A Meta-Analysis of the Impact of African Elephants on Savanna Vegetation

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ABSTRACT Large herbivores such as elephants (*Loxodonta africana*) apparently have a negative impact on woody vegetation at moderate to high population densities. The confounding effects that fire, drought, and management history have may complicate assignment of such impacts to herbivory. We reviewed 238 studies published over 45 years and conducted a meta-analysis based on 21 studies that provided sufficient information on response of woody vegetation to elephants. We considered size and duration of studies, elephant densities, rainfall, fences, and study outcomes in our analysis. We detected a disproportionate citation of 20 published studies in our database, 15 of which concluded that woody vegetation responded negatively to elephants. Our analysis showed that high elephant densities had a negative effect on woody vegetation but that rainfall and presence of fences influenced these effects. In arid savannas, woody vegetation always responded negatively to elephants. In transitional savannas, an increase in elephant densities did not influence woody vegetation response. In mesic savannas, negative responses of woody vegetation increased when elephants occurred at higher densities, whereas elephants confined by fences also had more negative effects on woody plants than elephants that were not confined. Our analysis suggested that rainfall and fences influenced elephant density related impact and that research results were often site-specific. Local environmental conditions and site-specific objectives should be considered when developing management actions to curb elephant impacts on woody vegetation. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):892–899; 2008)

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Large herbivores, such as the African elephant (*Loxodonta africana*), may transform savanna landscapes especially where their movements are confined (Dublin et al. 1990, Cumming et al. 1997, Trollope et al. 1998, Western and Maitumo 2004, van Aarde et al. 2006). Such changes in the landscape may induce loss of local species, which Caughley (1976) and others referred to as the elephant problem (Western 2006). In some instances, this problem motivated culling to reduce elephant numbers and their impact on other species in several sub-Saharan conservation areas (Feely 1965, Pienaar et al. 1966, Astle 1971, Hanks et al. 1981, Whyte et al. 1998).

The response of vegetation to elephants is difficult to interpret as it may be influenced by drought, fire, disease, other herbivores, and trampling (Gillson and Lindsay 2003, Skarpe et al. 2004, Wiseman et al. 2004), all of which independently or in combination could transform woodlands into grasslands (Walker et al. 1981, Illius and O'Connor 1999, Gillson 2004). In the absence of elephants or where they occur at low densities, savannas may also be transformed from woodlands to grasslands, but the confounding role of species other than elephants complicate the expected response of woodlands to reduced elephant numbers (Dublin et al. 1990, Pickett et al. 2003).

There are clear cases, however, of the impacts of elephant browsing in natural and planned experiments. The die-off of elephants in Tsavo National Park in Kenya was followed by a recovery of woodlands typical of the region (Leuthold 1996). Similarly, an increase of woody species on exclusion plots maintained in Amboseli National Park clearly reflects the resilience of this ecosystem (Western and Maitumo 2004). We could not find studies that assessed how vegetation responded to elephant numbers that were reduced by culling per se, a common management prescription to reduce loss of woody vegetation (see van Aarde et al. 2006 and references therein).

Managing the alleged impact of elephants is riddled with ethical, political, economic, and ecological implications and is often motivated by information from studies carried out elsewhere (Bulte et al. 2004, Hambler et al. 2005). Inferences made from elephant impact studies could be complicated and confounded by poor replication, lack of suitable controls, confounding environmental factors, and response variables that are incorrectly assigned to elephants. Rigorous scientific information on which to evaluate elephant impact and to motivate their management is lacking (Owen-Smith et al. 2006, van Aarde and Jackson 2007). This lack of information complicates management decisions, especially those presumed to be founded on scientific-based decision processes (Gordon et al. 2004, Pullin et al. 2004).

We reviewed the present literature on the impact of elephants on vegetation and used meta-analysis to evaluate the findings of independent studies, which allowed us to reanalyze and compare published results from impact studies conducted across the distributional range of elephants and under varying climatic and management conditions (Cooper and Hedges 1994, Gates 2002). We assessed 1) which studies were most influential in shaping current opinion on managing the impact of elephants, 2) how study design and its duration influenced conclusions, and 3) how elephant density, savanna type (based on rainfall), and confinement influenced response of woody vegetation to elephants in

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Table 1. The 20 most-cited studies, in order of their ranked scores, that investigated effect of elephants on woody vegetation.

