Chapter 6

Manuscript prepared for submission to the Proceedings of the Royal Society B: Biological Series

A meta-analysis of elephant impact

Robert A.R. Guldemond and Rudi J. van Aarde

Over most of Africa, elephant numbers have declined in the previous two centuries. Yet, those managing the 260,000 elephants in southern Africa often consider culling them as high elephant numbers are deemed harmful to biological diversity. Our review of scientific studies does not support this notion. A handful of studies dominate the literature. These show that elephants have a negative effect on tree densities. Short-term studies show that elephants have an immediate effect on plants. Long-term studies do not support this notion. Elephants also do not decrease the diversity of other species present in the system. The underlying premise for culling elephant is not justified.

Keywords: elephant impact; perceptions; plants; diversity; scale

1. INTRODUCTION

Across Africa, hunting and poaching have drastically reduced the number of elephants (*Loxodonta africana* Blumenbach and *L. cyclotis* Matchie) (Spinage 1973; Stiles 2004). The establishment of protected areas, their fencing and the provision of water has allowed elephant populations to rebound (Douglas-Hamilton 1987; Caughley *et al*. 1990). Fencing conceivably interfered with the role dispersal has in controlling population growth (see Chafota & Owen-Smith 1996) and water provision may enhance survival of juvenile elephants (Shrader *et al*. in review). Confining high densities of elephants may transform woodlands into shrublands or grasslands that may induce local disappearances of other species. This is what Caughley (1976) and others referred to as the “elephant problem”. Examples include Dublin *et al*. (1990), Cumming *et al*. (1997), Trollope *et al*. (1998), van de Vijver *et al*. (1999) and Western & Maitumo (2004).

At issue is whether managers should reduce elephant numbers to maintain biological diversity (e.g. Whyte *et al.* 2003). Several sub-Saharan conservation authorities have opted to cull elephants (Feely 1965; Pienaar 1966; Astle 1971; Hanks *et al*. 1981; Whyte *et al*. 1999). Gillson & Lindsay (2003), Goheen *et al*. (2004), Skarpe *et al*. (2004) and Wiseman *et al*. (2004) provide an alternative opinion. The impacts of elephants on vegetation depend on a large number of confounding variables. Global climate change, frequent fires, drought, disease and trampling may also reduce tree densities and transform woodlands into grasslands (e.g. Walker *et al*. 1981; Noy-Meir 1982; Gillson 2004).

We used meta-analytic techniques (Cooper & Hedges 1994) to synthesize the impact of elephants on components of biological diversity. We

(1) Establish which studies were most influential in shaping opinion on the impact of elephants,

(2) Investigate what effects elephants have on vegetation,

(3) Establish if elephant also affects other components of savannas, such as vertebrates and insects,

(4) Investigate how the duration of the study and selection of response variables influenced the published findings.

Our results suggest that a biased citation of selected studies generated current perceptions. Certainly, elephants have adverse effects on individual plants. Despite that, we found that most evidence is inconclusive for the general negative impact on vegetation, other vertebrate and insect taxa.

2. METHODS

Computerised databases, references lists and the African Elephant Bibliography (http://www.elephant.chebucto.net/index.cgi) provided the information for our analyses. We considered only primary studies published up to 2004 in English peer-reviewed journals. To reduce dependence and bias we excluded symposium presentations and abstracts, newsletters, books and chapters in books, post-graduate theses and internal reports. We excluded studies conducted under artificial conditions such as zoological gardens and the response of exotic species to elephants. We documented the year of publication, study site, duration of the study, the design (e.g. replication and controls), and the number of times each study was subsequently cited. Author opinions were grouped into negative or non-negative (positive, neutral) classes.

Finally, we grouped together the response variables used by the studies into (1) individual plant structure (e.g. cover, height, crown/ basal diameter), (2) damage indices (percentage debarking, canopy removals) (3) population (densities, mortality, survival) and (4) community variables (diversity indices) separately for plants, vertebrates (mammals and birds) and insect taxa. For convenience in discussing our results, we will call all reductions in abundance, density, biomass cover, species richness etc, plus all increases in damage, as “reductions in abundances”. That is, henceforth, “abundance” becomes a catchphrase for all the various ways in which elephants affect other species.

