

Growth and age determination of African savanna elephants

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Keywords

Loxodonta africana africana; shoulder height; sub-Saharan Africa; Von Bertalanffy growth curve.

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Received 24 May 2005; accepted 14 November 2005

doi:10.1111/j.1469-7998.2006.00108.x

Abstract

Understanding the population dynamics of savanna elephants depends on estimating population parameters such as the age at first reproduction, calving interval and age-specific survival rates. The generation of these parameters, however, relies on the ability to accurately determine the age of individuals, but a reliable age estimation technique for free-ranging elephants is presently not available. Shoulder heights of elephants were measured in 10 populations in five countries across southern and eastern Africa. Data included shoulder height measurements from two populations where the age of each individual was known (i.e. Addo Elephant National Park, South Africa and Amboseli National Park, Kenya). From the known-age data, Von Bertalanffy growth functions were constructed for both male and female elephants. Savanna elephants were found to attain similar asymptotic shoulder heights in the 10 populations, while individuals in the two known-age populations grew at the same rate. The Von Bertalanffy growth curves allowed for the accurate age estimation of females up to 15 years of age and males up to 36 years of age. The results indicate that shoulder height can serve as an indicator of chronological age for elephants below 15 years of age for females and 36 years of age for males. Ages derived from these growth curves can then be used to generate age-specific population variables, which will help assess the demographic status of savanna elephant populations across Africa.

Introduction

Savanna elephants *Loxodonta africana africana* live in landscapes ranging from deserts to forests across Africa (Blanc *et al.*, 2003). Populations apparently respond to variation in habitat quality through differences in age at first reproduction, length of calving interval and survival rates (e.g. Laws, 1969). To estimate these population parameters, the age of individuals within a population needs to be accurately estimated. Methods for determining the ages of elephants rely on changes in back length (Croze, 1972), shoulder height (e.g. Laws, 1966; Douglas-Hamilton, 1972; Jachmann, 1988; Lee & Moss, 1995) and hind foot length (Western, Moss & Georgiadis, 1983; Lee & Moss, 1995) with age. Rates of tooth eruption have also been used to estimate the age of dead or immobilized elephants (e.g. Laws, 1966; Sikes, 1966; Hanks, 1972a; Fatti *et al.*, 1980; Jachmann, 1988).

Only a few studies have assessed growth for elephants of known ages (e.g. Western *et al.*, 1983; Lee & Moss, 1995). Not surprisingly, no study has related ages to patterns and rates of tooth eruption on living free-ranging elephants. The

original study of Laws and colleagues (Laws, 1966, 1969; Laws, Parker & Johnstone, 1975) on shot elephants in Uganda developed tooth-ageing techniques based on a number of assumptions about the population and its age structure. Studies from captivity and elsewhere have noted problems with the original age estimating criteria, and some corrections can now be applied (Lang, 1980; Jachmann, 1988). However, the use of tooth ages may still contain significant errors and confound growth and population studies that depend on age (e.g. Laws, 1969; Hanks, 1972a, 1979; Lindeque, 1988; Lindeque & van Jaarsveld, 1993; Whyte, 2001). Two long-term studies on individually recognized, known-age elephants living in Amboseli National Park (Lee & Moss, 1995; Moss, 2001) and Addo Elephant National Park (Whitehouse & Hall-Martin, 2000) should allow for the development of reliable methods for determining the ages of elephants in the wild.

Before our study, the extent of variation in growth among savanna elephant populations was unknown. Elephant growth represents an unusual pattern for mammals, in that growth in some bony tissues is indeterminate (Haynes, 1991). Consequently females attain their maximum stature

only after 25 years of age with epiphyseal fusion in their long bones, whereas males appear to grow in height (albeit slowly) until they are in their 40s. The spine, and hence back length, of both males and females continues to grow until death (Haynes, 1991). Comparisons of terminal (or asymptotic) height between populations suggest that there may be some genetic or developmental differences across Africa (Hanks, 1972a; Sherry, 1978; Jachmann, 1986; Lee & Moss, 1995). At the same time, however, similarities in the rates of growth or in the shape of the growth curve across these populations are striking (Douglas-Hamilton, 1972; Laws *et al.*, 1975; Malpas, 1977; Western *et al.*, 1983). Population variation in asymptotic height could result from differences in growth rates, differences in the duration of growth or both. As there are so few studies of growth on known-age elephants, we cannot yet determine which genetic, nutritional or social factors are likely to be influential in determining the relationship between size (or stature) and age. Here, we review the relationship between shoulder height and age. We then evaluate growth in shoulder heights for known-age elephants in Amboseli National Park and Addo Elephant National Park. We also compare the shoulder heights of adult elephants across 10 populations.

