Changes in elephant numbers in major savanna populations in eastern and southern Africa

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Abstract

This paper presents an analysis of changes in elephant population estimates selected from the two most recent reports of the African Elephant Database (AED). Sites selected for analysis were restricted to surveyed areas in which successive estimates had been made using comparable methods. The resulting selection consisted of surveys conducted in eastern and southern Africa between 1994 and 2002, which together cover a large percentage of the total elephant population for which estimates are available in these two regions. The results suggest a significant overall increase ($p < 0.0002$) for the eastern and southern African sites combined. The overall increase in the southern African estimate was significant ($p < 0.0004$), but the increase in eastern African estimates was not statistically significant. It is concluded that savanna elephant populations in eastern and southern Africa are more likely to have increased than to have declined in the years leading up to the *African Elephant Status Report 2002*; important caveats become evident, however, when interpreting these findings.

Résumé

Cet article analyse les changements dans les estimations de populations d'éléphants selon les plus récents rapports de la Base de Données de l'Eléphant africain (BDEA). Les sites choisis pour cette analyse ont été limités aux aires étudiées dans lesquelles on a fait des estimations successives en utilisant des méthodes comparables. Les résultats de la sélection reprennent des études menées en Afrique orientale et australe entre 1994 et 2002 qui, ensemble, couvrent un grand pourcentage de la population d'éléphants pour laquelle des estimations existent dans ces deux régions. Les résultats suggèrent une augmentation générale significative ($p < 0,0002$) pour les deux sites combinés. L'augmentation globale pour les estimations en Afrique australe était significative ($p < 0,0004$), mais l'augmentation des estimations en Afrique orientale n'était pas statistiquement significative. On en conclut que les populations d'éléphants de savane en Afrique orientale et australe sont plus susceptibles d'avoir augmenté que diminué durant les années qui ont précédé le *Rapport 2002 sur le Statut de l'Eléphant africain* ; il reste d'importantes mises en garde, cependant, quant à l'interprétation de ces découvertes.

Introduction

A question of major interest to decision-makers involved in the conservation and management of African elephants is whether the elephant population on the continent as a whole is increasing or decreasing. Since its inception in 1986, the African Elephant Database (AED), probably the most comprehensive effort to monitor the distribution and abundance of any widely distributed species of mammal in the wild, has been periodically reporting on the status of African elephant populations throughout the species' range. Data for the AED are obtained from a wide variety of sources ranging from systematic aerial counts to ad hoc guesses, and the reliability of the estimates varies accordingly. To characterize this variability, the AED separates elephant numbers into four categories of certainty—*definite, probable, possible* and *speculative*—according to fixed rules (see Blanc et al. 2003 for details). In this system, if all elephant populations were systematically surveyed, giving unbiased estimates with measured precision, the sum of the *definite* and *probable* categories would be an accurate statement of true elephant numbers.

The reported numbers under the *definite* and *probable* categories in the continental, all regional and most national sections in the *African Elephant Status Report* (AESR) 2002 (Blanc et al. 2003) are higher than the corresponding numbers reported in the *African Elephant Database 1998* (Barnes et al. 1999). These changes, however, do not necessarily reflect real overall increases in elephant numbers, and a casual comparison of these figures is likely to be misleading for a number of reasons.

Many of the continent's elephant populations have never been systematically surveyed. Most elephant surveys tend to concentrate in and around protected areas, although up to 80% of elephant range may lie outside them. Any changes reported are only derived from a subset of all elephant populations and may therefore not reflect overall changes in numbers. The extent of unsurveyed range across the continent may amount to as much as 50% of total elephant range in Africa (Blanc et al. 2003), but even this estimate is subject to considerable uncertainty. Elephant distribution data for the AED are obtained from questionnaire replies and other potentially unreliable sources, which can quickly become outdated. To quantify this uncertainty, the AED has recently begun to categorize elephant range into three categories of reliability: *known* range, *possible* range and *doubtful* range.

