J. Zool., Lond. (2005) **266**, 89–94 Printed in the United Kingdom doi:10.1017/S0952836905006631

Measures of dung bolus size for known-age African elephants (*Loxodonta africana*): implications for age estimation

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(Accepted 5 October 2004)

Abstract

The availability of a population of mostly known-age African elephants *Loxodonta africana* from Amboseli National Park, Kenya, provided a unique opportunity to assess the use of dung bolus diameter for estimating age. A predictive equation for estimating dung bolus diameters from elephants of known age was derived and was found to follow the typical growth pattern exhibited by changes in shoulder height and foot length. The relationship between measurements of dung bolus and age was particularly strong when growth rates were high (age 0–25 years). The dung bolus growth curve from Amboseli elephants was similar to that derived from another wild population of African elephants, suggesting that dung bolus diameter can be used to assess age structure in areas where it is impossible to construct independent prediction curves of age and dung bolus.

Key words: *Loxodonta africana*, age estimation, Amboseli, dung bolus, growth curve

INTRODUCTION

Techniques for age estimation are critical for the accurate study of many aspects of population biology in any organism. Demographic studies require measures of age-specific fertility and mortality (Moss, 2001). Behavioural studies are enhanced if behaviour can be understood in the context of growth and development (e.g. Poole & Moss, 1981; Lee, 1986; McComb *et al*., 2001). For threatened or endangered populations, knowing the age structure of the population is critical for estimating the impact of poaching, hunting, culling or changes in habitat (Sukumar, 1989).

Assigning age estimates can be difficult, particularly if the study organism is large and long-lived. Birth registration and individual recognition, the only method for assigning exact age, may require decades before a reasonable fraction of the population is known. Because of the importance of age estimates for population studies, other methods are required for large, long-lived species. Elephants represent a key example of such a species. Elephant populations have undergone dramatic fluctuations in recent decades as a result of poaching pressure and habitat change (Brooks & Buss, 1962; Barnes & Kapela, 1991; Anderson & Eltringham, 1997). Several methods have been used to estimate age to describe population age structure and dynamics accurately.

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Elephant age has been estimated using measurements of shoulder height (Hanks, 1972; Sukumar, Joshi & Krishnamurthy, 1988; Lindeque & Jaarsveld, 1993; Lee & Moss, 1995), back length (Croze, 1972), molar tooth wear and progression (Laws, 1966; Jachmann, 1988; Lindeque, 1991), hind footprint length (Western, Moss & Georgiadis, 1983; Lindeque & Jaarsveld, 1993; Lee & Moss, 1995) and dung bolus circumference or diameter (Jachmann & Bell, 1984; Reilly, 2002; Morgan & Lee, 2003). Each of these techniques has drawbacks. Most are only practical in open habitats where visibility is good and animals can be photographed (e.g. back length or shoulder height). Ageing using photogrammetric techniques requires expensive equipment and is prone to measurement error, decreasing the precision with which individuals can be aged. Measuring footprint length requires special ground conditions that preserve footprints well. Measuring molar wear and progression will require that animals be killed or immobilized. These drawbacks make these techniques difficult or inappropriate for routine monitoring of elephant populations in Africa and Asia. Age estimation using dung bolus diameter is simple to use and yields relatively reliable results. Furthermore, it is advantageous in areas where visibility is low (forest and woodland) and elephants cannot be closely approached, or in situations where it is not possible to obtain age by other means (e.g. when elephants crop raid at night).

While a number of investigators have censused elephant populations using estimates of dung pile density, dung degradation rate and defecation rate (e.g. Jachmann &

Bell, 1984; Merz, 1986; Fay & Agnagna, 1991; Tchamba, 1992), to our knowledge only two published studies have used dung bolus diameters to estimate the age structure of an elephant population: one in Malawi using African savanna woodland elephant dung (Jachmann & Bell, 1984) and one in a Sumatran population of Asian elephants (Reilly, 2002). These studies demonstrate the promise of using measurements of bolus size to estimate age, but they use data from either captive (Jachmann & Bell, 1984) or semi-captive animals (Reilly, 2002) or from individuals whose ages are based upon estimates from photogrammetric techniques (Jachmann, 1980, 1986). Moreover, the paucity of knowledge of inter-population and inter-species (for Sumatran elephants) variability in growth rates and the reliability of using predictive equations derived from one population on another, currently limits the application of these findings to other populations where ages are unknown.