Methods

Growth analyses

We collated all available data from the literature on the relationship between shoulder height and age of savanna elephants (see Table 1). When possible we extracted the parameters of calculated growth curves. We interpolated shoulder height at birth using growth curves specific to each study. Our data do not allow for a robust statistical comparison; therefore we only report the means and coefficients of variation (CV) of these parameters.

We used a digital photogrammetric method (Shrader, Ferreira & van Aarde, 2006) to measure shoulder heights for adult females (those with at least two calves) and adult males in 10 elephant populations in five African countries (Botswana, Kenya, Namibia, South Africa and Zambia; Fig. 1). We compared the frequency distributions of these shoulder heights using a Kruskal–Wallis test after testing for homogeneity of variances using F_{\max} tests.

We also measured the shoulder heights of 57 known-age elephants in the Addo Elephant National Park (33°26'S, 25°45'E; South Africa) and of 298 such elephants in the Amboseli National Park (2°40'S, 37°16'E; Kenya). The year of birth was known for all individuals born from 1976 to the present (i.e. 27 years) in Addo (Whitehouse & Hall-Martin, 2000) and from 1970 to the present (i.e. 34 years) in Amboseli (Lee & Moss, 1995). Elephants were identified either through comparisons with identification photographs or by research personnel who could identify individuals. We used a paired t -test to compare age-specific mean shoulder heights for these populations.

We constructed sex-specific Von Bertalanffy (1938) curvilinear growth functions [$h_i = h_b + (H_\infty - h_b)(1 - e^{-kt})$], where

h_i is shoulder height, h_b is shoulder height at birth, H_∞ is asymptotic shoulder height, k is a constant determining the rate of growth and t is the age of an individual; see Hanks 1972a] using GraphPad Prism version 3.00 (Windows, GraphPad Software, San Diego, CA, USA, www.graphpad.com). There are, however, several potential problems with this curve. The first is that it approximates growth from conception, while it is fit to stature after birth (Lee & Moss, 1995). We, however, scale the curve by bounding it to a lower value linked to stature at birth, h_b , that should minimize the effect of this approximation. The second is that it assumes that there is a terminal or asymptotic stature, which may not be the case for male elephants (Lee & Moss, 1995). Thus, population comparisons of H_∞ may be heavily skewed by the number of older individuals in the sample.

Age determination

We used a Monte Carlo simulation to derive 100 random shoulder heights for males and females in each of 60 one-year age classes from 1 to 60 years. To generate these, we added the age-specific shoulder height for each age (generated using our known-age growth curve) to the product of the residual error of the growth function and a normally distributed random number between 0 and 1 (Gentle, 1943). This resulted in random shoulder heights for each age, which were constrained within bounds defined by the residuals. Data for females and males were organized separately into 5 cm height classes. The mean, standard deviation and variance were then calculated for each age class to determine the precision with which we could derive age from shoulder height measurements. Finally, confidence intervals for the predicted ages were calculated from these simulated data.

Results

Growth in shoulder height

We located 15 studies in the literature that reported changes in shoulder height with age (Table 1). From these studies, 19 curves were generated for males and 18 for females. Most of these curves were based on the Von Bertalanffy (1938) growth curve (Table 1). Predictions of the asymptotic shoulder height for males ranged from 265 to 451 cm ($\bar{x} = 328$, CV = 15.6, calculated only from the 13 non-replicated curves), whereas those for females ranged from 232 to 300 cm ($\bar{x} = 261$, CV = 6.6). Predictions for shoulder height at birth also varied widely, with values for males ranging from 86 to 253 cm ($\bar{x} = 105$, CV = 14.6) and those for females ranging from 90 to 120 cm ($\bar{x} = 105$, CV = 9.3). The aberrant value for shoulder height at birth resulted from our extrapolation based on that of Laws *et al.* (1975), who used data from males >20 years in their growth model. Growth rate constants were highly variable (\bar{x} for males = 0.083, CV = 50.2; \bar{x} for females = 0.123, CV = 14.5), suggesting that this measure is the least precise across the populations.