Many important populations are surveyed infrequently or have been surveyed only once. In consequence, any one report of the AED may repeat some estimates from the previous report because these are still the most up to date available. This makes using total numbers invalid as a measure of change, as constancy of numbers at some sites reflects only the same information carried forward from one status report to the next. The totals in the *definite* and *probable* categories may decline where an out-of-date estimate has been degraded to the *speculative* category and no more recent information is available. Conversely, where a population is surveyed for the first time, the resultant increase in the total is due not to population increase but to the inclusion of new information. False increases (or decreases) may also happen when the boundary of the study area changes between surveys, although the site name remains the same. When only parts of the ranges of elephant populations are included in the surveyed area, changes in estimates may be caused by elephant movements rather than real changes in population size.

Even where two successive surveys of the same area are available, misleading changes may be observed when different methods, liable to different levels of accuracy or bias, are used in the two consecutive surveys. Variation in survey conditions—like the time of the year or even the use of different survey crews—may result in changes in numbers of elephants seen, thus contributing to differences recorded over time.

In addition many estimates come from sample surveys and are therefore subject to statistical sampling error. As a result, differences between successive estimates could be due purely to chance but still make a large contribution to the differences between totals.

Despite these problems, it is possible to select those sites where surveys have been repeated using comparable methods and to conduct a formal comparison of elephant numbers over time restricted to a segment of the continental population. As it turns out, a large proportion of the known elephant populations in eastern and southern Africa can be included in such a sample. This paper presents the results of such an analysis using data taken from the AED 1998 and the AESR 2002.

Methods

Site selection

Survey data were obtained from the two most recent reports of the AED (Barnes et al. 1999; Blanc et al.

2003). Data from previous reports of the African Elephant Database (such as Said et al. 1995) were not used in this analysis, as there were few sites with comparable data across all three reports. Surveys were regarded as comparable if they met the following conditions:

- Similar survey methods or methods with similar levels of accuracy were used in both time periods. All guesses were excluded.
- Approximately the same elephant range was covered in both surveys. However, where a discrete population of elephants was censused in its entirety in both surveys, the estimates were regarded as comparable even if the total areas were different. In some cases, adjacent input zones reported in the AED 1998 were combined to match larger input zones reported in the AESR 2002.

Although some total ground counts and individual recognition studies met the above criteria, the majority of the sites in the sample were covered by aerial surveys. Systematic aerial surveys fall into two broad categories: sample counts and total counts. In the former, a representative sample of the study area is usually covered by counting animals along transects of known width on either side of flight lines. The overall density of elephants recorded in the transects is used to calculate a population estimate with confidence limits for the entire study area. The width of the confidence interval depends on the number and distribution of animals in the study area as well as on the sampling design and intensity (Norton-Griffiths 1978). Aerial total counts, on the other hand, aim to record every elephant in a study area by flying closely spaced flight lines to cover the entire area. Since it is assumed that every animal is counted, aerial total counts give no estimates of precision. However, as some animals are always likely to be missed, total counts tend to result in undercounts and as such represent a minimum estimate of the true number of animals present. Nevertheless, for the purposes of this analysis, all total counts were treated as sample counts with zero variance (Norton-Griffiths 1978).

Two important sites in eastern Africa were excluded from the analysis, as their inclusion would have biased the overall results. The Ruaha–Rungwa ecosystem in Tanzania with an estimated 24,682 ± 6495 (estimate ± 1.96 × SE) elephants in 2002 was excluded because the 1998 estimate (13,021 ± 4300) is believed to have been an undercount (Conservation Information and Monitoring Unit 2002). Similarly, the difference between the 1998 and 2002 dung count survey estimates for Mount Kenya (4022 ± 1083 and 2911 ± 640 respectively), is not due to changes in elephant density but rather to an improvement in the estimate of the area available to elephants in the ecosystem (H. Vanleeuwe, pers. comm.)