This study assesses the utility and limitations of using measurements of dung bolus to estimate age in African elephants. A predictive equation for measurements of elephant bolus diameter is derived from wild elephants *Loxodonta africana* of known ages in Amboseli National Park, Kenya. It was found that age does predict dung bolus diameter, indicating that this measure can in turn be used to estimate age where needed. Our data are also compared to growth data from other populations.

METHODS

Study population

This study was carried out in the Amboseli National Park, Kenya, which covers an area of $392\,km^2$, and is part of the larger Amboseli basin ecosystem, which extends for *c.* $3500\,km^2$. The Amboseli elephants represent one of the best-studied wild populations in Africa. The Amboseli basin supported a population of 1087 individually recognized elephants in 1999 (Moss, 2001). Since the inception of the Amboseli Elephant Research Project (AERP) in 1972, dates of birth (month and year) have been recorded for most individually recognized elephants; hence all animals up to age 30 years in the dataset reported here have ages known within 2 weeks, with only a few exceptions (Moss, 2001). For elephants born before this date, dates of birth are estimated using at least 2 ageing methods, including footprint length, back length, shoulder height, or visual estimates based on head morphology, as well as on general patterns of growth in these individuals over the past 3 decades (Moss, 2001). Individuals born between 1968 and 1972 (31–35 years old in the dataset reported here) have age estimates that are likely to be within $\pm$ 1 year, while individuals born before 1968 ($>$ 35 years in the data reported here) have age estimates likely to be within $\pm$ 2.5–5 years (Moss, 2001).

Note that 81% of our dung samples came from individuals aged 0–35 years for whom age was known to within 1 year. Owing to the slow growth rates of older individuals, the magnitude of uncertainty in age for individuals born before 1972 (before birth registration) is relatively small and does not alter our recommendations concerning the use of dung boli for age estimation (see Discussion).

Field methods

Measurements of dung bolus diameter were collected opportunistically from elephants of known and estimated age and known sex from July 2002 to July 2003 during a study of the behaviour of elephant family groups. Only intact boli (typically only 1 per pile) from fresh dung piles were used. Boli were considered 'intact' if no apparent deformations existed owing to impact with the ground. The shape of a dung bolus approximates that of a cylinder with slightly elliptical ends. The long and short axes of the elliptical ends were measured, and then the mean of these 2 measures taken as the diameter for a bolus. This method is simpler than measuring circumference (Jachmann & Bell, 1984) and potentially more accurate than using only maximum diameter (Reilly, 2002).

Data analysis

Measurements of the dung-bolus diameter and the age data were fitted to a von Bertalanffy growth model (VBGM) using a least-squares non-linear regression method (Norusis, 2000). Changes in dung bolus diameter with age, a proxy for growth in anal size, follows a typical growth pattern in elephants (Jachmann & Bell, 1984; Reilly, 2002; Morgan & Lee, 2003). Separate models were fitted to data from male and female elephants because the 2 sexes exhibit different growth patterns (Laws, Parker & Johnstone, 1975).

For individual elephants, there are 2 main potential sources of variability in bolus size: variability within defecations and variability across defecations. Because the magnitude of this variability could potentially influence the precision of age estimates, multiple measurements of boli were taken within the same dung pile, and boli from two independent defecations of the same individual were also measured whenever possible. For within-defecation variance, the mean difference between 2 boli from a single defecation was calculated. Between-defecation differences in dung boli from the same individual were tested for using a Wilcoxon signed-rank test for matched pairs.