Table 1 Parameters for growth curves published for savanna elephants

Locality	<i>n</i>	Measure	Age	Curve	H_{∞}	<i>k</i>	t_0	h_b	Reference
a) Males									
Luangwa Valley	59	Lying	Laws (1966)	Von Bertalanffy	451 ± 59	0.025 ± 0.006	-11.84 ± 1.80	116 ^a	Hanks (1972a)
Khartoum Zoo	1	Captive	Known (3–28 years)	Von Bertalanffy	409 ± 33	0.053 ± 0.009	-4.46 ± 1.17	86 ^a	Benedict (1936)
Murchison Falls	14	Lying	Laws (1966)	Von Bertalanffy	317	–	–	–	Laws (1966)
Murchison Falls	335	Lying	Laws (1966)	Von Bertalanffy	317	–	–	–	Laws & Parker (1968)
Murchison Falls	168	Lying	Laws (1966) (0–20 years)	Von Bertalanffy	265	0.114	-3.95	96 ^a	Laws <i>et al.</i> (1975)
Murchison Falls	167	Lying	Laws (1966) (> 20 years)	Von Bertalanffy	307	0.166	-10.48	253 ^a	Laws <i>et al.</i> (1975)
Queen Elizabeth Captive animals	11	Lying	Laws (1966)	Von Bertalanffy	298	–	–	–	Laws (1966)
		Captive	Known	Von Bertalanffy	302	–	–	–	Flower (1947), Bellinge & Woodley (1964), Johnson & Buss (1965), Perry (1953), Taylor (1955)
Amboseli	170	Photoscale II	Known	Von Bertalanffy	304	0.071	-5.34	96 ^a	Lee & Moss (1995)
Basle Zoo	2	Captive ^b	Known (1–21 years)	Von Bertalanffy	331	0.096	-3.44	93 ^a	Lang (1980)
Hwange Etosha	–	–	–	–	350	–	–	–	Haynes (1991)
Etosha	242	Lying	Laws (1966)	Von Bertalanffy	345	0.05	-8.86	123 ^a	Lindeque & van Jaarsveld (1993)
Etosha	242	Lying	Jachmann (1988)	Von Bertalanffy	337	0.07	-6.67	126 ^a	Lindeque & van Jaarsveld (1993)
Kruger	203	Lying	Laws (1966)	Von Bertalanffy ^c	323 ± 5	0.064 ± 0.003	-7.03 ^a	117 ± 2	I. J. Whyte (unpubl. data)
Kruger	402	Standing (calliper)	Laws (1966)	Von Bertalanffy ^c	275 ± 3	0.124 ± 0.004	-4.23 ^a	113 ± 1	I. J. Whyte (unpubl. data)
					<i>a</i>	<i>b</i>	<i>r</i>		
Etosha	242	Lying	Laws (1966)	Gompertz	336	0.40	0.93	135 ^a	Lindeque & van Jaarsveld (1993)
Etosha	242	Lying	Jachmann (1988)	Gompertz	331	0.39	0.94	129 ^a	Lindeque & van Jaarsveld (1993)
Etosha	242	Lying	Laws (1966)	Logistic	333	1.39	0.91	139 ^a	Lindeque & van Jaarsveld (1993)
Etosha	242	Lying	Jachmann (1988)	Logistic	327	1.47	0.88	132 ^a	Lindeque & van Jaarsveld (1993)
b) Females									
Luangwa Valley	153	Lying	Laws (1966)	Von Bertalanffy	249 ± 9	0.097 ± 0.003	-6.39 ± 0.39	115 ^a	Hanks (1972a)
Diksie (Zoo)	1	Captive	Known (0–27 years)	Von Bertalanffy	274 ± 4	0.122 ± 0.004	-3.82 ± 0.34	102 ^a	Short (1969)
Murchison Falls	31	Lying	Laws (1966)	Von Bertalanffy	274	–	–	–	Laws (1966)
Murchison Falls	458	Lying	Laws (1966)	Von Bertalanffy	274	–	–	–	Laws & Parker (1968)
Murchison Falls	458	Lying	Laws (1966)	Von Bertalanffy	252	0.099	-6.00	113 ^a	Laws <i>et al.</i> (1975)
Murchison Falls	458	Lying	Laws (1966)	Von Bertalanffy	252 ± 8	0.159	-2.62	90 ^a	Laws <i>et al.</i> (1975)
Queen Elizabeth	5	Lying	Laws (1966)	Von Bertalanffy	272	–	–	–	Laws (1966)
Amboseli	224	Photoscale II	Known	Von Bertalanffy	232	0.128	-3.98	93 ^a	Lee & Moss (1995)
Basle Zoo	4	Captive ^d	Known (1–26 years)	Von Bertalanffy	268	0.124	-3.38	92 ^a	Lang (1980)
Hwange	–	–	–	–	300	–	–	–	Haynes (1991)