One of the sites in eastern Africa, Samburu District (Kenya), was included in the sample despite an increase in precision due to a change in survey method between the AED 1998 (aerial sample count) and the AESR 2002 (aerial total count). However, since total counts tend to result in undercounts the inclusion of Samburu District in the analysis is justified on the basis that the 2002 total count estimate is larger than the upper 95% confidence limit of the 1998 sample count.

The above criteria resulted in a selection of 51 sites in eastern (13 sites; table 1) and southern Africa (38 sites; table 2). The geographical location of the selected sites is shown in figure 1. A small number of comparable surveys also existed in Central and West Africa (1 site in Central Africa—Garamba National Park—and 7 sites in West Africa, 5 of which are part of the same population in Burkina Faso). However, these sites were excluded from the analysis as they represented very small fractions of total *known* plus *possible* range in eastern Africa (0.2%) and in southern Africa (2%). The analysis reported here is, in consequence, restricted to sites in eastern and southern Africa.

The combined area covered by the selected surveys represents 21% of total *known* plus *possible* for eastern Africa and 23% for southern Africa, but only 11% of the total current *known* and *possible* elephant range estimate for the continent. The sites include some of the best-managed and best-studied parks on the continent and cannot therefore be considered a representative sample of sites with elephants in Africa as a whole. However, the total number of elephants in these sites (353,687) represents a high proportion (77%) of total continental numbers under the *definite* and *probable* categories reported in the AESR 2002 (461,091).

Differences and rates of change

Estimates were added separately for each dataset and differences between the two datasets were calculated at the levels of individual and combined regions. The statistical significance of these differences was judged by calculating the variance of the estimated difference and constructing a 95% confidence interval for the true difference. A difference was deemed significant if its