3. ANALYSIS

We developed a standardised ranking score for each study to ascertain the most influential studies. The mean difference between the age of a given study and those that cited it, were divided by the age (in years) of that study. We then divide this value by the number of times that it was cited. Consequently, the highest ranked studies were those cited most frequently and for the longest available period since its publication.

We used Cohen’s *d* (Gurevitch & Hedges 1993) to calculate the effect sizes separately for experimental (with elephant exclusion control plots) and observational studies (those without). We interpret the overall effect size as the “reductions in abundances” elephants have for the taxa. For experimental studies, Cohen’s *d* is the difference in the response variable between treatment (elephant presence) and control (elephant absence), divided by the pooled average standard deviation (Gurevitch & Hedges 1993). For those studies that assigned elephant presence as controls in their study designs, we reassigned the published information as treatment values. In the studies without controls, we divided the pooled average standard deviation by the difference in values of response variables between the beginning and end of each study. Only studies that reported sample sizes and indices of variability around the mean could be included in these analyses. Large differences and low variability will result in larger effect sizes (Gurevitch & Hedges 1993).

We used the *Q*-statistic in a mixed model analysis of variance to investigate heterogeneity amongst response variables. The *Q*-statistic is a measure of the degree to which the study outcomes (in this case Cohen's *d*) of the response variables share a common effect size (see Gurevitch & Hedges 1993 for further details). Here we defined the analysis units (*k*) as all the extractable response variables published in each study. Using the rank-correlation method of Begg & Mazumdar (1994) and calculating the 'fail-safe number' of Rosenthal (1991), we assess publication bias for the effect size values. The number of published response variables with non-significant outcomes in order to nullify the overall effect size constitutes the 'fail-safe number'. This serves as a measure of the robustness of the meta-analysis.

4. RESULTS

Our search yielded 230 articles in 57 journals published from 1961 to 2004 (Appendix B). The number of papers published per year increased with time ($F_{1,43} = 98.63$, $p < 0.0001$) and covered 72 sites across sub-Saharan Africa. Most studies (80.1%) lasted fewer than five years. Only 15.1% of the published studies included controls, that is, areas without elephants.

The 20 most influential publications account for 50.9% of all citations in our database (table 6.1), the rest of the 230 articles share the remainder. These highly ranked publications had a mean age of 27 ± 9.8 (SD) years, but age had no significant

Table 6.1. The twenty most influential publications, the number of times studies in our database cited them and the calculated importance ratio for each study.

Study	Number of citings	Importance ratios
1. Laws 1970	60	37.1
2. Caughley 1976	57	34.9
3. Buechner & Dawkins 1961	44	25.7
4. Anderson & Walker 1974	33	24.7
5. Van Wyk & Fairall 1969	31	21.9
6. Dublin *et al*. 1990	34	21.1
7. Pellew 1983	30	18.0
8. Croze 1974	29	17.7
9. Barnes 1983	28	17.1
10. Wing & Buss 1970	30	16.4
11. Jachmann & Bell 1985	24	15.7
12. Jachmann & Croes 1991	15	10.0
13. Cumming *et al*. 1997	16	9.4
14. Ben-Shahar 1993	17	9.0
15. Glover 1963	18	8.7
16. Field 1971	19	8.4
17. Thompson 1975	13	8.2
18. Leuthold 1977	14	7.3
19. Penzhorn *et al*. 1974	11	7.0
20. Guy 1981	11	6.8