The VBGM is useful for fitting vertebrate growth data (Xiao, 2000; Megalofonou, Yannopoulos & Dean, 2003; Oshitani, Nakano & Tanaka, 2003) and has been used extensively in modelling elephant growth (Hanks, 1972; Laws *et al.*, 1975; Sukumar, Joshi & Krishnamurthy, 1988; Lindeque & Van Jaarsveld, 1993; Lee & Moss, 1995; Reilly, 2002). The VBGM is expressed using the equation:

$$L_t = L_\infty\{1 - \exp[-\mathrm{K}(t - t_0)]\}$$

where L_t is bolus diameter at age t, L_∞ is the asymptotic bolus diameter, K is the coefficient of catabolism (growth decay constant) and t_0 is the theoretical age at which dung

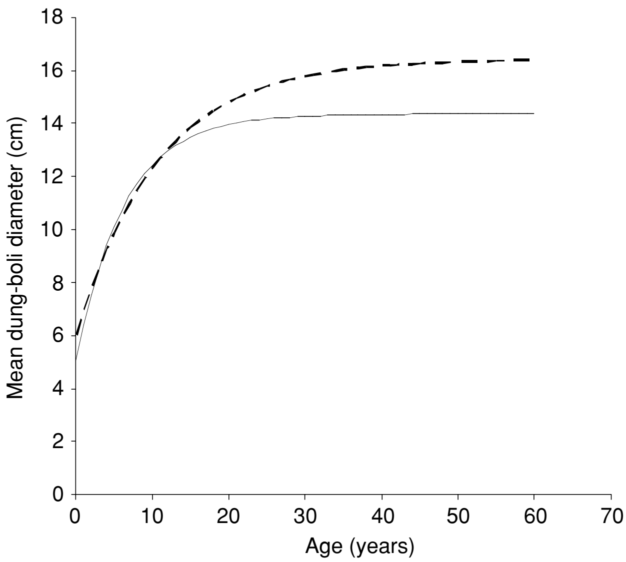

Fig. 1. A comparison of predicted growth curves based on dung boli diameter for male (dotted line) and female (solid thin line) elephants *Loxodonta africana* from Amboseli National Park (growth curves derived from 28 males and 51 females).

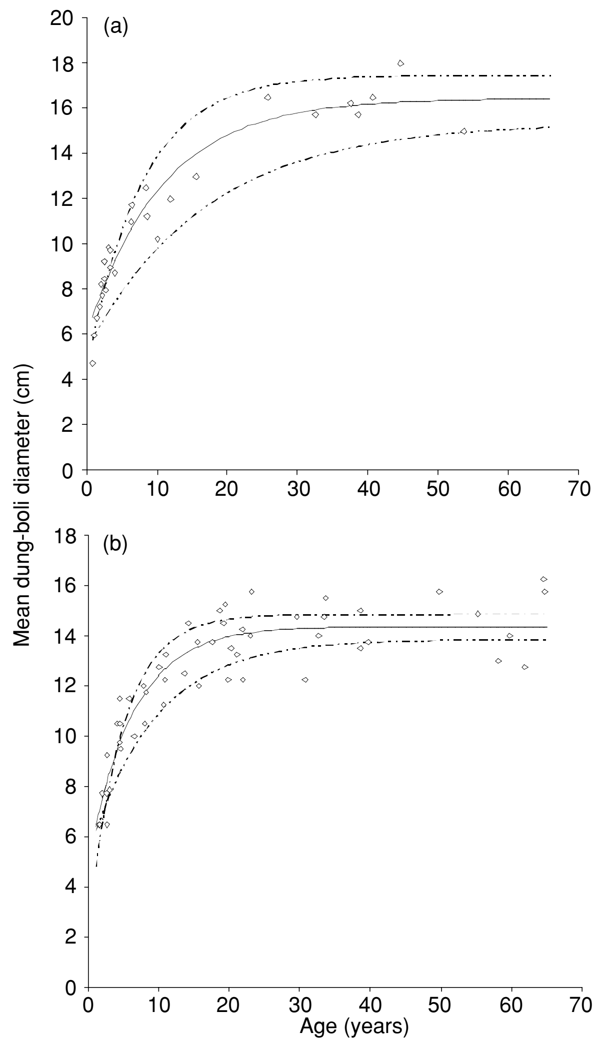

Fig. 2. Predicted growth curves (solid lines) with 95% confidence intervals (broken lines) based on mean dung bolus diameter of *Loxodonta africana* with actual observations (open squares): (a) males; (b) females.