Table 1 Continued

Locality	<i>n</i>	Measure	Age	Curve	H_{∞}	<i>k</i>	t_0	h_b	Reference
Etosha	315	Lying	Laws (1966)	Von Bertalanffy	262	0.11	-4.99	111 ^a	Lindeque & van Jaarsveld (1993)
Etosha	315	Lying	Jachmann (1988)	Von Bertalanffy	263	0.13	-4.05	108 ^a	Lindeque & van Jaarsveld (1993)
Kruger	267	Lying	Laws (1966)	Von Bertalanffy ^c	250 ± 1	0.124 ± 0.003	-4.56 ^a	108 ± 2	I. J. Whyte (unpubl. data)
Kruger	540	Standing (calliper)	Laws (1966)	Von Bertalanffy ^c	246 ± 1	0.138 ± 0.003	-4.51 ^a	114 ± 1	I. J. Whyte (unpubl. data)
Etosha	315	Lying	Laws (1966)	Gompertz	<i>a</i>	<i>b</i>	<i>r</i>	117 ^a	Lindeque & van Jaarsveld (1993)
Etosha	315	Lying	Jachmann (1988)	Gompertz	261	0.45	0.87	112 ^a	Lindeque & van Jaarsveld (1993)
Etosha	315	Lying	Laws (1966)	Logistic	259	1.15	0.85	120 ^a	Lindeque & van Jaarsveld (1993)
Etosha	315	Lying	Jachmann (1988)	Logistic	260	1.24	0.82	116 ^a	Lindeque & van Jaarsveld (1993)

Von Bertalanffy: $h_t = H_{\infty}(1 - e^{-k(t-t_0)})$, where *k* is the growth rate, *t* is the age and t_0 is the theoretical age at which animals will have a shoulder height of zero. Gompertz: $h_t = ab^{t^r}$, where *a* and *b* are constants and *r* is growth rate. Logistic: $h_t = a/(1 + br^t)$. h_b is estimated height at birth.

^aEstimated from published curves.

^bOne hundred and thirty-four combined measurements.

^cFitted using a rewritten Von Bertalanffy curve: $h_t = h_b + (H_{\infty} - h_b)(1 - e^{-kt})$.

^dTwo hundred and fifty combined measurements.

Note that, where possible, we have included standard errors of parameters.

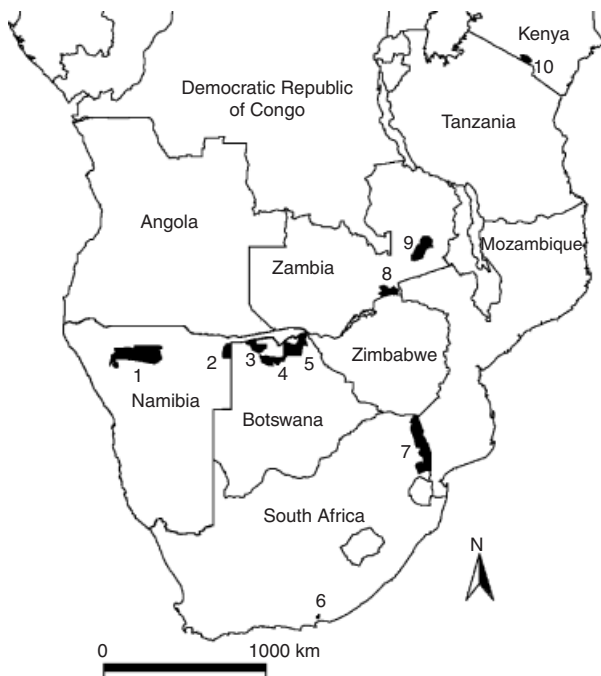


Figure 1 Locations of the 10 sampled savanna elephant populations. Sites were located in five countries across sub-Saharan Africa (i.e. Namibia, Botswana, South Africa, Zambia and Kenya) and comprise (1) Etosha National Park, (2) Khaudum Game Reserve, (3) Ngamiland 11, (4) Moremi Wildlife Reserve, (5) Chobe National Park, (6) Addo Elephant National Park, (7) Kruger National Park, (8) Lower Zambezi National Park, (9) South Luangwa National Park and (10) Amboseli National Park.

Inter-population variability could result from differences in ecological conditions that affect growth rates throughout life. However, problems with data or analyses may be responsible for at least some of these differences. Several studies based curves on ages determined from the molar eruption criteria developed by Laws (1966). Only three studies used measurements from known-age elephants and two of these were based on repeated measures of a few captive elephants, most of which were less than 30 years of age. The three studies (Laws, 1966; Laws & Parker, 1968; Laws *et al.*, 1975) that used data collected at Murchison Falls in Uganda reported different parameters for growth curves. Because one intention was to explore early rather than later growth rates in males, the differences in parameters are not surprising (e.g. Laws *et al.*, 1975), but do reflect the sensitivity of growth curves to analytical technique. Using different growth curves and two age determination techniques, Lindeque & van Jaarsveld (1993) generated little variation in the asymptotic shoulder heights of adults but large variation in shoulder heights at birth.