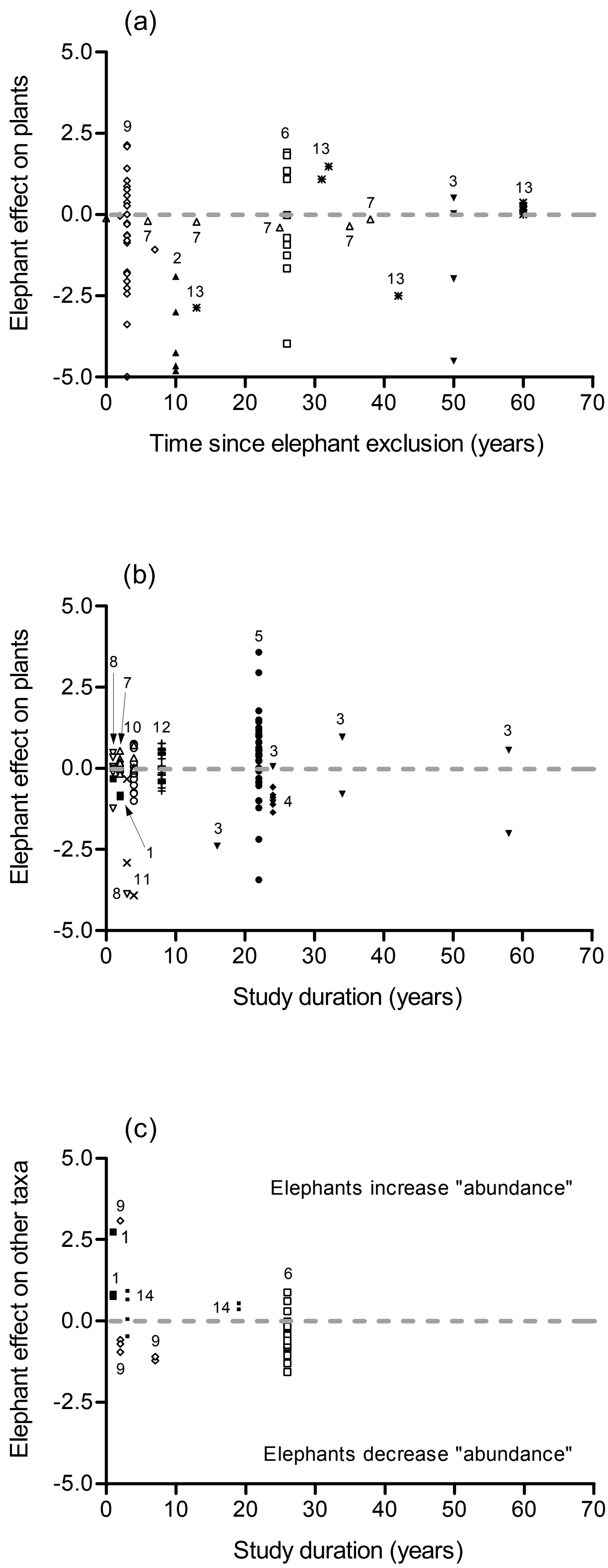

Fig. 6.1 Elephants either increase and/ or decrease plant "abundance" in

Fig. 6.1 (continue) experimental (a) and observational (b) studies. Other vertebrate and insect taxa (c) show a similar pattern for all the studies combined. Data points above the horizontal dashed line in each figure represent where elephants increase "abundance" – see methods for details. Numbers on the graphs represents the different study sites; 1 = Northern Botswana, 2 = Sweetwaters Game Reserve, 3 = Kruger National Park, 4 = Murchison Falls National Park, 5 = Kibale National Park, 6 = Mana Pools National Park, 7 = Sengwa Wildlife Research Area, 8 = Nazinga Game Reserve, 9 = Mpala Research Centre, 10 = Tsavo National Park, 11 = Amboseli National Park, 12 = Ithala Game Reserve, 13 = Addo Elephant National Park, 14 = Tembe Elephant Park. Data from Augustine & McNaughton 2004; Barnes 2001; Birkett 2002; Botha *et al*. 2002; Buechner & Dawkins 1961; Chapman *et al*. 1997; Cumming *et al*. 1997; Eckhardt *et al*. 2000; Fenton *et al*. 1998; Goheen *et al*. 2004; Guy 1981; Herremans 1995; Jachmann & Croes 1991; Keesing 1998; Leuthold 1977; Lombard *et al*. 2001; Mapaure & Campbell 2002; McGeoch *et al*. 2002; Musgrave & Compton 1997; Novellie 1988; Parker & Witkowski 1999; Western & Maitumo 2004; Wiseman *et al*. 2004.

influence on its ranking ($F_{1,18}$ = 3.22, p = 0.089). Sixteen of these influential studies concluded that elephants had decreased abundance of taxa. (We use abundance in the special sense defined above). A significantly lower number (56%) of all 230 studies came to the same conclusion (χ^2 = 5.50, 1 d.f., $p < 0.01$).