bolus diameter is 0 (Hanks, 1972). To derive a growth model that fits our data, SPSS version 10.0.1 (SPSS, 1999) was used to estimate parameter values (L_∞, K and t_0) using an iterative non-linear regression approach. The Levenberg–Marquardt algorithm was used to modify parameter values (L_∞, K and t_0) during each iteration to achieve the minimum sum-of-squares for the model. The significance-of-fit of these equations to the data was verified using the corrected R^2 with a runs test on the residuals for each equation (Motulsky & Christopoulos, 2003). The difference between the male and female growth parameters determined from the VBGM was tested using the likelihood ratio test (Kimura, 1980; Cerrato, 1990).

Finally, the boli circumferences (c) reported for an elephant population in Kasungu National Park, Malawi (Jachmann & Bell, 1984) was converted into estimates of mean diameter (d) with the equation: $d = c/\pi$. The predicted growth curves for dung-boli diameter from the Kasungu and Amboseli populations were compared using a 2-sample Kolmogorov–Smirnov test to examine whether predicted equations derived for 1 elephant population can be used to predict another.

RESULTS

The relationship between mean dung bolus diameter and age follows a typical growth pattern for African elephants. From ages 0 to 12 years, dung bolus diameters from male and female elephants are indistinguishable, and increase rapidly between diameters of 5–6 cm to $\sim$11 cm (Fig. 1). Dung bolus size for male elephants continues to increase until age 25 years, at which point the rate of increase markedly declines; males apparently approach the asymptotic anal size between ages 46–56 (Fig. 2a). In contrast to males, growth rate as estimated by dung bolus size slows for females at age 20 years and approaches asymptotic dung bolus diameter between ages 30 and 35 (Fig. 2b). The derived growth parameters of the VBGM (Table 1) for male and female elephants fit the data for age and mean dung-bolus diameter (males $R^2 = 0.929$, $n = 28$; females $R^2 = 0.844$, $n = 51$). The distributions of data around the curves were random, indicating good fit of VBGM to our data ($Z = 0.000$, $P = 1.000$; $Z = 0.427$, $P = 0.669$, Wald–Wolfowitz runs test; Fig. 2a, b). Although other researchers have shown that males and females have different growth curves (e.g. Lee & Moss, 1995), a statistical difference between growth parameters of the two sexes was not detected in this study ($\chi^2 = 6.392$, d.f. $= 3$, $P = 0.094$; likelihood ratio test). This is probably because of a high variance around the line-of-fit for male

Table 1. Growth parameters of the von Bertalanffy growth model based on diameter of dung boli produced by elephants *Loxodonta africana* of known and estimated age and sex from Amboseli National Park, Kenya. L_∞ is the asymptotic dung bolus diameter, K is a growth constant and t_0 is the theoretical age when dung bolus diameter equals zero

	Males ($n = 28$)				Females ($n = 51$)			
Parameter	Estimate	Asymptotic SE	95% LCI	95% UCI	Estimate	Asymptotic SE	95% LCI	95% UCI
L_∞	16.433	0.509	15.383	17.482	14.354	0.249	13.854	14.854
K	0.093	0.017	0.058	0.123	0.158	0.025	0.107	0.209
t_0	− 4.909	1.229	− 7.441	− 2.378	− 2.722	0.925	− 4.582	− 0.862

elephants resulting from small sample size and similarity between sexes during the first 12 years.

Homoscedasticity was confirmed for both male and female lines-of-fit by testing age against the square of the residuals of dung boli diameter (for males $R^2 = 0.037$, $P = 0.168$; females $R^2 = 0.001$, $P = 0.861$) and the mean variance within an age class was determined to be 1.077 cm and 1.019 cm for females and males, respectively. Within single defecations from the same individual, the mean difference in any two dung bolus diameters was small (mean ± SD = 0.333 ± 0.129 cm, range 0.25–0.5 cm, $n = 6$ piles from which two boli were measured). Dung boli produced by the same individuals within 6 months of each other did not have significantly different diameters ($Z = -1.187$, $n = 7$ piles, $P = 0.235$; Wilcoxon signed-rank test for matched pairs; mean difference ± SD = 1.375 ± 0.955 cm, range 0.25–2.5 cm).