In many studies, shoulder heights were primarily measured on culled elephants lying on their sides. However, four growth functions were generated using shoulder heights of standing individuals. Differences in growth functions may arise depending on whether the elephant is standing or lying. These differences may be the result of (1) measuring along the curve of the body, (2) failing to push the leg into a straight position or (3) the leg being slightly longer because of no weight on it. In Kruger National Park, asymptotes generated using data obtained from lying individuals (I. J. Whyte, unpubl. data) were larger than those for standing individuals (♂: lying – 323 cm, standing – 275 cm; ♀: lying – 250 cm, standing – 246 cm).

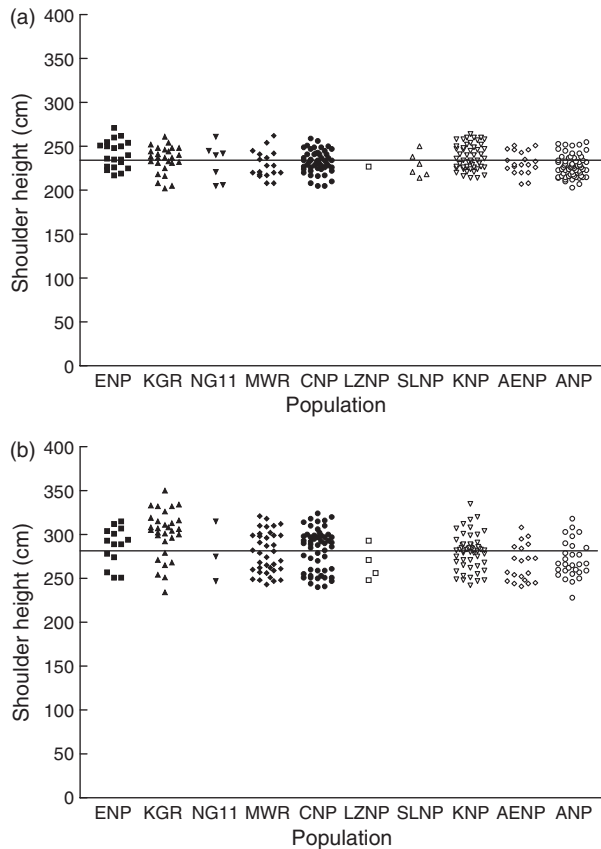


Figure 2 Shoulder heights for (a) adult females ($n=264$ individuals) and (b) adult males ($n=245$ individuals) in 10 savanna elephant populations. Adult females were accompanied by at least two calves whereas adult males were not associating with a breeding herd. Line indicates mean shoulder height. ENP, Etosha National Park; KGR, Khaudum Game Reserve; NG11, Ngamiland 11; MWR, Moremi Wildlife Reserve; CNP, Chobe National Park; LZNP, Lower Zambezi National Park; SLNP, South Luangwa National Park; KNP, Kruger National Park; AENP, Addo Elephant National Park; ANP, Amboseli National Park.

Adult shoulder heights did not differ among the 10 populations sampled during the present study (Kruskal–Wallis $H_9 = 8.00$, $P = 0.43$ and $H_8 = 13.87$, $P = 0.09$ for females and males, respectively; Fig. 2). The variance across populations in adult male shoulder height (F_{\max} test: $F_{9,3} = 3.00$, $P = 0.19$) was similar, but differed for females (F_{\max} test: $F_{9,63} = 3.02$, $P < 0.01$). Age-specific shoulder heights for females and males separately did not differ significantly between Addo Elephant National Park in South Africa and Amboseli National Park in Kenya (females: paired $t_{24} = 1.50$, $P = 0.15$; males: paired $t_{14} = 0.78$, $P = 0.45$; Fig. 3).

The combined data sets from Amboseli National Park and Addo Elephant National Park predicted that asymptotic female shoulder height ranged from 227 to 234 cm, whereas that for males ranged between 291 and 342 cm (Table 2).