Only 15 experimental (k = 86) and 13 observational (k = 141) studies published adequate information for our meta-analyses. For all the taxa combined, our results show that elephants do not affect their abundances (d = -0.07 ± 0.01, $p < 0.05$, 95% CI: -0.20 to 0.46, k = 227). However, when consider separately, experimental studies indicate that elephants significantly decrease plant abundance (d = -0.50 ± 0.03, $p < 0.05$, 95% CI: -0.19 to -0.81, k = 59). With the observational studies (no elephant exclusion), elephants increase plant abundance non-significantly (d = 0.04 ± 0.01, $p < 0.05$, 95% CI: -0.11 to 0.19, k = 132). Elephants further, had no apparent effect on taxa other than plants (e.g. mammals, birds and insects; d = -0.08 ± 0.03, $p <$ 0.01, 95% CI: -0.40 to 0.23, k = 34).

Study site characteristics may also influence these outcomes. While most of the data for plants show that elephants decrease abundance, for sites 6, 7, 9 and 13, there is no consistent pattern (figure 6.1a). At these sites, there are equal increases and decreases in plant abundance. Interestingly though, duration of experimental studies also influence outcomes – those conducted over a short duration showed decreases in abundance. Longer studies showed either no overall effect or even increase in abundance. The study at site 3 (figure 6.1a), where elephants reduce plant abundance over a 50-year period, suffered from poor replication (n = 2).

Similarly, for the studies without controls (figure 6.1b), plant variables tended towards an equal distribution of increasing and decreasing plant abundance (sites 5, 7, 8, 10 and 12), irrespective of time-period. In addition to this, the initial overall increase in abundance elephants have for other taxa, such as for insects, also seems to decline with study duration, with study site 6 having equal responses above and below the neutral effect line (figure 6.1c). In general, though, study site confounds the result — studies with short duration are at different sites than studies conducted over longer periods.

It is clear from figure 6.1a-c that plants and other taxa vary greatly in their responses to elephants (amongst plants: Q = 1956.6, 225 d.f., $p < 0.0001$; between taxa: Q = 492.3, 2 d.f., $p < 0.0001$). Studies that focussed on how elephants decrease plants abundance mostly (90%) concentrated their efforts at individual (structural) and population (mortality and survival) indices. This is in contrast to those investigating the decrease in abundance for other taxa, with 70% of the responses reported at the community level.

Publication bias is prevalent in experimental studies (r_s = -0.31, $p < 0.001$), but not for observational studies (r_s = 0.04, p = 0.54). However, the 'fail-safe' number for experimental (2696) and observational studies (6883) both exceeded the number of published variables necessary to nullify the overall effect size (570 and 1065 respectively). We therefore consider our assessment robust.

5. DISCUSSION

The elephant-diversity debate is contentious. Elephants' inducing structural changes in woody plants largely fuels the debate (e.g. Dublin *et al.* 1990; Cumming *et al.* 1997; Ben-Shahar 1998). Although savannas are in a continuing state of flux (Gillson 2004; Stephenson 2004), some consider such changes as unacceptable (Pienaar *et al.* 1966; Astle 1971; Cumming *et al.* 1997; Whyte 2004). However, support for the standpoint is not universal (e.g. Gilson & Lindsay 2003). Our meta-analyses challenge some of the existing perceptions of the consequences elephants may have for savannas.

Interest and studies on the “elephant problem” have increased since 1961. A fraction of publications (20 of 230) dominates the debate on impact, as more than half the pertinent literature refers to them. This bias towards citing papers concluding that elephants have a negative effect on vegetation, may partly explain some of our current perceptions and interpretations of the “elephant problem”. Citation bias is common in science (Gates 2002). Factors include the directionality and magnitude of results, journal quality, article length, number of authors per article and institutional prestige (Møller & Jennions 2001; Murtaugh 2002; Leimu & Koricheva 2005). We argue that the interpretation in the directionality of results has contributed to the bias in the elephant-diversity debate.

This is of concern as it provides a rationale for conservation bodies to justify reducing elephant numbers as a management activity (e.g. Feely 1965; Pienaar *et al*. 1966; Astle 1971; Hanks *et al*. 1981; van Aarde *et al.* 1999; Whyte 2004) with political and economic implications (e.g. Bulte *et al*. 2004; Hambler *et al*. 2005). Our assessment shows that only half of all studies concluded that elephants had negative consequences for components in their environment. Management driven by an unbiased assessment should also consider the positive effects of elephants (e.g. Cochrane 2003; Goheen *et al*. 2004).