The distribution of the predicted values of dung bolus diameter for known-age male and female Amboseli elephants does not differ from predicted values based on age estimates of the Kasungu elephants (males, $Z = 0.424$, $P = 0.994$; females, $Z = 0.707$, $P = 0.699$; Fig. 3a, b).

DISCUSSION

Changes in dung bolus diameter with age in Amboseli elephants follows the typical pattern observed for changes in shoulder height and hindfoot length with elephant age. During the first 12 years of life, bolus growth is similar between the sexes. The growth rates for males and females begin to differ thereafter, with female growth slowing dramatically by 20 and reaching an asymptotic value at 35 years of age. Growth in males slows by the age of 25 and continues to decline until it reaches an asymptote at age 55. This pattern of longer growth duration for male than for female elephants has been reported by researchers using all other available methods of age estimation (e.g. Lindeque & Van Jaarsveld, 1993; Lee & Moss, 1995).

Although the overall male and female curves do not differ significantly in our dataset, age prediction beyond 12 years of age (when males begin to increase in size faster than females) is complicated by these gender specific growth rates. If gender of the individual is known, age prediction can still be useful until age 20 (females) or 25 (males). These observations suggest that dung bolus diameter is most reliable for predicting elephant age when growth rates are high (i.e. when individuals are young). Because smaller changes in dung bolus diameter translate into potentially large age differences as growth approaches an asymptote, all older individuals (above 20 or 25) should be grouped into one age class. Despite differences in the

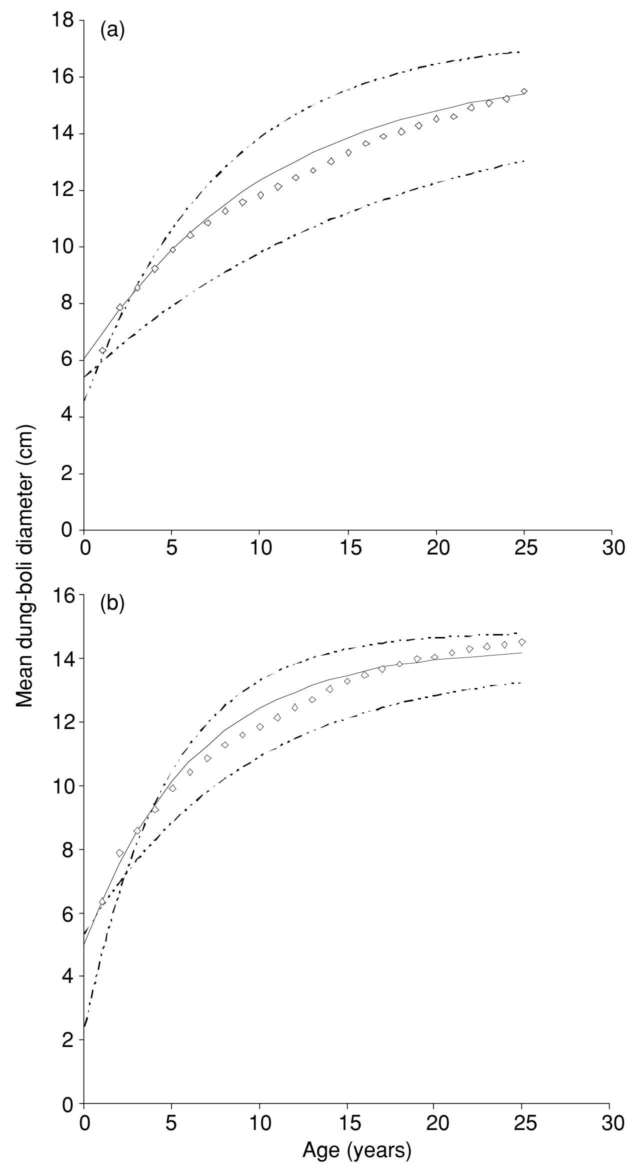

Fig. 3. A comparison of Amboseli's predicted growth curves (solid line) and 95% confidence interval (broken lines) with Kasungu's predicted growth curve (open squares) for *Loxodonta africana*: (a) males; (b) females. Kasungu data were obtained from Jachmann & Bell (1984) and converted into mean boli diameter.

shape of the male and female growth curves, it should be noted that if good estimates of the overall sex ratio can be obtained, researchers can still assess the sex-specific population age structures from dung bolus diameters (see Jachmann & Bell, 1984: 136).

