

A Rapid Method to Estimate Population Variables for African Elephants

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ABSTRACT We developed a noninvasive method to estimate reproductive and survival parameters for free-ranging African savannah elephants (*Loxodonta africana africana*) and used these to estimate finite population growth rates. We used published data from 2 populations with known growth rates and birth and survival histories to validate our technique. Based on body measurements, our method yielded estimates of age at first and last calving, calving interval, and age-specific survival rates that were similar to those determined during long-term studies at both Addo Elephant National Park and Amboseli National Park. Our technique generated population data required to estimate population growth rates. The method may be particularly useful where censuses yield imprecise estimates or where long-term population data are unavailable. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):822–829; 2008)

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Population growth rate reflects the collective response of groups of individuals to resource availability and interspecific interactions (Sibly et al. 2003) and is often calculated from a series of population estimates. Estimates of growth rates, however, are sensitive to the quality of such time series (Gerrodette 1987). For African elephants (*Loxodonta africana*), the calculation of growth rates from time-series data can be problematic because only 19% of the 384 population estimates in a recent status report came from total counts (Blanc et al. 2007). Nearly half (41%) of these estimates were guesses, whereas 34% were from formal counts. For elephants, most sample-based surveys yield estimates that vary in precision (Barnes 2002). Indeed, in the most recent African Elephant Status Report (Blanc et al. 2007), 75 of 89 aerial sample counts yielded confidence limits that ranged from 10% to 376% of the mean (median = 65.3%). Estimates with such low precision may lack power to detect trends (Gerrodette 1987), given that elephant populations usually grow at 4–5% per year (e.g., Blanc et al. 2005).

Population growth rates can also be derived from survival and fecundity estimates (e.g., matrix models; Calow et al. 1997, Sibly and Smith 1998, Caswell 2001). Identifying the relative contribution of age-specific fecundity and survival to growth may help identify the most important factors influencing population dynamics. Estimates of age-specific fecundity can be derived from age at first reproduction, from intervals between births, and from age of reproductive senescence, but these data are usually difficult to obtain (e.g., Hanks 1972, Smuts 1975, Dunham 1988, Whyte et al. 1998, Whyte 2001). Additionally, ages of individual elephants may also be difficult to estimate, further complicating calculation of fecundity and survival rates (Shrader et al. 2006a). Long-term observational studies of known individual elephants can overcome the inaccuracies

of age estimation, but such long-term studies require considerable effort and can be expensive (e.g., Whitehouse and Hall-Martin 2000, Moss 2001, Wittemyer et al. 2005a, Shrader et al. 2006a). Our objective was to explore an alternative approach to estimating population parameters for free-ranging elephants.

STUDY AREA

Amboseli National Park

Amboseli National Park (2°40'S, 37°16'E) was 390 km², located in southern Kenya, and comprised acacia (*Acacia* spp.) woodlands, open grasslands, patches of palm fields, permanent and semipermanent swamps, and a seasonally flooded lake bed (Moss and Poole 1983). Annual rainfall was 350 mm during 2 rainy seasons (Poole 1999). The park was not fenced and, as part of the Amboseli ecosystem, supported 1,100 elephants in 2002 (Blanc et al. 2003). Most elephants used open grasslands or swamps during the day (Poole 1999). Daytime temperatures averaged 25° C in the warmest months and ranged up to 33° C. The lowest minimum temperature in the coldest months was 11° C (Altman et al. 2002). Amboseli elephants have been studied intensively since 1970 (Moss 2001).

Addo Elephant National Park

Addo Elephant National Park is approximately 6,000 km southwest of Amboseli in southeastern South Africa (33°26'S, 25°45'E). Addo was 103 km² and fenced (Lombardt et al. 2001). The park supported 337 elephants in 2002 (Blanc et al. 2003). Valley bushveld or succulent thickets that comprised dense, spiny scrubland to low forest characterized the vegetation (Cowling 1984). The 400 mm of annual rain fell mostly in spring and autumn. Mean annual temperature was 18° C but sometimes rose to 45° C in midsummer. Winter temperatures seldom dropped below 0° C (Lombardt et al. 2001). Intense studies of the elephants in Addo started in 1976 (Whitehouse and Hall-Martin 2000).