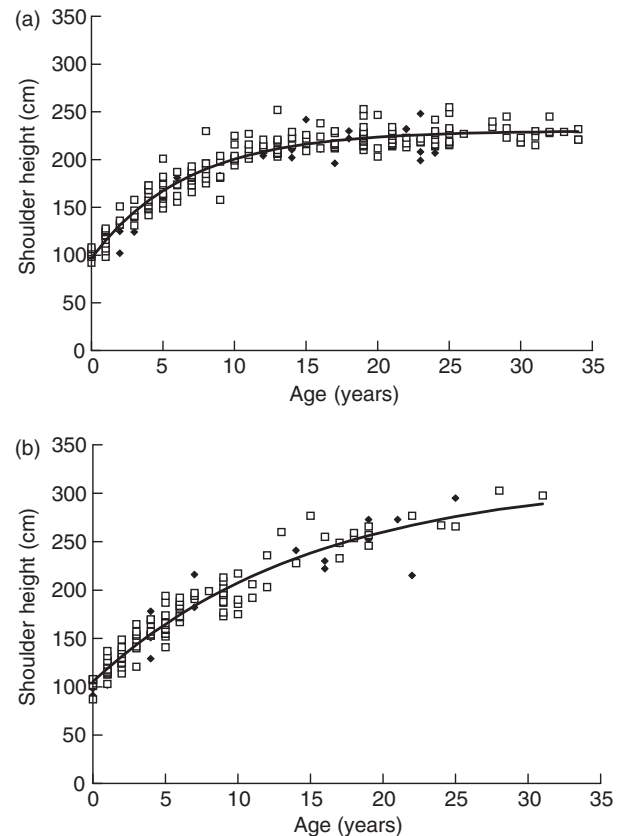


Figure 3 Shoulder height as a function of known age for female (a) and male (b) elephants from the Amboseli National Park in Kenya (□) ($n=192$ ♀♀ & 106 ♂♂) and the Addo Elephant National Park in South Africa (◆) ($n=30$ ♀♀ & 27 ♂♂). Sex-specific Von Bertalanffy (1938) curvilinear growth functions [$h_t = h_b + (H_\infty - h_b)(1 - e^{-kt})$, where h_t is shoulder height, h_b is shoulder height at birth, H_∞ is shoulder height at which adults stop growing, k is a constant determining the rate of growth and t is the age of an individual] were fitted to the combined data.

Age determination

The standard deviations of the ages estimated for elephants from their shoulder heights increased with increasing shoulder height (Fig. 4a and c). Standard deviations increased markedly and had values larger than 5 at shoulder heights >215 cm for females (F_{\max} test for equality of variances, $F_{2,99} = 16.83$, $P < 0.01$; Fig. 4b). For males, standard deviations changed at a more gradual rate (Fig. 4d) and exceeded a value of 5 at shoulder heights >290 cm. This suggests that shoulder height reflects age accurately for females up to 15 years (215 cm) and for males up to 36 years (290 cm) (Table 3).

Discussion

Our study supports earlier suggestions (e.g. Douglas-Hamilton, 1972; Laws *et al.*, 1975; Malpas, 1977; Western *et al.*, 1983) that the growth patterns of savanna elephants are

Table 2 Estimates of parameters derived for male and female growth curves [$h_t = h_b + (H_\infty - h_b)(1 - e^{-kt})$] using shoulder heights of known-age elephants in Amboseli National Park (≤ 34 years old) and Addo Elephant National Park (≤ 27 years old)

	Males ($n=133$)			Females ($n=222$)		
	Estimate	SE	95% CI	Estimate	SE	95% CI
h_b	105.4	2.8	99.87–110.9	96.9	2.9	91.3–102.5
H_∞	316.6	12.94	291.3–342.0	230.2	1.8	226.8–233.6
k	0.066	0.008	0.052–0.081	0.150	0.008	0.135–0.166
R^2		0.93			0.91	

h_t is measured shoulder height, h_b is shoulder height at birth, H_∞ is asymptotic shoulder height, k is growth rate, t is age in years, SE is standard error, CI is confidence interval and R^2 is coefficient of determination.