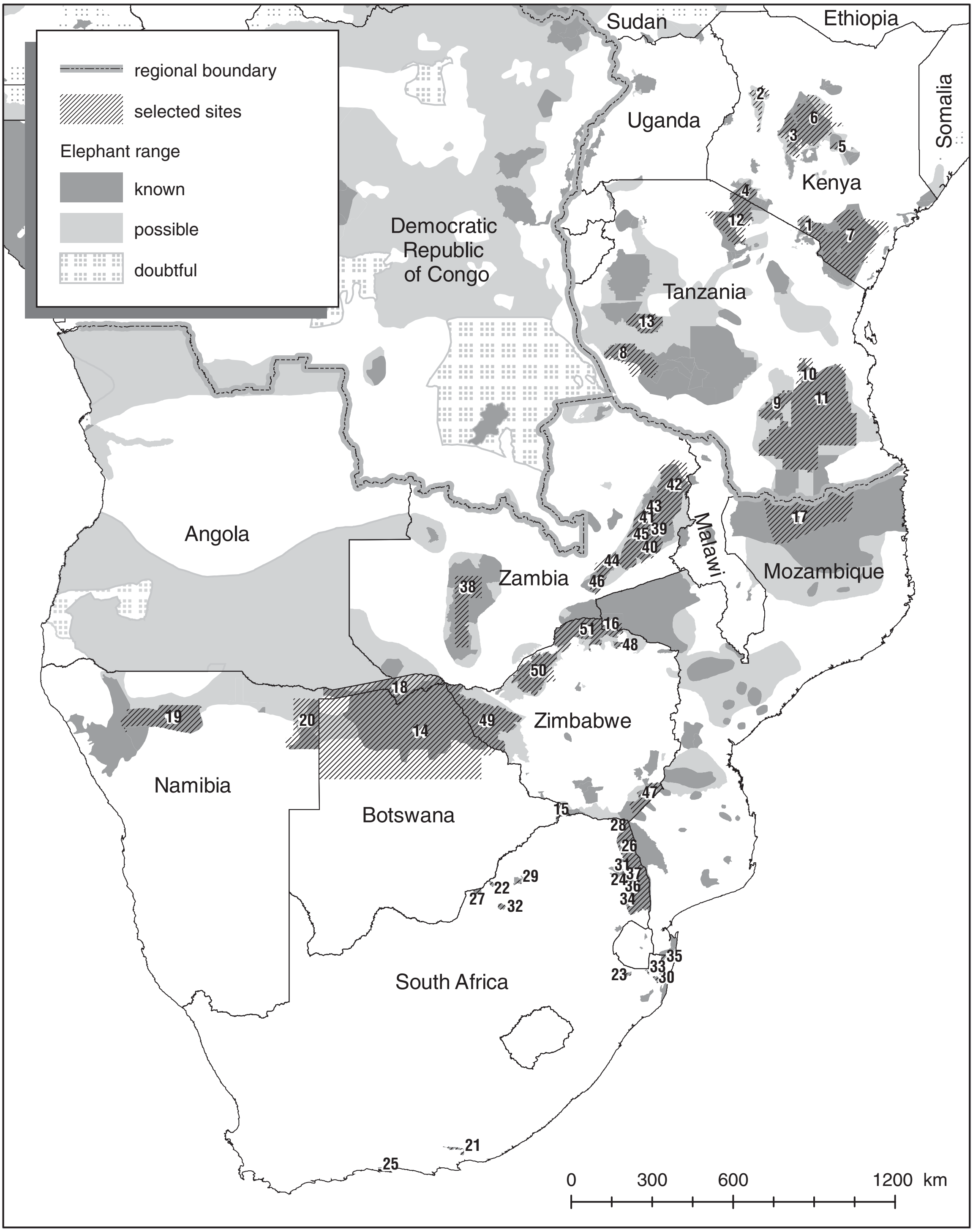

Figure 1. Location of the sites included in the analysis and elephant range from Blanc et al. (2003). Numbers refer to sites listed in tables 1 and 2.

Table 1. Eastern African sites used in this study and summary survey results

Survey zone	Year of survey	Survey method	Estimate	95% CL (±)	Area (km^2)
Kenya					
1. Amboseli	1998	IR1	980	0	5,547
	2002	IR1	1,100	0	5,547
2. Kerio Valley	1997	AT3	652	0	4,616
	2002	AT3	490	0	4,616
3. Laikipia	1996	AT3	2,436	0	7,000
	2002	AT3	3,241	0	8,406
4. Masai Mara	1998	AT3	1,450	0	3,488
	2002	AT3	2,116	0	3,488
5. Meru and Bisanadi	1997	AT3	360	0	2,849
	2002	AT2	372	0	2,053
6. Samburu District	1996	AS2	1,224	898	21,095
	2002	AT2	2,206	0	20,073
7. Tsavo	1994	AT3	7,371	0	38,300
	2002	AT3	9,221	0	37,382
Tanzania					
8. Katavi–Rukwa	1995	AS2	4,998	2,360	13,341
	2002	AS3	5,751	4,549	11,862
9. Kilombero	1994	AS2	1,903	514	6,928
	2002	AS3	6,203	4,639	6,006
10. Mikumi	1994	AS2	700	309	3,215
	2002	AS3	1,144	923	3,069
11. Selous	1994	AS2	49,571	11,025	81,838
	2002	AS3	57,886	14,518	80,287
12. Serengeti	1998	AT3	2,015	0	16,860
	2000	AT3	1,631	0	16,860
13. Ugalla River	1996	AS2	761	655	6,524
	1999	AS3	1,177	615	7,252
Total eastern sites	1996*	–	74,421	11,345	211,601
	2002*	–	92,538	15,944	206,901
Difference	6*		18,117	19,569	–4,700

Survey method codes: IR – individual registration; GT – ground total count; AT – aerial total count; AS – aerial sample count. The number that accompanies the survey method code gives an indication of survey quality, ranging from 1 to 3 (best to worst). For more details, see Blanc et al. (2003). The 95% CL (±) column denotes the standard error of the estimate times 1.96.
* median value

95% confidence interval did not overlap zero. In particular, an increase was considered significant if the lower bound of the 95% confidence interval was greater than zero. To calculate *p* values, a *t*-statistic was calculated as the ratio of the estimated difference to its standard error. This approach is similar to a matched-pairs *t*-test in that the sum of the differences between individual pairs is compared against the pooled variance of the dataset, but the measure of variation used in this case originates from the sum of the internal variances of sample counts and not from the variance of differences across sites.