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METHODS

Data

The social structure for elephants defined our sampling approach. Females live in herds containing several females and their immature offspring (Douglas-Hamilton 1972, Moss and Poole 1983, Moss 1988). Males disperse at maturity and remain mostly solitary, whereas females remain in their natal group (Moss and Poole 1983). In some instances, herds subdivide, but female-calf associations stay intact until the calf is 10 years old. At other times, social groups fuse to form bond groups (Moss and Poole 1983), which usually consist of related individuals (Archie et al. 2006). Although our sampling focused on female herds for which we did not know fission-fusion status, stability of female-calf associations ensured little bias in our sampling of female elephants (Wittemyer et al. 2005b).

To construct age structures, we sampled 13 herds encountered in Addo and 34 in Amboseli, which included 163 and 313 individuals, respectively, and, therefore, exceeded the Caughley (1977) recommendation that ≥ 150 individuals be used to construct age distributions. Our fieldwork took place during the dry season (Sep 2003 for Addo and Oct 2004 for Amboseli) when elephants associate with permanent water (Owen-Smith 1996). Our survey routes followed tourist roads, and we sampled each area and group only once.

To develop and verify our rapid elephant population assessment (REPA) technique, we used published data from 2 elephant populations that are geographically distinct and widely separated—Addo (Whitehouse and Hall-Martin 2000) and Amboseli (Moss 2001). These data, based on individual life histories, include survival rates, fecundity schedules, and intrinsic growth.

Analyses

Age distributions.—We assigned age (x_i) to each elephant by comparing shoulder height (b_i) to the sex-specific growth curves of Shrader et al. (2006a) resolved to 1-year age-classes for animals up to 15 years old. Because of variability in shoulder heights of adult elephants, we assigned animals apparently >15 years to one age class (Shrader et al. 2006a). To incorporate uncertainty in age estimates, we used error structures of the parameters for the Von Bertalanffy shoulder-height growth function for elephants to assign age to each individual 1,000 times (Shrader et al. 2006a). We used Monte Carlo simulations (Gentle 1943) to draw random values from the growth function's parameter distributions and regrouped individuals into 1-year age-classes after every repetition.

Our analyses focused on females. We smoothed and expanded age frequencies to include the large >15 -year-old age class by assuming elephants do not live >60 years (Wiese and Willis 2004). We defined

$$\sum_x^w n_x = n_0 a^x \left[\frac{(1 - a^{(w-x+1)})}{(1 - a)} \right] \quad (1)$$

as the sum of frequencies of females that were x years to w

years old. Here n_x = number of females x years old, and n_0 = frequency of breeding females times fecundity. Frequencies decay at a rate a , our smoothing parameter, as age increases ($a = s/\lambda$, where s = survival, λ = finite growth rate; Eberhardt 1988; Fig. 1a). We defined a series of $\sum_{i=x}^w n_i$ by increasing x at increments of 1 up to 15 and setting $w = 60$. We then estimated the decay rate (a) and its variance [$\text{var}(a)$] across all elephant ages using maximum likelihood and assuming a normal distribution (Edwards 1972; analytical algorithms from Hood 2005).

Reproductive variables.—We estimated age at first calving and calving intervals from ages of individuals in female-calf associations that included first year calves under adult females, calves close to maternal sides of adult females, and calves following adult females. We made no distinction between females and used the mean difference in ages of calves that associated with adult females as an estimate of birth intervals. Allomothering (Lee 1987), weaning, and calf mortalities could confound our estimate of calving interval. To account for some cases of allomothering, we excluded intervals <2 years because gestation is 22 months followed by several months of apparent lactational anoestrous (Hodges et al. 1994). To control for weaning, we used only those calves that were <10 years old because these calves usually associate with their mothers (Douglas-Hamilton 1972, Moss 1988). However, we could not account for calf mortalities. Birth interval, therefore, reflected both birth rates and calf survival.

We used the mean difference in the age of the oldest calves and that of their mothers to estimate age of first calving (x_{first}). For this part of the analysis, we used data from females up to 25 years old. Calf mortalities may bias calving interval, so to incorporate uncertainty in assigning ages to individual elephants, particularly those of females up to 25 years old (Shrader et al. 2006a), we used Monte Carlo simulations (Gentle 1943) and recalculated mean calving interval, age at first calving, and their standard errors after each of 1,000 repetitions. We then averaged the estimates and their standard errors for calving interval and age at first calving from these repetitions.