Our assessment supports the notion that elephants have a significant effect on plants. This makes sense as through feeding, they damage individual trees, shrubs and seedlings (e.g. Barnes 1980, 1983; Lewis 1986; Jachmann & Croes 1991). The impacts of elephants on plants are largely immediate, and this may contribute to short-term studies illustrating a negative effect. Such short-term studies that continued for less than five years dominate (80%) our database and may ignore the recovery of vegetation. This is not unique, as short time periods dominate ecological studies in general (see Weatherhead 1986; Tillman 1989). Our analyses agree with Caughley (1976), Dublin (1991), Lock (1993) and Leutholds' (1996) assertions that increased study duration eliminates the apparent negative impact of elephants. Based on short-term studies, the ecological conclusions we reach, as well as our subsequent management actions, are biased and may be inappropriate.

The effect of elephants differs between the taxa included in our analyses (see Q-statistics). It is therefore inappropriate to consider the impact on one taxon as representative across other taxa, or on biological diversity. In addition, one cannot separate the responses measured in elephant studies from the contribution made by other herbivores or events such as fire and rainfall (e.g. Ben-Shahar 1998; Dublin *et al*. 1990; Cumming *et al*. 1997; Trollope *et al*. 1998; van de Vijver *et al*. 1999). Responses may also vary from site to site, further confining the interpretation of findings and the role of elephant in African savannas. One should consider the 'full suite' of community level responses. This may alter the perspectives of studies focussing on single species or even taxa. Only seven of the studies included in our assessment, however, reported response to elephants at this level. We need more information before we can comment on the consequences elephants may have at the community level. We found no overall support for the notion that elephants reduce species diversity (Cumming *et al*. 1997; Whyte 2004), despite their apparent adverse effects for individual plants. It is naive to link their apparent impact on individual plants to biological diversity in general. We therefore conclude that the interpretation of selected studies generate current perceptions.

Future quantitative assessments must rely on rigorous experimental protocols (for example Underwood 1997; Quinn & Keogh 2002) that include a range of spatiotemporal scales (Levin 1992; May 1994), the investigation of all relevant response variables (this study) and appropriate statistical information (Gurevitch & Hedges 1993). We disregarded half of all the studies in this meta-analysis that had proper experimental designs, but lacked sufficient statistical reporting.

Equilibrium based agro-economic arguments dictate the debate surrounding elephant management (confine movements, alleviate environmental constraints and impose constant values on animal populations; e.g. Macnab 1985). This no longer makes sense and we need to allow scale-dependent processes (Lewin 1986; Western *et al*. 1989) to drive conservation management (Gillson & Lindsay 2003). These may include plans to allow acting out dispersal and meta-population dynamics by establishing sink populations through range expansion into marginal areas. This could also allow for seasonal alleviation of 'high' elephant densities on a temporal scale, and initiates recovery periods for other components part of the larger system.

The study is part of a PhD prepared by the senior author. CERU provided financial and logistical support through grants received from the National Research Foundation, the US Fish & Wildlife Service, the Peace Parks Foundation and the International Fund for Animal Welfare. The preparation of the manuscript benefited from inputs by Stuart Pimm and Tim Jackson.

REFERENCES

Anderson, G. D. & Walker, B. H. 1974 Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *J. Sth. Afr. Wildl. Manage. Assoc.* **4**, 1–14.

Astle, W. L. 1971 Management in Luangwa Valley. *Oryx* **11**, 135–139.

Augustine, D. J. & McNaughton, S. J. 2004 Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J. Appl. Ecol.* **41**, 45–58.

Barnes, M. E. 2001 Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *J. Arid Environ.* **49**, 541–554.

Barnes, R. F. W. 1980 The decline of the baobab tree in Ruaha National Park, Tanzania. *Afr. J. Ecol.* **18**, 243–251.

Barnes, R. F. W. 1983 Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *J. Appl. Ecol.* **20**, 521–540.

Begg, C. B. & Mazumdar, M. 1994 Operating characteristics of a rank correlation test for publication bias. *Biometrics* **50**, 1088–1101.

Ben-Shahar, R. 1993 Patterns of elephant damage to vegetation in northern Botswana. *Biol. Conserv.* **65**, 249–256.

Ben-Shahar, R. 1998 Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecol.* **136**, 189–194.

Birkett, A. 2002 The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *Afr. J. Ecol.* **40**, 276–282.

Botha, J., Witkowski, E. T. F. & Shackleton, C. M. 2002 A comparison of anthropogenic and elephant disturbance on *Acacia xanthophloea* (fever tree) populations in the Lowveld, South Africa. *Koedoe* **45**, 9–18.

