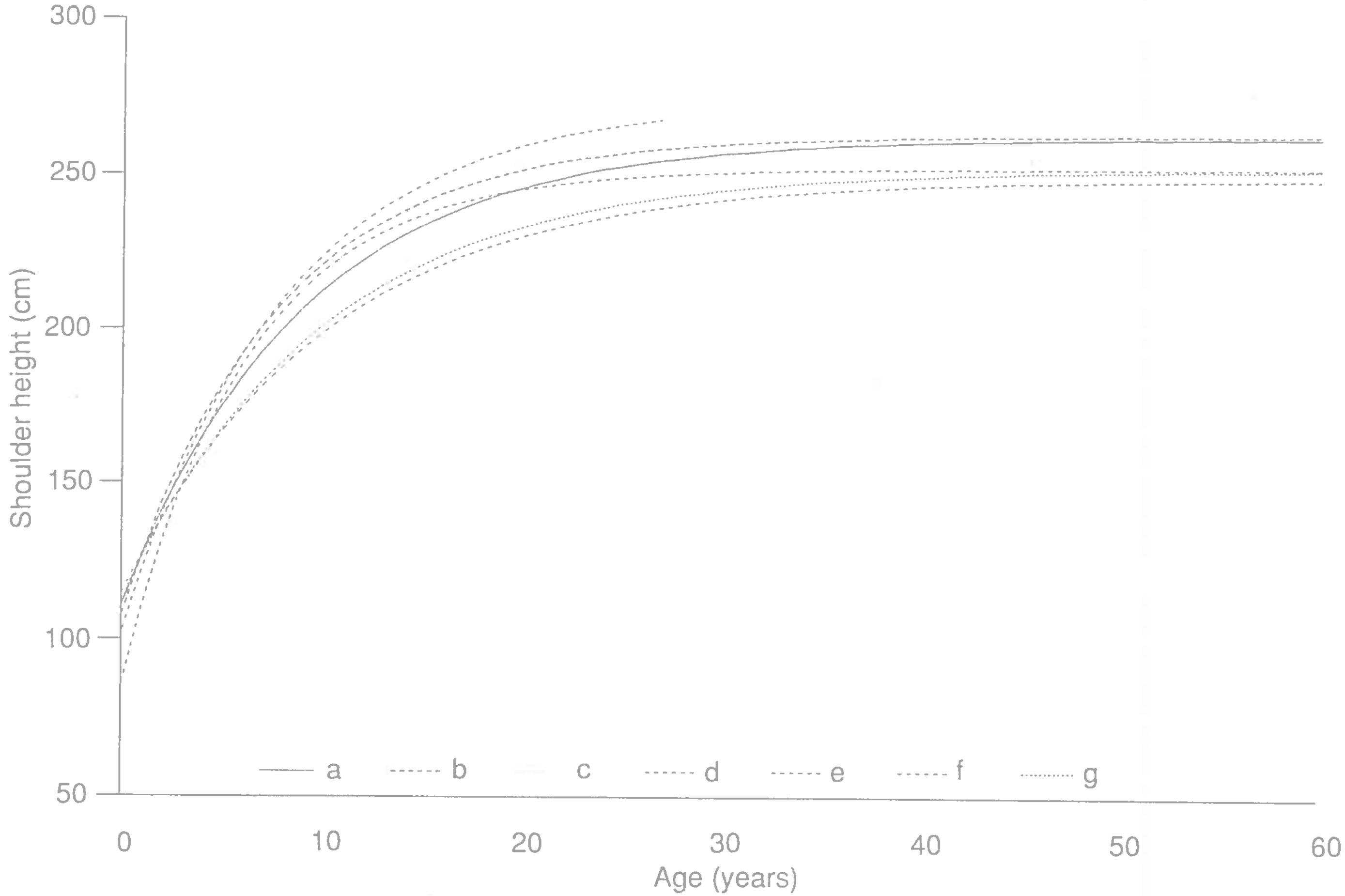

FIG. 3. Von Bertalanffy growth curves for post-natal growth in shoulder height in female African elephants; a = Etosha N.P. and age estimation following Laws (1966); b = Etosha N.P. and age estimation following Jachmann (1988); c = captive elephants (Lang, 1980; Jachmann, 1988); d = Malawi (Jachmann, 1988); e = Zambia (Hanks, 1972); f = captive female 'Diksie' (Short, 1969; Hanks, 1972); g = Uganda (Laws, Parker & Johnstone, 1975).