To express the difference as a rate of change, the finite rate of the increase λ (Caughley 1977) was estimated from the ratio λ^t of the pooled estimates from the AED 1998 ($\hat{N}_0$) and the AESR 2002 ($\hat{N}_1$):

$$\lambda^t = \frac{\hat{N}_1}{\hat{N}_0} \qquad \text{(Eq. 1)}$$

where t is the time interval in years. As the time interval between surveys in the AED 1998 dataset and the AESR 2002 dataset varied from one site to another (see under Results below), it was adjusted by calculating t as the average time interval between surveys weighted by the number of elephants in the AED 1998 dataset.

The finite rate of increase λ is therefore estimated by

$$\hat{\lambda} = \left(\frac{\hat{N}_1}{\hat{N}_0}\right)^{\frac{1}{t}} \qquad \text{(Eq. 2)}$$

From this the estimated mean annual per cent rate of increase $\hat{R}$ can be calculated as

$$\hat{R} = \left(\hat{\lambda} - 1\right) \times 100 \qquad \text{(Eq. 3)}$$

To construct a 95% confidence interval around the estimated rates of change, the variance of the ratio of population estimates was approximated using a second-order Taylor series expansion (Schreuder et al. 2004):

$$Var\left(\frac{\hat{N}_1}{\hat{N}_0}\right) = \left(\frac{\hat{N}_1}{\hat{N}_0}\right)^2 \left[\frac{Var(\hat{N}_0)}{\hat{N}_0^2} + \frac{Var(\hat{N}_1)}{\hat{N}_1^2} - \frac{2\,Cov(\hat{N}_0, \hat{N}_1)}{\hat{N}_0 \hat{N}_1}\right] \qquad \text{(Eq. 4)}$$

Table 2. Southern African sites used in this study and summary survey results

Survey zone	Year of survey	Survey method	Estimate	95% CL (±)	Area (km^2)
Botswana					
14. Northern Botswana	1995	AS3	89,227	13,406	122,922
	1999	AS2	120,604	21,237	146,050
15. Tuli	1994	AS1	831	456	885
	2001	AT2	1,262	0	885
Mozambique					
16. Magoe South	1995	AS2	137	187	2,824
	2001	AS2	1,264	1,359	2,824
17. Niassa	1998	AS2	8,707	1,937	42,349
	2002	AS2	13,061	2,433	42,341
Namibia					
18. Caprivi	1995	AS2	4,883	1,247	19,290
	1998	AS2	4,576	1,223	18,259
19. Etosha	1995	AS1	1,189	410	22,270
	2000	AS2	2,100	774	19,269
20. Kaudom/Nyae Nyae	1995	AS2	1,085	545	15,020
	2000	AS2	1,966	973	12,107
South Africa					
21. Addo Elephant	1998	AT1	272	0	513
	2002	AT1	337	0	513
22. Atherstone	1997	AT3	24	0	136
	2002	AT3	32	0	136
23. Itala	1997	GT1	45	0	297
	2002	GT1	61	0	297
24. Klaserie	1997	AT3	303	0	628
	2002	AT2	467	0	628
25. Knysna	1997	IR1	3	0	300
	2002	IR1	4	0	300
26. Kruger	1998	AT3	8,869	0	19,624
	2002	AT2	10,459	0	19,624
27. Madikwe	1998	AT3	282	0	700
	2002	AT3	318	0	700
28. Makuya	1997	AT3	8	0	165
	2002	AT2	27	0	165
29. Marakele	1998	IR1	48	0	380
	2002	IR1	91	0	380
30. Mkuzi	1997	IR1	25	0	380
	2002	IR1	28	0	380
31. Phalaborwa	1997	AT3	42	0	41
	2002	AT2	23	0	41
32. Pilanesberg	1997	AT3	87	0	553
	2002	AT3	142	0	553
33. Pongola	1997	IR1	20	0	119
	2002	IR1	33	0	119
34. Sabie Sand	1997	AT3	311	0	572
	2002	AT2	757	0	572
35. Tembe Elephant	1997	AT3	115	0	300
	2002	AT3	140	0	300