Estimating age of last calving (x_{last} ; i.e., when 50% of F in that age class stopped calving) was more complex (Fig. 1b). We reasoned that age at last calving would be reflected by the age of the oldest female with a calf minus the age of her calf. We first estimated frequency of females at age of first birth (x_{first}):

$$n_{\text{first}} = n_0 a^{x_{\text{first}}} \quad (2)$$

using the decay rate (a) previously estimated from the age distribution. If all females bred from ages x_{first} to x_{last} , then frequency of females that had calves (N_B) is

$$N_B = \sum_{x_{\text{first}}}^w n_x - \sum_{x_{\text{lastcalf}}+1}^w n_x \quad (3)$$

where $w = 60$, and x_{lastcalf} = latest age when females still had an associating calf. Substituting, using equation 1, allowed us to rewrite equation 3:

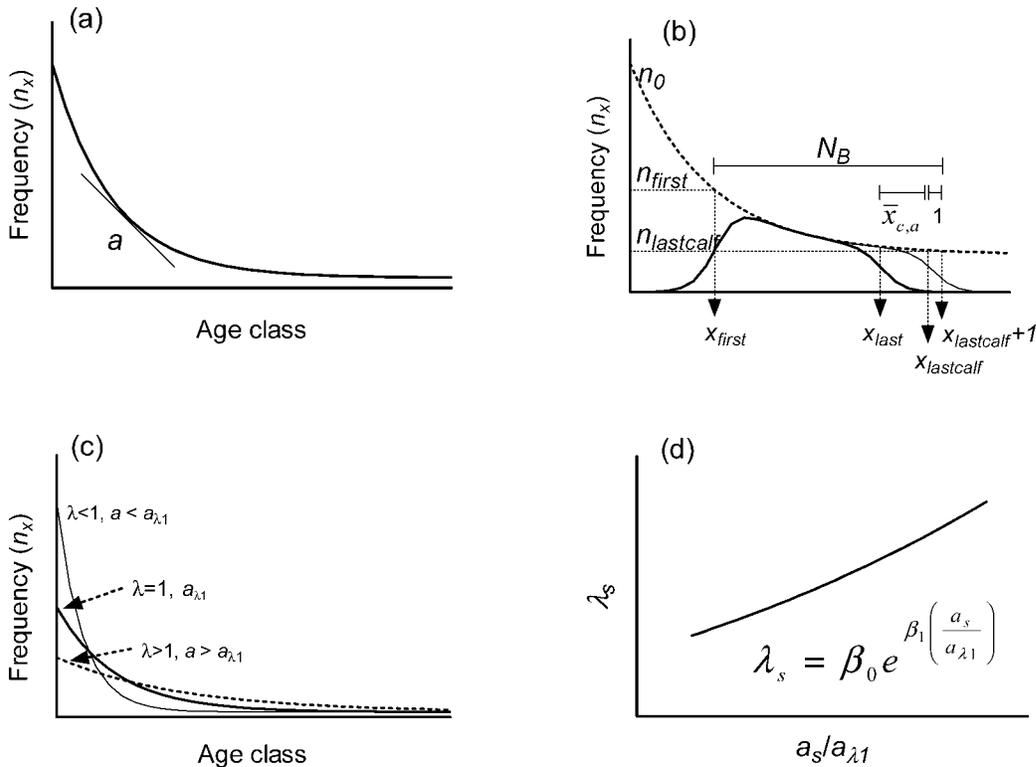


Figure 1. Line diagrams of our approach to estimate demographic parameters for elephants. (a) An age distribution has a characteristic parameter, a , that defines the rate of decay in frequencies (n_x) with age. (b) We used this decay rate that describes age distribution (broken line), the age at first calving (x_{first}), and the frequency of adult females with calves (N_B) to estimate the age when cows gave birth to their last calf (x_{last}). The frequency of breeding females will typically increase and later decrease (bold solid line). However, the age at which we observed the females without their last calves ($x_{lastcalf+1}$) will be older (solid line) than when they gave birth to those calves (x_{last}). The difference is the average age of the last calves still associating with a female ($\bar{x}_{c,a}$) to which we added 1 year. (c) The observed decay rate (a) is larger for increasing populations at a given fecundity than the decay rate when $\lambda = 1$ ($a_{\lambda 1}$) and vice versa. (d) Simulated λ_s should scale exponentially with $a_s/a_{\lambda 1}$ for a given fecundity schedule.