Buechner, H. K. & Dawkins, H. C. 1961 Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* **42**, 752–766.

Bulte, E., Damania, R., Gillson, L. & Lindsay, K. 2004 Space – the final frontier for economist and elephants. *Science* **306**, 420–421.

Caughley, G. 1976 The elephant problem – an alternative hypothesis. *E. Afr. Wildl. J.* **14**, 265–283.

Caughley, G., Dublin, H. & Parker, I. 1990 Projected decline of the African elephant. *Biol. Conserv.* **54**, 157–164.

Chapman, C. A., Chapman, L. J. Wrangham, R., Isabirye-Basuta, G. & Ben-David, K. 1997 Spatial and temporal variability in the structure of a tropical forest. *Afr. J. Ecol.* **35**, 287–302.

Chafota, J. & Owen-Smith, N. 1996 Options for the management of elephants in northern Botswana. *Pachyderm*, **22**, 67-73.

Cochrane, E. P. 2003 The need to be eaten: *Balanites wilsoniana* with and without elephant seed-dispersal. *J. Trop. Ecol.* **19**, 579–589.

Cooper, H. & Hedges, L. V. 1993 Research synthesis as a scientific enterprise. In *The handbook of research synthesis* (ed. H. Cooper & L. V. Hedges), pp. 3–14. New York: Russell Sage Foundation.

Croze, H. 1974 The Seronera bull problem. II. The trees. *E. Afr. Wildl. J.* **12**, 29–47.

Cumming, D. H. M., Fenton, M. B., Rautenbach, I. L., Taylor, R. D., Cumming, G. S., Cumming, M. S., Dunlop, J. M., Ford, A. G., Hovorka, M. D., Johnston, D. S., Kalcounis, M., Mahlangu, Z. & Portfors, C. V. R. 1997 Elephants, woodlands and biodiversity in southern Africa. *S. Afr. J. Sci.* **93**, 231–236.

Douglas-Hamilton, I. 1987 African elephants: population trends and their causes. *Oryx* **12**, 11–24.

Dublin, H. T. 1991 Dynamics of the Serengeti-Mara woodlands: An Historical Perspective. *Forest and Conservation History* **35**, 169–178.

Dublin, H. T., Sinclair, A. R. E. & McGlade, J. 1990 Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Anim. Ecol.* **59**, 1147–1164.

Eckhardt, H. C., van Wilgen, B. W. & Biggs, H. C. 2000 Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *Afr. J. Ecol.* **38**, 108–115.

Feely, J. M. 1965 A game-cropping scheme in the Luangwa Valley. *Zool. Afr.* **1**, 227–230.

Fenton, M. B., Cumming, D. H. M., Rautenbach, I. L., Cumming, G. S., Cumming, M. S., Ford, G., Taylor, R. D., Dunlop, J., Hovorka, M. D., Johnston, D. S., Portfors, C. V., Kalcounis, M. C. & Mahlanga, Z. 1998 Bats and the loss of tree canopy in African woodlands. *Conserv. Biol.* **12**, 399–407.

Field, C. R. 1971 Elephant ecology in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.* **9**, 99–123.

Gates, S. 2002 Review of methodology of quantitative reviews using meta-analysis in ecology. *J. Anim. Ecol.* **71**, 547–557.

Gillson, L. 2004 Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity* **1**, 281–298.

Gillson, L. & Lindsay, K. 2003 Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. *Environmental Science & Policy* **6**, 411–419.

Glover, J. 1963 The elephant problem at Tsavo. *E. Afr. Wildl. J.* **1**, 30–39.

Goheen, J. R., Keesing, F., Allan, B. F., Ogada, D. & Ostfeld, R. S. 2004 Net effects of large mammals on Acacia seedling survival in an African savanna. *Ecology* **85**, 1555–1561.

Gurevitch, J. & Hedges, L. H. 1993 Meta-analysis: combining the results of independent experiments. In *Design and Analysis of Ecological Experiments* (ed. S. M. Scheiner & J. Gurevitch), pp. 378–398. New York: Chapman & Hall Inc.

Guy, P. R. 1981 Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *J. Appl. Ecol.* **18**, 507–519.

Hambler, C., Henderson, P. A. & Speight, M. R. 2005 Elephants, Ecology, and Non-equilibrium? *Science* **307**, 673–374.