where *Var* is the variance and *Cov* the covariance. In this analysis, however, the errors in the estimates are uncorrelated and the covariance can therefore be taken to be zero.

Results

Table 3 presents a summary of changes in elephant numbers, while table 4 summarizes the rates of change. Results are discussed in detail below, first for both regions combined and then for each region in turn.

Southern and eastern African sites combined

Surveys selected from the AED 1998 were conducted between 1994 and 1998; the median survey year was 1997. For surveys selected from the AESR 2002, survey years ranged from 1998 to 2002, the median year being 2002. The time difference between surveys ranged from a minimum of 2 years to a maximum of 8, with a median of 5 years (25% quartile: 4 years; 75% quartile: 5 years). The weighted mean time between surveys was 5.097 years. The total area surveyed increased slightly from the AED 1998 to the AESR 2002 by 37 km^2, or 0.006%.

A significant proportion of the selected sites (41 out of 51, or 80.4%) reported higher estimates in the AESR 2002 dataset than in the AED 1998 dataset (sign test, Z = 4.20, $p < 0.0001$). The estimated total number of elephants in the tabulated sites increased from 282,895 in the 1998 dataset to 353,687 in the 2002 dataset, a difference of 70,792 or 25%. The standard error of the difference was 14,464. Taking t to be 1.96, this gives a 95% confidence interval of +35,863 to +141,584 for the overall difference in the tabulated

Table 2. (continued)

Survey zone	Year of survey	Survey method	Estimate	95% CL (±)	Area (km²)
36. Timbavati	1997	AT3	322	0	784
	2002	AT2	372	0	494
37. Umbabat	1997	AT3	134	0	144
	2002	AT2	88	0	144
Zambia					
38. Kafue	1997	AS2	4,482	3,222	22,400
	2001	AS3	2,194	5,590	16,929
39. Luambe and Lumimba	1996	AS3	763	811	4,462
	1999	AS2	1,053	551	4,462
40. Lupande	1996	AS2	892	1,394	4,840
	2002	AS2	975	587	4,959
41. Munyamadzi	1996	AS2	102	210	3,300
	2000	AS3	1,108	500	3,292
42. Musalangu	1996	AS3	305	690	17,350
	2001	AS3	1,121	898	17,350
43. North Luangwa	1996	AS3	3,033	2,252	4,636
	2000	AS3	3,750	1,076	4,636
44. Sandwe and Chisomo	1996	AS2	818	1,597	4,920
	1999	AS2	128	155	750
45 South Luangwa	1996	AS2	7,942	2,930	9,050
	2002	AS2	4,459	1,519	8,448
46. West Petauke	1996	AS3	2,435	2,773	4,140
	1999	AS2	897	1,399	905
Zimbabwe					
47. Gonarezhou, Malipati	1996	AS2	3,842	1,692	5,435
and Mahenye	2001	AS2	4,992	1,577	5,346
48. Mavuradonha and	1997	AS1	120	120	617
Great Dyke	2001	AS2	13	26	617
49. NW Matabeleland[a]	1997	AS2	36,280	7,308	25,074
	2001	AS2	49,310	6,028	25,072
50. Sebungwe[b]	1997	AS2	13,386	1,241	15,597
	2001	AS2	13,989	2,098	15,622
51. Zambezi Valley	1995	AS2	17,105	2,580	14,842
	2001	AS2	18,948	2,463	17,127
Total southern sites	1997*	–	208,474	16,959	387,859
	2002*	–	261,149	23,441	392,596
Difference	5*	–	52,675	28,933	4,737