$$N_B = n_0 a^{x_{first}} \left(\frac{1 - a^{w-x_{first}+1}}{1-a} \right) - n_0 a^{x_{lastcalf}} \left(\frac{1 - a^{w-x_{lastcalf}+1}}{1-a} \right), \quad (4)$$

which simplifies to

$$N_B = n_{x_{first}} \left(\frac{1}{1-a} \right) - n_{x_{lastcalf}+1} \left(\frac{1}{1-a} \right), \quad (5)$$

because

$$\frac{1 - a^{w-x_{first}+1}}{1-a} = \frac{1}{1-a}, \quad (6)$$

when w becomes infinite. We rewrote equation 5 to find

$$n_{x_{lastcalf}+1} = n_{x_{first}} - N_B(1-a). \quad (7)$$

From the decay rate (a), we found $x_{lastcalf} + 1$, when the frequency of females was $n_{x_{lastcalf}+1}$ through

$$x_{lastcalf} + 1 = \frac{1}{\log a} \log \left(\frac{n_{x_{lastcalf}+1}}{n_{x_{first}}} \right) + x_{first}. \quad (8)$$

These females stopped breeding at an age when their last calves were born. We thus defined x_{last} as

$$x_{last} = \frac{1}{\log a} \log \left(\frac{n_{x_{lastcalf}+1}}{n_{x_{first}}} \right) + x_{first} - 1 - \bar{x}_{c,a} \quad (9)$$

where $\bar{x}_{c,a}$ was the average age of the calf recorded with females >230 cm at the shoulder (the asymptote of F growth reached at 43 yr of age) that had only one calf. We assumed that large females with one calf had stopped breeding. As with age at first calving, calf mortality may also influence the estimate of age at last calving. To estimate $\text{var}(x_{last})$, we used 1,000 Monte Carlo simulations (Gentle 1943) drawing values for a , x_{first} , and $\bar{x}_{c,a}$ from their respective distributions.

We corrected for sex ratios at birth assumed to be one and defined an approximated fecundity (m' , see influence of unaccounted calf mortality earlier) as half the inverse of the calving interval. Age-specific fecundity in elephants is relatively constant up to age 40, after which it declines slightly (Moss 2001). For simplicity, we gave all age classes $\geq x_{first}$ and $\leq x_{last}$ the same m' value irrespective of age.

Population growth.—We assumed that the recorded smoothed age distribution was stable (Udevitz and Ballachey 1998). Our observations did not allow an independent estimate of first year survivorship, l_0 , so that

$$\lambda = \sum_{x=1}^{w-1} \frac{n_x}{n_0} l_0 m' \quad (10)$$

adapted from Michod and Anderson (1980) could not estimate the finite population growth λ . To address this, we argued that a hypothetical population with stable numbers (i.e., $\lambda = 1$) and the same survivorship for elephants of all ages will have survival $s = a_b$, the decay rate of age frequencies (Eberhardt 1988). When all ages had the same survival (s), equation 10 reduced to

$$\lambda = \sum_{x=1}^{w-1} a_b^x s m' \quad (11)$$

because $a_b \approx n_{x+1}/n_x$. At $\lambda = 1$, $s = a_b$, and $m' = 0$ for ages $< x_{first}$ and $> x_{last}$, so that equation 11 reduced further to

$$1 = m' \sum_{x_{first}}^{x_{last}} a_b^{x+1}, \quad (12)$$

from which we solved a_b . We termed this the zero-growth decay rate ($a_{\lambda,1}$) for a hypothetical population with the same fecundity schedule as our observed population and that is numerically stable (i.e., $\lambda = 1$). Any other hypothetical population that has a decay $a_{b'} > a_{\lambda,1}$ for the same fecundity schedule should have a growth rate $\lambda > 1$, indicative of an increasing population. Conversely, when $a_{b'} < a_{\lambda,1}$, then we expected $\lambda < 1$ (Fig. 1c).