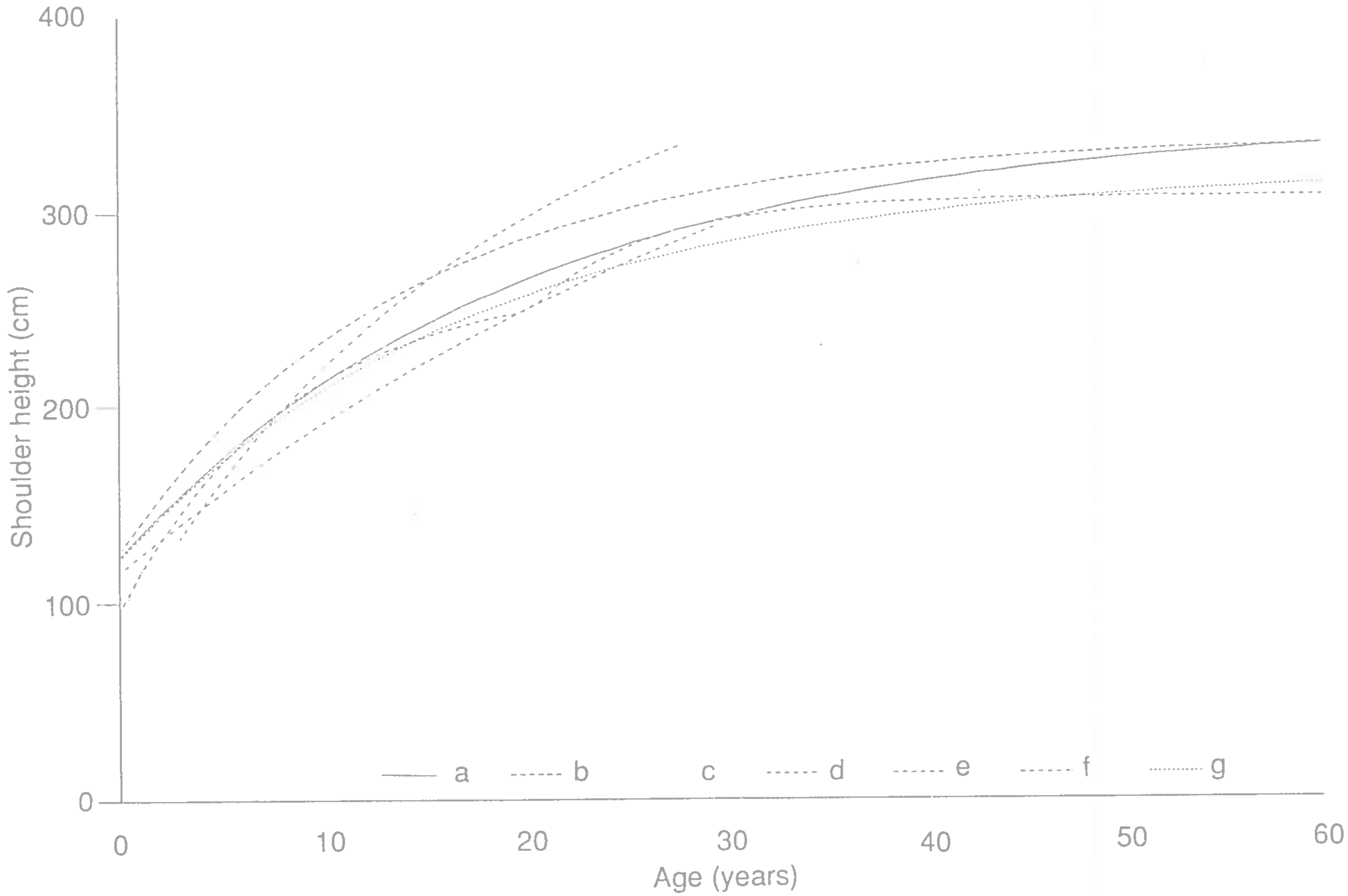

FIG. 4. Von Bertalanffy growth curves for post-natal growth in shoulder height in male African elephants; a = Etosha N.P. and age estimation following Laws (1966); b = Etosha N.P. and age estimation following Jachmann (1988); c = captive elephants (Lang, 1980; Jachmann, 1988); d = Malawi (Jachmann, 1988); e = Zambia (Hanks, 1972); f = captive male 'Kartoum' (Hanks, 1972); g = Uganda (Laws, Parker & Johnstone, 1975).

The short period before self-retarding growth is expressed after birth until the inflection point is reached in calculated growth curves indicates that growth before birth is relatively complete in elephants, although there is much variation in the birth mass and gestation length of African elephants (Kiltie, 1982). Very large mammals typically invest proportionally less in their always precocial offspring after birth, resulting in comparatively slow growth of neonates, and in elephants requiring a degree of alloparental care to supplement maternal investment (Case, 1978; Western, 1979; Dublin, 1983; Bennett & Harvey, 1985; Martin & MacLarnon, 1985; Lee, 1987; Owen-Smith, 1988).

The correspondence between growth curves derived by Von Bertalanffy equations from different populations is illustrated in Figs 3 and 4. All previous studies used linear solutions to the Von Bertalanffy equation, which are less accurate than the non-linear methods used in the present study (Vaughan & Kanciruk, 1982; Zullinger *et al.*, 1984), which may influence any direct comparison. Estimates of variance and correlation coefficients were usually absent in earlier reports. Laws & Parker (1968) suggest that the rate of growth might vary within a population over time, or between populations, as a factor related to nutrition, stress and overcrowding. McCullagh (1969), Malpas (1977) and Sherry (1978) found appreciable differences in growth rate between nearby populations and growth rates *per se* might facilitate the contentious subdivision of elephants into populations and sub-populations. Published variation in growth constants and rates (Fig. 3) cannot, however, be used with confidence due to a lack of standardization in analytical procedures.

It would seem, however, that elephants in Etosha N.P. do grow taller than the other populations represented in Figs 3 and 4, which is consistent with the former classification of elephants into different sub-species based in part on their larger size. The type locality for the 'Kaokoveld elephant *L. a. zukowskyi*' (Strand, 1924) is in present-day Etosha N.P. (Shortridge, 1934). Captive elephants appear to grow much faster than wild ones based on Figs 3 and 4, and also in Krumrey & Buss (1968), Hanks (1972) and Brownlee & Hanks (1977); and those represented in Figs 3 and 4 would have reached exceptional asymptotes. The captive female elephants of Lang (1980), however, reached their growth plateaus at 15–16 years of age, some 25 years earlier than wild elephants. We regard the growth rates obtained from these captive elephants as abnormal due to their artificial zoo environments, and express doubt over the validity of applying the rates of molar progression of these individuals to any wild population. The age schedule of Jachmann (1988) might therefore not be valid, nor the apparently faster growth rates resulting from the use of this age schedule on free-living elephants.

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