See footnote to table 1 for survey method codes and additional details.
[a] Includes the following survey zones: Hwange, Matabeleland and Matetsi
[b] Includes the following survey zones: Binga, Chete, Chirisa, Chizarira, Kariba, Lusulu, Matusadona, North Gowke and Sijarira
*median value

populations, a statistically significant difference (t = 3.97; $p < 0.0002$). This translates to an annual rate of increase of 4.48%, with a 95% confidence interval ranging from +2.17% to +6.60%.

To examine whether the significant difference was simply a consequence of increases in a few very large populations, the analysis was repeated excluding sites with very large increases in absolute numbers. The sites excluded were northern Bo- tswana (with a difference of +31,377), northwest Matabeleland (+13,030) and Selous (+8,315). The results of the analysis on this reduced dataset still show a significant difference of between +5,137 and +31,003 elephants ($t = 2.74$, $p < 0.01$). In view of this, the three sites were included in subsequent analyses.

Eastern Africa

Surveys reported in the AED 1998 were conducted between 1994 and 1998, and all but one of the surveys reported in the AESR 2002 were carried out in 2002. The time difference between surveys in the selected sites in eastern Africa ranged from 2 to 8 years, with a median time difference of 6 years and a weighted mean time difference of 7.45 years. The total reported surface area surveyed in the selected sites declined between the AED 1998 and the AESR 2002, by 4700 km² (–2.22%), but all the sites that registered declines in area reported higher elephant estimates in the latter.

The AESR 2002 reports higher elephant estimates for 11 of the 13 selected eastern African sites with an estimated difference of 18,117 elephants. While the 95% confidence interval of the difference (–1452 to +36,234) includes the value zero, and the result is therefore not statistically significant ($t = 1.82$, $p > 0.05$), the range of probabilities lies mostly on the positive side of zero. This is also true of the estimated annual rate of increase (2.97%, range –0.59% to 5.87%), making an overall increase substantially more likely than a decline in numbers.

Table 3. Results of the analysis of differences in elephant populations in the selected sites

Region	Area (km²)	Median survey year	Estimate	Difference	Variance of estimate	Standard error of difference	*t*	*p*
Eastern	211,601	1996	74,421	18,117	33,505,371	9,984	1.815	>0.05
Africa	206,901	2002	92,538		66,174,523			
Southern	387,859	1997	208,474	52,675	74,870,543	14,762	3.568	<0.001
Africa	392,596	2002	261,149		143,037,079			
Total	599,460	1997	282,895	70,792	108,375,914	17,821	3.972	<0.0002
	599,497	2002	353,687		209,211,602			

Source: AED 1998; AESR 2002

Table 4. Results of the analysis of rates of change in elephant populations in the selected sites

Region	Weighted time difference (years)	Annual rate of change (%)	Variance of ratio	Lower 95% CL of rate (%)	Upper 95% CL of rate (%)
Eastern Africa	7.449	2.97	0.02137	–0.59	5.87
Southern Africa	4.257	5.43	0.00600	2.28	8.31
Total	5.097	4.48	0.00473	2.17	6.60

Source: AED 1998; AESR 2002

Southern Africa

The median time difference between the selected surveys in southern Africa was 5 years, with a minimum difference of 3 years and a maximum of 7. The weighted mean time difference between surveys was 4.26 years. The total surveyed area increased by 4737 km^2 (+1.22%).

Out of 38 sites selected in southern Africa, 30 reported higher estimates in the AESR 2002 with increases ranging from a single elephant (Knysna, South Africa) to over 30,000 (northern Botswana). The remaining 8 sites reported lower estimates in the AESR 2002, ranging from a decrease of 19 elephants in Phalaborwa (South Africa) to 3483 in South Luangwa (Zambia).