Hanks, J., Densham, W. D., Smuts, G. L., Jooste, J. F., Joubert, S. C. J., le Roux, P. & Millstein, P. le S. 1981 Management of locally abundant mammals: the South African experience. In *Problems in management of locally abundant wild animals.* (ed. P. A. Jewell & S. Holt), pp. 21–55. New York: Academic Press.

Herremans, M. 1995 Effects of woodlands modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. Ecography **18**, 440–454.

Jachmann, H. & Bell, R. H. V. 1985 Utilization by elephants of the Brachystegia woodlands of the Kasungu National Park, Malawi. *Afr. J. Ecol.* **23**, 245–258.

Jachmann, H. & Croes, T. 1991 Effects of browsing by elephants on the Combretum/ Terminalia woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biol. Conserv.* **57**, 13–24.

Keesing, F. 1998 Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia* **116**, 381–389.

Laws, R. M. 1970 Elephants as agents of habitat and landscape change in East Africa. *Oikos* **21**, 1–15.

Leimu, R. & Koricheva, J. 2005 What determines the citation frequency of ecological papers? *Trends Ecol. Evol.* **20**, 28–32.

Leuthold, W. 1977 Changes in tree populations of Tsavo East National Park, Kenya. *E. Afr. Wildl. J.* **15**, 61–69.

Leuthold, W. 1996 Recovery of woody vegetation in Tsavo National Park, Kenya, 1970–94. *Afr. J. Ecol.* **34**, 101–112.

Levin, S. A. 1992 The problem of pattern and scale in ecology. *Ecology* **73**, 1943–1967.

Lewin, R. 1986 In ecology, change brings stability. *Science* **234**, 1071–1073.

Lewis, D. M. 1986 Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *Afr. J. Ecol.* **24**, 227–241.

Lock, J. M. 1993 Vegetation change in Queen Elizabeth National Park, Uganda: 1970-1988. *Afr. J. Ecol.* **31**, 106–117.

Lombard, A. T., Johnson, C. F., Cowling, R. M. & Pressey, R. L. 2001 Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biol. Conserv.* **102**, 191–203.

Macnab, J. 1985 Carrying capacity and related slippery shibboleths. *Wildl. Soc. Bull.* **13**, 403–410.

Mapaure, I. N. & Campbell, B. M. 2002 Changes in the miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *Afr. J. Ecol.* **40**, 212–219.

May, R. M. 1994 The effects of spatial scale on ecological questions and answers. In *Large-scale ecology and conservation biology.* (ed. P. J. Edwards, R. M. May & N. R. Webb), pp. 1–18. Oxford: Blackwell Science.

McGeoch, M. A., van Rensburg, B. J. & Botes, A. 2002 The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *J. Appl. Ecol.* **39**, 661–672.

Møller, A. P. & Jennions, M. D. 2001 Testing and adjusting for publication bias. *Trends Ecol. Evol.* **16**, 580–585.

Murtaugh, P. A. 2002 Journal quality, effect size, and publication bias in meta-analysis. *Ecology* **83**, 1162–1166.

Musgrave, M. K. & Compton, S. G. 1997 Effects of elephant damage to vegetation on the abundance of phytophagous insects. *Afr. J. Ecol.* **35**, 370–373.

Novellie, P. 1988 The impact of large herbivores on the grassveld in the Addo Elephant National Park. *S. Afr. J. Wildl. Res.* **18**, 6–10.

Noy-Meir, I. 1982 Stability of plant-herbivore models and possible applications to savanna. In *Ecology of Tropical Systems* (ed. B. J. Huntley & B. H. Walker), pp. 591–609. Berlin: Springer-Verlag.

Parker, A. H. & Witkowski, E. T. F. 1999 Long-term impacts of abundant perennial water provision for game on herbaceous vegetation in a semi-arid African savanna woodland. *J. Arid Environ.* **41**, 309–321.

Pellew, R. A. P. 1983 The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *Afr. J. Ecol.* **21**, 41–74.

Penzhorn, B. L., Robbertse, P. J. & Olivier, M. C. 1974 The influence of the African elephant on the vegetation of the Addo Elephant National Park. *Koedoe* **17**, 137–158.

Pienaar, U de V., van Wyk, P. & Fairall, N. 1966 An aerial census of elephant and buffalo in the Kruger National Park and the implications thereof on intended management schemes. *Koedoe* **9**, 1–10.