We argued that if we could find the relationship between deviation of $a_{b'}$ from $a_{\lambda,1}$ and λ for a hypothetical population with the same fecundity schedule as our observed population, then we could estimate λ for our observed population through deviation of the observed decay rate a from $a_{\lambda,1}$. Elephants have low mortality rates (Whitehouse and Hall-Martin 2000, Dudley et al. 2001, Moss 2001, Wittemeyer et al. 2005a), so we varied survival rate (s_b) between 0.6 and 0.995 to find a series of $a_{b'}$ values for hypothetical populations with our recorded fecundity (m'). We then input these values into a Leslie Matrix to estimate a simulated finite growth rate (λ_b) as the matrix's dominant Eigen value (Caswell 2001). We calculated the simulation's decay rate ($a_{b'}$) from

$$\lambda_b = s_b m' \sum_{x_{first}}^{x_{last}} a_{b'}^x \quad (13)$$

and repeated this with new s_b values to find 100 pairs of $a_{b'}/a_{\lambda,1}$ and λ_b for a given fecundity schedule.

Because decay rates were close to 1, we defined

$$\frac{a_{b'}}{a_{\lambda,1}} \approx \frac{1 + \ln(a_{b'})}{1 + \ln(a_{\lambda,1})} \quad (14)$$

and rearranged it to

$$\frac{a_{b'}}{a_{\lambda,1}} [1 + \ln(a_{\lambda,1})] - 1 = \ln(a_{b'}). \quad (15)$$

However, $a_{b'} = s_b/\lambda_b$, so equation 15 transformed to

$$1 + \ln(s_b) - \frac{a_{b'}}{a_{\lambda,1}} [1 + \ln(a_{\lambda,1})] = \ln(\lambda_b). \quad (16)$$

We rewrote this equation 16 to

$$\lambda_b = e^{1 + \ln(s_b)} \times e^{-[1 + \ln(a_{\lambda,1})] a_{b'} / a_{\lambda,1}}. \quad (17)$$

By setting $\beta_0 = e^{1 + \ln(s_b)}$ and $\beta_1 = -[1 + \ln(a_{\lambda,1})]$, the relationship between $a_{b'}/a_{\lambda,1}$ and λ_b took an exponential form (Fig. 1d) defined by

$$\lambda_b = \beta_0 e^{\beta_1 (a_{b'} / a_{\lambda,1})}, \quad (18)$$

for which we found $\ln(\beta_0)$ and β_1 through linear least-squares regression of $\ln(\lambda_b)$ against $\ln(a_{b'}/a_{\lambda,1})$. Because $0 > s_b \leq 1$, the coefficient of determination typically converged to 1 and suggested little residual error that could influence estimates of λ_b . From this relationship, the observed decay rate (a substituted $a_{b'}$) gave an estimate of λ for the fecundity schedule and age structure we recorded.

Equation 18 suggested that variance in the estimate of finite population growth rate [$\text{var}(\lambda)$] was the combined consequences of variance in the observed decay rate (a), previously calculated as $\text{var}(a)$ through maximum likelihood, and variance in zero growth decay rates [$\text{var}(a_{\lambda,1})$], which is equivalent to the variance of m' [$\text{var}(m')$; see eq 12]. To estimate $\text{var}(m')$, we calculated the lower ($LCL_{m'}$) and upper confidence limits ($UCL_{m'}$) of m' as

$$CL_{m'} = \frac{0.5}{\bar{i} \pm 1.96\sigma_i}, \quad (19)$$

where \bar{i} was the calving interval with its standard error σ_i defined earlier. From equation 19, we could estimate variance of m' as

$$\text{var}(m') = \left\{ \frac{1}{2} \left[\left(\frac{m' - LCL_{m'}}{1.96\sqrt{v}} \right) + \left(\frac{UCL_{m'} - m'}{1.96\sqrt{v}} \right) \right] \right\}^2, \quad (20)$$

where v was the number of observations we used to estimate \bar{i} . We estimated $\text{var}(\lambda)$ through Monte Carlo simulation (Gentle 1943) using 1,000 random values of a and m' drawn from their distributions defined by $\text{var}(a)$ and $\text{var}(m')$ as input values for equation 18.

Survival rates.—In large mammals, survival rates are normally lowest during the first few years of life (Gaillard et al. 1998, Gaillard et al. 2000). Elephants differ in that many die in their first year, less so the next 1–5 years, and more so after they are weaned (Lee and Moss 1986). Therefore, age frequencies may not always decay at a constant rate (a) with age. We thus used equation 1 to estimate a decay rate (a_z) and its variance [$\text{var}(a_z)$] separately for age classes 1–5 years, 6–10 years, 11–15 years, and >15 years old using maximum likelihood (Edwards 1972; Microsoft Excel macro from Hood 2005). In some small populations, near 100% survival was noted (Mackey et al. 2006). We assumed that a_z will not exceed $0.995/\lambda$ because some elephants will die even when environmental conditions are good. We estimated survival rate for an age class as $s_z = a_z \lambda$ (see Eberhardt 1988) with $\text{var}(s_z)$ via Monte Carlo simulations (Gentle 1943).