Study	No. of papers that cited the study	Ranked scores *I*
Laws 1970	62	38.0
Caughley 1976	58	34.7
Buechner and Dawkins 1961	45	26.1
Dublin et al. 1990	40	25.4
Anderson and Walker 1974	34	24.9
van Wyk and Fairall 1969	31	21.3
Pellew 1983	34	21.0
Croze 1974	32	20.1
Jachmann and Bell 1985	27	17.8
Barnes 1983	28	16.4
Wing and Buss 1970	30	15.9
Glover 1963	19	9.5
Jachmann and Croes 1991	15	9.3
Cumming et al. 1997	17	9.2
Field 1971	20	9.1
Thompson 1975	13	8.9
Ben-Shahar 1993	17	8.3
Leuthold 1977	15	8.0
Ben-Shahar 1996	14	8.0
Guy 1981	12	7.5

African savannas. We define elephant effect as the response of woody plants to elephants as recorded by authors.

METHODS

Data Collection

We consulted the *African Elephant Bibliography*, *Biological Abstracts*, *Institute for Scientific Information Web of Knowledge*, *Science Citation Index*, *Wildlife Ecology Studies Worldwide*, and the *Zoological Records* electronic databases using "elephants," "trees," "vegetation," "woody plants," "damage," or "impact" as keywords in our search. We only considered studies that were written in English and published prior to 2006. As studies often report results in >1 medium we reduced dependence and bias by excluding symposium presentations and abstracts, newsletters, books and chapters, postgraduate theses, and internal reports. We also did not consider studies conducted in zoological gardens or studies that reported on species exotic to African savannas.

We found 238 peer-reviewed studies that met the above criteria. For all of these studies, we documented year of publication, study site, duration of study (yr), and number of replicates and controls. To determine which studies in our database were most frequently cited, we cross-referenced them with one another by listing for each study all references that were also in our database. We also grouped each study into a negative, positive, and no response category. Here we considered all responses that indicated reductions in numbers, density, biomass, cover, species richness, or any increase in damage by elephants, and bush thickening or encroachment, as negative and grouped these in the negative response category. We regarded the opposite response as positive and all of these were distinguished from studies that showed no response. We also noted the authors' inference on elephant management and distinguished between studies where authors recommended management from those where authors did not.

From the 238 studies, we included only those that reported number of replicates and provided measures of variability around mean values in our meta-analysis (Gurevitch and Hedges 1993). For these studies, we obtained estimates of elephant densities from published and unpublished sources for the time as close as possible to the year of investigation. For long-term studies, we used the highest value for elephant density during the study. We obtained annual rainfall values for the study sites from Hijmans et al. (2005). Based on these and following the

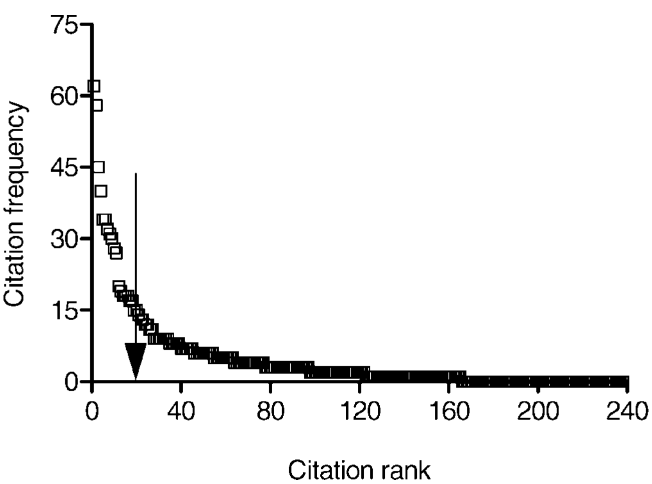

Figure 1. Citing frequency (of studies of the effect of elephants on woody vegetation) as a function of rank, where rank is determined by the number of times a study was cited, corrected for its age. Studies to the left of the arrow account for 50% of the number of the cross-references between the 238 publications included in our analysis.