Quinn, G. R. & Keogh, M. J. 2002 *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Rosenthal, R. 1991 *Meta-analytic procedures for social research*. London: Sage Publications.

Shrader, A.M., Pimm, S.L. & van Aarde, R.J. (in review) The effect of rainfall on the survival of savanna elephants across southern Africa.

Skarpe, C., Aarrestad, P. A., Andreassen, H. P., Dhillion, S. S., Dimakatso, T., du Toit, J. T., Halley, D. J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G., Modise, D., Moe, S. R., Mojaphoko, R., Mosugelo, D., Motsumi, S., Neo-Mahupeleng, G., Ramotadima, M., Rutina, L., Sechele, L., Sejoe, T. B., Stokke, S., Swenson, J. E., Taolo, C., Vandewalle, M. & Wegge, P. 2004 The return of the giants: ecological effects of an increasing elephant population. *Ambio* **33**, 276–282.

Spinage, C. A. 1973 A review of ivory exploitation and elephant population trends in Africa. *E. Afr. Wildl. J.* 11, 281–289.

Stephenson, P. J. 2004 The future for elephants in Africa. In *Terrestrial Ecoregions of Africa and Madagascar: A Conservation Assessment* (ed. N. Burgess, J. D'Amico Hales, E. Underwood, E. Dinerstein, D. Olson, I. Itoua, J. Schipper, T. Ricketts & K. Newman), pp. 133–136. Washington DC: Island Press.

Stiles, D. 2004 The ivory trade and elephant conservation. *Environ. Conserv.* **31**, 309–321.

Thompson, P. J. 1975 The role of elephants, fire and other agents in the decline of a *Brachystegia boehmii* woodland. *J. Sth. Afr. Wildl. Manage. Assoc.* **5**, 11–18.

Tilman, D. 1989 Ecological experimentation: strengths and conceptional problems. In *Long-term studies in Ecology* (ed. G. E. Likens), pp. 136–157. New York: Springer.

Trollope, W. S. W., Trollope, L. A., Biggs, H. C., Pienaar, D. & Potgieter, A. L. F. 1998 Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe* **41**, 103–112.

Van Aarde, R., Whyte, I. & Pimm S. 1999 Culling and the dynamics of the Kruger National Park African elephant population. *Anim. Conserv.* **2**, 287–294.

Van de Vijver, C. A. D. M., Foley, C. A. & Olff, H. 1999 Changes in the woody component of an East African savanna during 25 years. *J. Trop. Ecol.* **15**, 545–564.

Van Wyk, P. & Fairall, N. 1969 The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* **12**, 57–89.

Underwood, A. J. 1997 *Experiments in Ecology. Their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press.

Walker, B. H., Ludwig, D., Holling, C. S. & Peterman, R. M. 1981 Stability of semi-arid savanna grazing systems. *J. Ecol.* **69**, 473–498.

Weatherhead, P. J. 1986 How unusual are unusual events? *Am. Nat.* **128**, 150–154.

Western, D., Pearl, M. C., Pimm, S. L., Walker, B., Atkinson, I. & Woodruff, S. 1989 An agenda for conservation action. In *Conservation for the twenty-first* *century* (ed. D. Western & M. C. Pearl), pp. 304–323. Oxford: Oxford University Press.

Western, D. & Maitumo, D. 2004 Woodland loss and restoration in a savanna park: a 20-year experiment. *Afr. J. Ecol.* **42**, 111–121.

Whyte, I. J. 2004 Ecological basis of the new elephant management policy for Kruger National Park and expected outcomes. *Pachyderm* **36**, 99–108.

Whyte, I., van Aarde, R. & Pimm, S. L. 1999 Managing the elephants of Kruger National Park. *Anim. Conserv.* **1**, 77–83.

Whyte, I. J., van Aarde, R. J. & Pimm, S. L. 2003 Kruger elephant population: its size and consequences for ecosystem heterogeneity. *In The Kruger experience: ecology and management of savanna heterogeneity* (ed. J. T. du Toit, K. H. Rogers, and H. C. Biggs), pp. 332–348. Washington: Island Press.

Wing, L. D. & Buss, I. O. 1970 Elephants and forests. *Wildl. Monogr.* **19**, 1–92.

Wiseman, R., Page, B. R. & O'Connor, T. G. 2004 Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *S. Afr. J. Wildl. Res.* **34**, 25–37.