Growth studies of shoulder height and foot length in Amboseli revealed that the ages at which individuals grow fastest, and approach asymptotic values, are similar to those observed in this study (see Lee & Moss, 1995). Lindeque & Van Jaarsveld (1993) found a similar growth schedule in Namibian elephants based on growth in shoulder height and hind footprint length.

Despite the similarities in results between ageing methods, each method has different strengths and is prone to different sources of error. All estimates of age will be affected by the underlying natural variation within each age class for all methods, though the extent to which the variation differs between measures is unknown. Comparing the accuracy of different methods is difficult because no elephant growth study has explicitly reported variance in age estimation. Reilly (2002) provided side-by-side growth curves of the different methods from the same population of Sumatran elephants that suggested different growth variables may have similar variation around the lines of best fit.

In Sumatran elephants, variability between boli from the same individual is low (SD was < 4.5% and 3.3% of mean bolus size for one male and one female, respectively) (Reilly, 2002). Reilly's results add strength to our result that variability within and between dung piles for the same individual is low, even though Asian and African elephants represent different genera. In comparison, the shoulder height method has numerous sources of measurement error (Lee & Moss, 1995), and footprint length may be affected by substrate (Western *et al*., 1983). When ageing an individual, repeated sampling helps minimize this measurement error, but in many situations this may not be an option. Although it is difficult to compare the cumulative effect of these sources of variation for any given method, each method probably provides a reasonable age estimate that should not be regarded as an exact age.

A comparison of the bolus-based growth curves of Amboseli and Kasungu elephants shows that the curves have a similar shape and strongly suggests that they may be used interchangeably (Fig. 3). Despite similarities in growth schedules between populations, researchers using the predictive equation from the Amboseli data should be cautious when applying it to forest elephants *L. cyclotis* who have markedly different morphologies, and presumably, growth rates. Morgan & Lee (2003) suggest a 35–40% height difference between forest and savanna elephants. The difference between maximum bolus diameters of the two populations, however, is only 11% (18 cm in Amboseli savanna elephants and 16 cm in Petit Loango forest elephants) and the difference between minimum diameters is 15% (4.75 cm in Amboseli and 4 cm in Petit Loango) (Morgan & Lee, 2003). More data on bolus size are required from forest areas to assess the extent to which populations vary in bolus size.

CONCLUSIONS

(1) Dung bolus diameter is suitable for estimating age for individual African savanna elephants. The smaller the dung diameter, the more accurately it can be used to predict age. The method is most accurate below the age of 20 and 25 years (for females and males, respectively), which in the Amboseli elephant population corresponds to a 13.96–15.42 cm bolus diameter.

(2) Combined with surveys on dung density, measurements of dung bolus diameter can be used to estimate the age structure of elephant populations, provided that as bolus diameter increases, broader age classes are used in assigning age. All individuals above the age of 20–25 years should be grouped in one age class.

(3) Growth equations for dung bolus diameter derived for one elephant population can, with caution, be applied to age other populations provided that the asymptotic and lower dung diameters are comparable.

Acknowledgements

We thank the Office of the President of Kenya for permission to work in Amboseli National Park, and the Kenya Wildlife Service for local sponsorship. The Amboseli Elephant Research Project provided invaluable scientific and logistical support, particularly from N. Njiraini and K. Sayialel, who contributed greatly to elephant identification and dung measurements in the field. This research was supported by the National Science Foundation (IBN0091612 S.C.A), the African Elephant Conservation Trust, and the Amboseli Elephant Research Project. We thank Hugo Jachmann for his helpful comments on the manuscript.

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