Validation.—We compared the Addo as well as the Amboseli known-age estimates of age at first calving and calving intervals to those we derived for Addo (Whitehouse

Table 1. Sequence of analytical steps required to estimate selected demographic variables for elephants from our study of free-ranging African elephants at Addo Elephant National Park, southeastern South Africa, in September 2003, and at Amboseli National Park, southern Kenya, in October 2004. We present the information needed and parameters generated by each step.

Step	Input	Output
Assign ages	b_i	x_i
Construct age distribution	x_i	n_x
Smooth age distribution	n_x	a
Estimate age at first calving	x_i of F and associating calves	x_{first}
Estimate calving intervals	x_i of associating calves	i
Estimate the age of a F's last calf	x_i of single calves with large F	$\bar{x}_{c,a}$
Count the F with calves	F and F-calf associations	N_B
Estimate no. of F at age of first calving	a	n_{first}
Estimate no. of F at latest age when they still had an associating calf	a, n_{first}, N_B	$n_{lastcalf}$
Estimate latest age when F still had an associating calf	$a, n_{first}, n_{lastcalf}, x_{first}$	$x_{lastcalf}$
Estimate age at last calving	$a, n_{first}, n_{lastcalf}, x_{first}, \bar{x}_{c,a}$	x_{last}
Estimate recruitment as a constant between age of first and last calving	x_{first}, x_{last}, i	m'
Estimate age decay when finite growth = 1 for obs recruitment	m'	$a_{\lambda,1}$
Simulate age decay with hypothetical survival rates for obs recruitment	m', s_b	a_b
Estimate finite growth from hypothetical survival rates and obs recruitment	m', s_b	λ_b
Find relationship between hypothetical λ and ratio of hypothetical decay to decay at zero growth	$a_{\lambda,1}, a_b, \lambda_b$	β_0, β_1
Estimate obs growth rate	$a, a_{\lambda,1}, \beta_0, \beta_1$	λ
Estimate age-specific decay rates	n_x within age group z	a_z
Estimate age-specific survival rates	a_z, λ	s_z

and Hall-Martin 2000) and Amboseli (Moss 2001), respectively, using Student's t -tests (Sokal and Rohlf 1995). When the confidence intervals for our estimates of age at last calving, age-specific survival rates, and population growth rate included previously published point estimates derived from long-term studies, we concluded that they were similar. Table 1 summarizes the sequence of analytical steps.

RESULTS

We measured 163 elephants in Addo, including 110 female-calf associations. Our sample comprised 313 elephants and their female-calf associations from Amboseli, where 1,190 elephants lived at the time. Addo's elephant population had 360 individuals at the time of our 7-day visit. We therefore sampled >20% of each population.

Our derived ages of first calving and those previously published for these 2 populations were similar (Table 2; Addo: $t_{66} = 1.08, P = 0.28$; Amboseli: $t_{100} = 1.95, P = 0.06$). Our estimates of calving intervals also did not differ from published values for both populations (Table 2; Addo: $t_{141} = 1.85, P = 0.07$; Amboseli: $t_{99} = 0.11, P = 0.91$). In both cases, confidence intervals of our estimates overlapped those reported by previous studies. In addition, our estimated confidence intervals for age at last calving encompassed point estimates of published values (Table 2).

Our estimates of survival were similar to those published for both parks from long-term studies (Table 2). At Amboseli, published survival rates for age 10–15 years were higher than our upper confidence limits for this age-class. Our estimated confidence limits for λ included finite growth rates published for both populations (Table 2). Our point estimate of λ for Addo (1.058) was 0.3% higher than the published value (1.055), and that for Amboseli (1.035) was 0.3% lower than estimated from known-histories (1.038).

DISCUSSION

Our REPA is a noninvasive, reliable alternative to costly and time-intensive monitoring programs to obtain demographic data for free-ranging elephant populations. For REPAs carried out in Addo and Amboseli, 10 survey days per population yielded estimates of demographic variables that were similar to those obtained during 3 decades of long-term elephant studies. Our method of extracting demographic information was fast and reasonably inexpensive, though analytically complex.