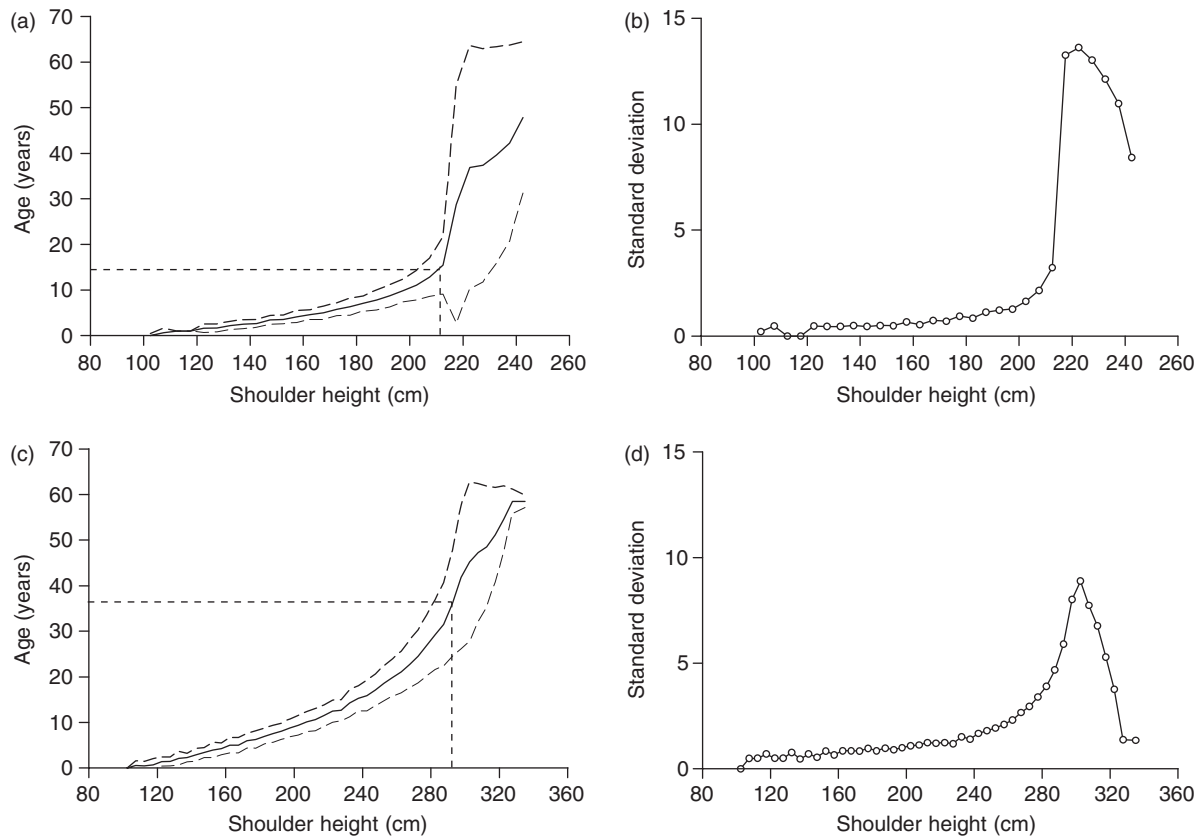


Figure 4 Ages calculated for shoulder heights of (a) female and (c) male elephants using Monte Carlo simulations of shoulder heights ($n=100$ for each 1 cm shoulder height class). Standard deviations (dashed lines) increased as estimated average age (solid line) increased. Deviations in ages estimated increased dramatically at 215 cm for females (b) and had values larger than 5. For males, deviations were larger than 5 at shoulder heights greater than 290 cm for males (d), suggesting accurate aging of an elephant up to 15 years for females and 36 years for males (dotted lines).

similar across large areas of Africa. The distributions of adult shoulder heights for elephants in 10 distinct and widely dispersed populations were similar. Age-specific shoulder heights were comparable for elephants in Addo Elephant National Park (South Africa) and Amboseli National Park (Kenya). These two populations are at least 6000 km apart and have been geographically isolated for at least a hundred years. We are therefore able to produce generalized growth curves as a means to determine age in free-ranging savanna elephants ♂: $h_t = 105.4 + (316.6 - 105.4)(1 - e^{-0.066t})$;

♀: $h_t = 96.9 + (230.2 - 96.9)(1 - e^{-0.150t})$. This is a necessary first step in the analyses of age-specific population variables.

It is important to note, however, that the accuracy of our ages and inter-population comparisons in stature are limited to relatively early in the elephant's life span, particularly that of females (15 years for females, 36 years for males). Other studies have found or at least suggested significant inter-population variation in asymptotic heights (Hanks, 1972a; Sherry, 1978; Jachmann, 1986; Morgan & Lee, 2003; see table 2 in Lee & Moss, 1995). Although some of

Table 3 Predicted ages and confidence limits (LCL, lower confidence limit; UCL, upper confidence limit) for elephants of known shoulder height estimated from our growth functions (see Table 2)

Shoulder height (cm)	Females			Males		
	Age (years)	95% LCL (years)	95% UCL (years)	Age (years)	95% LCL (years)	95% UCL (years)
≤ 105	0	0	1	0	0	1
> 105–110	1	0	1	0	0	1
> 110–115	1	1	1	1	0	1
> 115–120	1	1	2	1	0	2
> 120–125	2	1	2	1	1	2
> 125–130	2	1	2	2	1	2
> 130–135	2	2	3	2	1	3
> 135–140	3	2	3	2	2	3
> 140–145	3	2	3	3	2	4
> 145–150	3	3	4	3	2	4
> 150–155	4	3	4	4	3	5
> 155–160	4	3	5	4	3	5
> 160–165	5	3	6	5	4	6
> 165–170	5	4	6	5	4	6
> 170–175	6	5	7	6	5	7
> 175–180	6	5	8	6	5	8
> 180–185	7	6	9	7	6	8
> 185–190	8	6	10	8	6	9
> 190–195	9	7	11	8	7	10
> 195–200	10	8	12	9	7	10
> 200–205	11	8	14	9	8	11
> 205–210	13	9	17	10	8	12
> 210–215	15	10	23	11	9	13
> 215–220	28	11	60	11	10	14
> 220–225	Adult			12	10	15
> 225–230				13	11	15
> 230–235				14	12	17
> 235–240				15	13	18
> 240–245				16	13	19
> 245–250				17	14	20
> 250–255				19	15	22
> 255–260				20	16	24
> 260–265				21	17	25
> 265–270				23	18	27
> 270–275				25	19	30
> 275–280				27	21	33
> 280–285				29	22	37
> 285–290				31	24	41
> 290–295				36	26	48
> 295–300				42	27	60
> 300				Adult		