The total difference between estimates in the AED 1998 and the AESR 2002 for the southern African sites amounts to 52,675 with a 95% confidence interval of +23,742 to +81,608, a highly significant difference ($t = 3.57$, $p < 0.001$). The estimated mean annual rate of increase for the selected sites in this region is 5.43% with lower and upper 95% confidence limits of +2.28% and +8.31% respectively. The difference for southern Africa is of sufficient magnitude to make the combined results of eastern and southern African sites highly significant despite the lack of statistical significance for the eastern African sites alone.

Discussion

The results of this analysis strongly suggest an overall increase in the number of elephants in the tabulated sites in southern Africa as well as for the combined eastern and southern African sites between 1994 and 2002. Only within-survey variance is accounted for in this analysis, as variance due to changes in survey conditions and movement of elephants across survey boundaries cannot be measured, given only one pair of surveys per site. It is unlikely, however, that allowance for this could have reduced the results to non-significance. It should be emphasized that the results refer only to the relevant total numbers as there are insufficient data in most cases to make meaningful comparisons at the site level. Nevertheless, populations are believed to be increasing in many of the sites listed (see Barnes et al. 1999 and Blanc et al. 2003 for details on individual populations).

The number of elephants included in the selected sites from the AESR 2002 dataset represents a high proportion (68%) of the *definite* plus *probable* elephants for eastern Africa and southern Africa (97%) reported in Blanc et al. (2003), and accounts for virtually the entire elephant populations of some countries: Botswana, Namibia, South Africa and Zimbabwe. The analysis does, however, exclude most of Mozambique; substantial portions of elephant range in Kenya and Tanzania; and the entire ranges of Angola, Sudan and Uganda among others.

While the estimated annual rates of increase reported here are similar to those derived from detailed demographic studies (for example, Moss 2001; Wittemyer et al. 2005), and below the theoretical (7%) and observed (10%) long-term maxima (Calef 1988; Foley 2002), it is impossible to determine whether these changes are due solely to natural population growth, or the extent to which they may have been influenced by immigration into survey zones. The selection of sites for this analysis largely comprises protected areas, some of them surrounded by large areas of unsurveyed range. In view of increasing range loss due to habitat conversion in much of the continent (Parker and Graham 1989), net immigration into well-protected areas may be expected and the possibility that elephant movements may have contributed to the observed increases cannot therefore be ruled out. On the other hand, much of the excluded unsurveyed range is unlikely to contain high densities of elephants, and in some southern African countries elephants have expanded into new range in the past few years (Blanc et al. 2003). A large unidirectional bias is therefore unlikely.

Despite the limitations inherent in the data, this analysis suggests an overall increase in the number of elephants in southern African sites during the period covered by this comparative study. The likelihood is also high that the eastern African sites experienced an overall increase in elephant numbers during the period. This is a noteworthy finding, as the vast majority of the savanna subspecies of the African elephant are in southern and eastern Africa. It must be reiterated, however, that this says nothing about the situation in West or Central Africa, where data are insufficient to draw any conclusions; more extensive and regular survey work of consistent quality will be required to detect changes in elephant populations in the continent as a whole. Similarly, the results do not imply a uniform increase across all sites but merely an increase on average; some sites may have suffered a decline. Finally, it should not be assumed that elephant populations analysed in this study are continuing to increase at present as the period of the observed increase was centred around the late 1990s.

Doubts about the validity of the present results hinge on elephant movements into surveyed areas, the absence of information about the status of elephants in unsurveyed range, and in particular the extent to which the observed increases result from reproduction instead of immigration from unsurveyed areas. Coordinated surveys of entire populations, across international borders where necessary, would remove much of this uncertainty. Clearly, the need continues to obtain reliable estimates for *all* elephant range.

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