The first step of REPA involves deriving an age distribution for a population based on ages of individual elephants. Most published age distributions for elephants rely on one of several indices of age. Some studies used molar tooth eruption and wear criteria to assign age to individual elephants (e.g., Hanks 1972, Smuts 1975, Dunham 1988, Jachmann 1988). Others used measures of shoulder heights (e.g., Jachmann 1980, Jachmann 1988, McKnight 2000), footprint lengths (e.g., Western et al. 1983, McKnight 2000), diameters of dung boli (e.g., Jachmann & Bell 1984), and relative size measures (e.g., Leuthold 1976, Lewis 1984, Lindeque 1991, Damiba and Ables 1994) to assign ages. Some of these approaches may not estimate ages correctly because the age predicted by a specific measure was not tested against the actual age of an individual (Shrader et al. 2006a). We assigned individual ages by using a function that relates digital measures of shoulder heights of known-age elephants to age (Shrader et al. 2006a, b). Our technique can assign ages to individual elephants within 2 years of the actual age for females and males that are ≤ 15 years and ≤ 25 years old, respectively (Shrader et al. 2006a). In addition, we can simulate the likely age of an elephant given the confidence intervals for parameters of the growth functions that we used (see

Table 2. Validation of the rapid elephant population assessment (REPA) approach to estimating elephant population variables (\bar{x} and SE) using data collected in Addo Elephant National Park, southeastern South Africa, in 2003, and Amboseli National Park, southern Kenya, in 2004. s = annual survival rate. λ = finite growth rate.

Variable	REPA estimates			Whitehouse and Hall-Martin (2000)		
	Estimate	SE	95% CI	Estimate	SE	95% CI
Addo Elephant National Park						
s_{1-5yr}	0.995	0.016	0.958–0.995	0.995		
s_{5-10yr}	0.995	0.012	0.966–0.995	0.995		
$s_{10-15yr}$	0.995	0.013	0.965–0.995	0.995		
$s_{>15yr}$	0.995	0.011	0.968–0.995	0.990		
Age at first calving (yr)	13.8	0.83 ^a	12.12–15.37	13.0	0.25 ^d	12.51–13.49
Calving interval (yr)	4.0	0.33 ^b	3.32–4.62	3.8	0.10 ^e	3.60–4.00
Age at last calving (yr)	53.1	0.55 ^c	51.99–54.15	49.2	3.90 ^f	41.55–58.85
λ	1.058	0.011	1.036–1.080	1.055		
Amboseli National Park						
s_{1-5yr}	0.984	0.010	0.964–0.995	0.980		
s_{5-10yr}	0.995	0.008	0.974–0.995	0.994		
$s_{10-15yr}$	0.995	0.006	0.978–0.995	0.996		
$s_{>15yr}$	0.980	0.006	0.969–0.995	0.985		
Age at first calving (yr)	13.6	0.54 ^g	12.52–14.64	13.7		12.74–14.46
Calving interval (yr)	4.6	0.24 ^h	4.15–5.07	4.5		1.80–11.70
Age at last calving (yr)	53.5	0.68 ⁱ	52.07–56.97			52.00–56.00
λ	1.035	0.006	1.023–1.046	1.038		

^a $n = 18$.

^b $n = 20$.

^c $n = 7$.

^d $n = 66$.

^e $n = 164$.

^f $n = 5$.

^g $n = 43$.

^h $n = 54$.

ⁱ $n = 5$.

Shrader et al. 2006a). We thus limit the potential influence of age assignment on our estimates by making use of an age-related body measurement that we tested against real ages of individual elephants.

Our REPA provided age-specific estimates of reproductive variables commonly used to estimate fecundity. One such variable is age of sexual maturity, which we estimated, as others did before us, as the age when 50% of females bred (e.g., Laws 1969, Hanks 1972, Smuts 1975, Dunham 1988). Earlier studies relied on signs of ovulation or age-specific conception rates from killed elephants (Laws 1969, Hanks 1972, Smuts 1975, Dunham 1988), but first ovulation may not lead to conception and fetal mortality may occur before parturition, which may explain why age of sexual maturity derived from ovarian morphology may be lower than ages estimated using REPA. We acknowledge postweaning mortality may affect the difference between the age of a female and her oldest calf. In spite of this, ages at first calving that we derived for Addo and Amboseli were similar to those based on long-term longitudinal studies by Whitehouse and Hall-Martin (2000) and Moss (2001), respectively.