Upper and lower values for confidence intervals were calculated from simulated data (see text).

the differences between populations could be due to the use of deduced rather than real ages (Fatti *et al.*, 1980), others may reflect constraints on the length of the growth period, resulting in a smaller adult in later life. Both genetic (e.g. Morgan & Lee, 2003 for forest elephants *L. a. cyclotis*) and nutritional factors (e.g. Hanks, 1972a; Sherry, 1978; Jachmann, 1986) may cause differences in asymptotic size or in rates of growth. Although there are consistent genetic similarities among all savanna elephants by comparison with forest elephants (Roca *et al.*, 2001), there is also major population variation in some haplotypes (Uganda, Botswana:

Nyakaana & Arctander, 1999; Addo: Eggert, Rasner & Woodruff, 2002). Thus, it is likely that both ecological and nutritional factors as well as population differences could produce the observed variation in stature.

Maximum shoulder height of adult mammals can be influenced by severe nutritional limitations during the early growing stages (Berg & Butterfield, 1978; Batt, 1979). For elephant populations to experience consistent, ubiquitous and significant reduction in terminal stature, growth faltering must be evident across generations or be the result of a regular annual cycle of energetic and nutritional limitations.

Thus, we expect, as found here, that most savanna elephant populations will be relatively similar in height for age, at least until well into adulthood. However, elephants in some populations that either are limited in their access to nutrients essential for bone growth such as calcium or phosphorus (e.g. Kilimanjaro: Grimshaw & Foley, 1990) or experience annual cycles of energy limitations (e.g. Mikimi, Tanzania; P. C. Lee, pers. obs.) may be smaller than the general 'elephant' mean.

Our models predict the ages of female elephants with high precision up to a shoulder height of 215 cm (i.e. 15 years) and males up to 290 cm (i.e. 36 years). However, is this precision good enough to estimate demographic variables? Age-specific population parameters that induce between-population differences in population growth rates are evident within the age range for which we can reliably determine the age of individuals. Female elephants reach sexual maturity, or age at first conception, and age at first calving when ≤ 14 years old (Laws, 1966; Laws *et al.*, 1975; Moss, 1983, 2001; Jachmann, 1986; Whyte, 2001). Males, however, reach sexual maturity around the age of 25 (Hanks, 1972*b*; Laws *et al.*, 1975) and disperse from their family between 10 and 16 years of age (Lee & Moss, 1999). Calves of both sexes maintain close proximity to their mothers until they are 6–8 years of age (Lee, 1986), making estimates of inter-calf intervals possible. Age-specific survival can therefore be estimated for females up to 15 years of age and for males up to 36 years of age. As the survival rates of individuals > 12 years are consistent and relatively high (Woodd, 1999; Moss, 2001), it is possible to extrapolate survival rates for both males and females older than 36 and 15 years of age, respectively, to older ages. As a result, we suggest that it is possible to estimate age-specific demographic variables using our models of growth to derive age.

Our models produce a similar growth rate but a lower asymptote value than earlier studies (see Table 1). Ages generated from other growth curves are therefore likely to underestimate real age, lowering the ages of first reproduction and under-estimating age-specific survival rates. The generation of a single and accurate growth curve for savanna elephants implies that the statural growth and age determination techniques described here facilitate estimates of age-specific demographic parameters.

Acknowledgements

The study was conducted under the auspices of the Conservation Ecology Research Unit at the University of Pretoria, South Africa. We used grants made to Rudi van Aarde by the International Fund for Animal Welfare, the Peace Parks Foundation, the United States Fish & Wildlife Services and the National Research Foundation to fund the study. We would like to thank the personnel of the Amboseli Elephant Research Project, Conservation Foundation Zambia, Conservation Lower Zambezi and the Etosha Ecological Institute for their assistance. A special thanks to the Botswana Department of Wildlife and National Parks, Kenyan Wildlife Service, Namibia Ministry of Environment

and Tourism, South African National Parks and the Zambian Wildlife Authority for allowing us to conduct this research within their parks and reserves. Adrian Lister and an anonymous reviewer provided valuable comments.

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