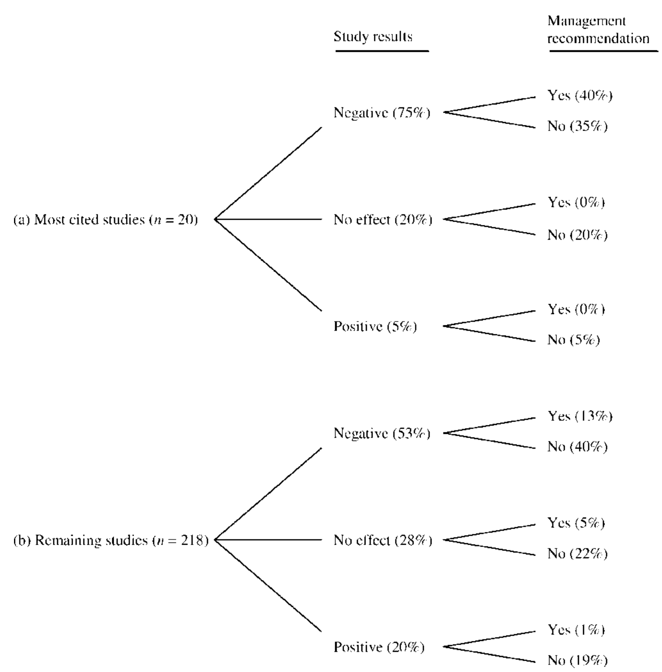

Figure 2. A chart that distinguishes study results on impact of elephants on woody vegetation from management recommendations. Study results distinguish between negative, positive, or no effect. Management recommendations emphasize reduction in elephant numbers.

Table 2. Name of the study site and country, rainfall, and savanna type of the 21 studies (of the effect of elephants on woody vegetation) that published sufficient information for our meta-analysis, with elephant densities at the time of study.

Study	Study site and country	Rainfall (mm/yr)	Savanna type	Elephant densities (no./km^2)
Augustine and McNaughton 2004	Mpala Research Centre, Kenya	575	Transitional	0.35
Barnes 2001	Chobe National Park, Botswana	506	Arid	2.42
Birkett 2002	Sweetwaters Game Reserve, Kenya	798	Mesic	1.10
Birkett and Stevens-Wood 2005	Sweetwaters Game Reserve, Kenya	798	Mesic	1.20
Botha et al. 2002	Kruger National Park, South Africa	579	Transitional	0.53
Buechner and Dawkins 1961	Murchison Falls National Park, Uganda	1,166	Mesic	3.49
Chapman et al. 1997	Kibale National Park, Uganda	1,111	Mesic	0.10
Cumming et al. 1997	Mana Pools, Zimbabwe	714	Transitional	1.70
Eckhardt et al. 2000	Kruger National Park, South Africa	579	Transitional	0.44
Goheen et al. 2004	Mpala Research Centre, Kenya	575	Transitional	0.35
Guy 1981	Sengwa Wildlife Research Area, Zimbabwe	600	Transitional	1.80
Herremans 1995	Chobe/Moremi, Botswana	506	Arid	2.00
Jachmann and Croes 1991	Nazinga Game Ranch, Burkina Faso	934	Mesic	2.50
Keesing 1998	Mpala Research Centre, Kenya	575	Transitional	0.35
Leuthold 1977	Tsavo (Royal) National Park, Kenya	706	Transitional	0.49
Lombard et al. 2001	Addo Elephant National Park, South Africa	376	Arid	2.40
Loth et al. 2005	Lake Manyara National Park, Tanzania	624	Transitional	0.01
Musgrave and Compton 1997	Addo Elephant National Park, South Africa	376	Arid	2.25
Novellie 1988	Addo Elephant National Park, South Africa	376	Arid	1.36
Western and Maitumo 2004	Amboseli Game Reserve, Kenya	467	Arid	0.20
Wiseman et al. 2004	Ithala Game Reserve, South Africa	790	Mesic	0.19

division of savannas proposed by Sankaran et al. (2005), we classified each study site as arid (<516 mm/yr), transitional (516–784 mm/yr), or mesic (>784 mm/yr) savannas.