Earlier studies that counted placental scars or that used the ratio of pregnant to nonpregnant females in a sample of killed elephants to estimate calving intervals did not verify values (Perry 1953, Laws 1969, Hanks 1972, Smuts 1975, Dunham 1988). Jachmann (1980) concludes that calf

mortality and adoption may bias estimates of age at first calving and calving intervals when using an approach similar to ours. However, the similarity of REPA-derived estimates of age at first calving and calving intervals to those based on known life-histories suggests that REPA does indeed yield reliable estimates.

Age structures derived from individuals whose ages were assigned using dental criteria may increase estimates of survival of young elephants because large (relatively old) skulls decay slower than small (young) ones when exposed to field conditions (Laws 1969, Jachmann 1980, Conybeare and Haynes 1984, Wittemyer et al. 2005a). We overcame the problem of age-assignment from skull inaccuracies by estimating ages of all animals within a herd using relationships that relate shoulder heights to known-age elephants (Shrader et al. 2006a). Furthermore, our survival estimates compared well with those known for both Addo (Whitehouse and Hall-Martin 2000) and Amboseli (Moss 2001) elephants through longitudinal studies, once again suggesting that our approach yields reliable survival estimates. We recognize, however, that the shape or a_x values of a smoothed age distribution may be sensitive to changes in age frequencies, especially when sample sizes are small, which may distort estimates of survival.

Published values for ages at first or last birth may be too young, intervals between births may be too short, and estimated survival rates may be too low because of age-

assignment criteria that previous studies used (e.g., Laws 1966, Sikes 1966, Sikes 1968, Lang 1980). Long-term studies of elephants of known age, such as those on the elephants of Addo, Amboseli, and Samburu, may yield the best estimates of fecundity and survival (Whitehouse and Hall-Martin 2000, Moss 2001, Wittemeyer et al. 2005a). Because our estimates of survival and fecundity are similar to previously published values, it is not surprising that our estimates of finite growth (λ) were also similar to those previously estimated for Addo and Amboseli elephants (Whitehouse and Hall-Martin 2000, Moss 2001).

Our approach to estimating survival and growth rates assumed stable age distributions (Caswell 2001), which could be limiting in cases where age structures are skewed (e.g., in newly established populations or in areas with intense poaching). When populations are disturbed in this manner, it may take time for demographic signals to be established in the population and, subsequently, to be detectable by REPA. Our method may also distort survival estimates when applied to small populations that may not have a stable age distribution.

We assumed that survival and fecundity were principal components of population growth (Gaillard et al. 2000) and that populations we studied were closed. This assumption may well be valid because fences around Addo and Maasai tribal lands surrounding Amboseli may limit elephant dispersal and reduce immigration and emigration effects. Few family groups have colonized Amboseli since 1970 (Moss 1988). However, assuming age distributions in female herds are an unbiased sample of a population's age distribution, movement of herds in and out of populations may have little influence on estimates derived from REPA, given sufficient sampling. A systematic survey of breeding herds across the distribution of elephants in a study area to ensure >150 females in the sample will be adequate to extract an age distribution (Caughley 1977).

MANAGEMENT IMPLICATIONS

Our REPA provides data that can be used to monitor how elephant populations respond to conservation management actions, such as antipoaching campaigns and culling. It also allows studies on population responses to natural events, such as the extended dry or wet cycles characteristic in parts of the range of elephants in Africa. Furthermore, imprecise population estimates are typical for elephant studies (Barnes 2002) and make it difficult to estimate growth rates reliably (Gerrodette 1987). Our REPA clearly overcomes the problem of imprecise population estimates because it yields narrow confidence limits as well as reliable estimates of demographic variables from a single short-term survey. The REPA method yields more demographic data than the standard aerial surveys typically applied to count elephants in Africa, which are expensive and yield little more than population estimates and distributional data. An option of combining our approach with aerial censuses to obtain demographic profiles of elephant populations can augment population estimates and distributional data, which may be

more cost efficient in a routine of less-frequent surveys interspersed by REPA to deduce elephant population responses to management.

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