Data Analysis

We calculated a ranking index I for each study in our database to determine the most influential studies in our database

$$I = C_i\left[A_i \Big/ \bar{a}_{i-j}\right]^{-1} \qquad (1)$$

where C_i = number of times the ith study was cited by others in our database, A_i = age of the ith study, and $\bar{a}_{i-j}$ = mean age difference between the ith study and all the jth studies that subsequently cited the former. The highest ranked studies were those cited most frequently and for the longest time following publication.

We used Cohen's d to calculate response of different plant variables to elephants (Gurevitch and Hedges 1993). Studies use different variables (e.g., counts, growth rates, and species richness) to measure elephant impact. Cohen's d is a dimensionless statistic that allows for comparing these variables between studies. For experimental studies (with elephant exclusion plots), Cohen's d was the difference in the response variable between treatment (elephant presence) and control (elephant absence), divided by the pooled average standard deviation. For each of the observational studies (those without elephant exclusion plots), which relied on data from time series, we calculated Cohen's d by dividing the pooled average standard deviation by the difference between the start and end values for each of the response variables used in the different studies.

We first explored how the number of replicates per study, study duration, and elephant densities influenced effect sizes. We then investigated how elephant densities under different management regimes (fenced and unfenced parks) may have affected response of vegetation (a measure of elephant impact) in each of the 3 savanna types.

RESULTS

The 238 peer-reviewed studies in our database were published in 60 journals from 1960 to 2005. Number of studies published per year increased over the 45 years and covered 73 study sites across sub-Saharan Africa. Most studies (72%) lasted <5 years and only 23% compared vegetation of areas with and without elephants.

The 238 studies cited one of the other studies on 1,117 occasions. Half of these cross-references consisted of the 20 most frequently cited studies (Table 1); the other 218 studies made up the remaining cross-references (Fig. 1). Of the 20 most frequently cited studies, 15 concluded that elephants had a negative impact on the variables considered (Fig. 2). Authors of 8 of these 15 studies recommended management of elephants (Fig. 2), which contrasted with opinions expressed by authors from the remaining publications. In the remaining 218 publications, 81% did not make any recommendations on managing elephant impact, although 53% of them had concluded a negative response of the variables (Fig. 2). Therefore, only 25% of the 238 studies recommended management intervention based on their conclusions that elephants had a negative impact on woody vegetation.

Only 21 (n) of the 238 studies published information on variables adequate for inclusion in our meta-analyses (Table 2). These 21 studies covered 14 sites, but studies from the same site were conducted independently (Table 2). Average rainfall for each of the study sites ranged between 376 mm and 1,200 mm rain per year and elephant densities ranged from <0.1 elephants/km^2 to 3.5 elephants/km^2 during their study periods.

These 21 studies included 194 (*k*) woody vegetation responses and we treated these as separate observations. From these we noted 87 positive and 98 negative vegetation responses (Fig. 3a–c). Increased replication did not influence vegetation responses (Fig. 3a). Long-term studies (>20 yr) from unfenced areas demonstrated more positive (65%) than negative (35%) responses, whereas 70% of responses from long-term studies in fenced areas were negative (Fig. 3b). Number of variables per study varied considerably and ranged from species-specific to general vegetation variables. We grouped the different response variables and separated count and structural measurements from the calculated population rates and community indices (Fig. 3c). Responses of vegetation were both negative and positive at low elephant densities but only negative at elephant densities >2 elephants/km^2 (Fig. 3c). However, responses also varied between savanna types and differed in fenced and unfenced areas.

Elephant densities in the arid savannas (<516 mm rain/yr) varied greatly and reached values of 2.4 elephants/km^2 in both fenced and unfenced sites. Responses of vegetation variables in arid savannas were negative at all sites ($n = 6$ studies; Fig. 4a). Elephants in transitional savannas (516–784 mm rain/yr) occurred at densities between <0.1 elephants/km^2 and 0.6 elephants/km^2 in fenced sites and up to 1.8 elephants/km^2 in unfenced sites. Effect sizes did not respond to density in unfenced sites ($n = 9$ studies; Fig. 4b). Our information on studies for fenced elephants at varying densities in transitional savannas was limited and prevented further analysis. In mesic savannas (>784 mm rain/yr) elephant densities ranged from 0.2 elephants/km^2 to 1.2 elephants/km^2 and from 0.1 elephants/km^2 to 3.5 elephants/km^2 in fenced and unfenced sites, respectively. Both fenced and unfenced areas were associated with positive and negative vegetation responses at low elephant densities and negative responses with an increase in elephant densities ($n = 6$ studies; Fig. 4c). Negative vegetation responses for fenced areas were recorded at lower elephant densities than for unfenced areas.

DISCUSSION

We detected a disproportionate citation of only a few published studies on elephant impact, with the majority of these cited studies concluding that woody vegetation responded negatively to elephants. Our analyses also showed that high elephant densities had a negative effect on woody vegetation but that rainfall and presence of fences influenced these negative effects. We challenge some of the existing

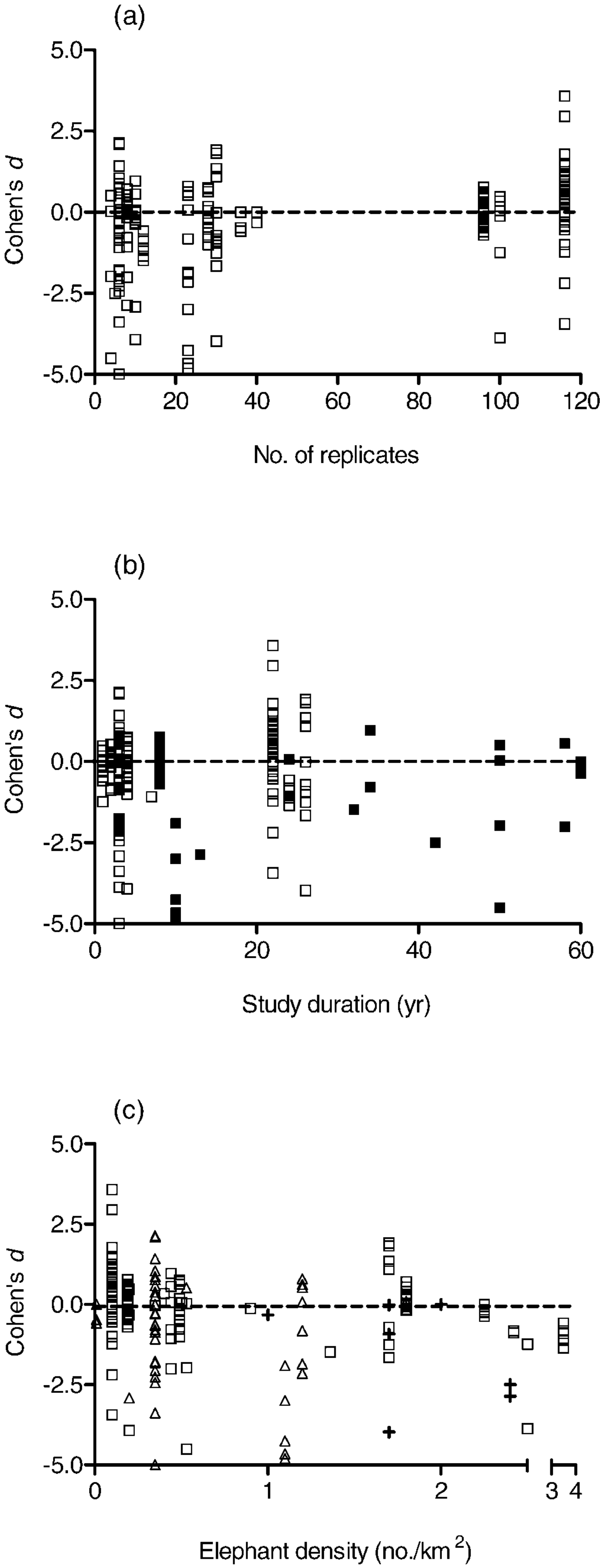

Figure 3. Cohen's *d* (an expression of effect of elephants on woody vegetation) as a function of (a) the number of replicates, (b) study duration, and (c) elephant density. Symbols indicate the 194 extracted response variables from the 21 studies we used in our analysis. Symbols below dashed lines represent cases where elephants had a negative effect, whereas symbols
←
above the line denote positive effects. Open and closed symbols in (b) denote values from unfenced and fenced study areas, respectively. Symbols in (c) represent 3 groups of variables; squares indicate count and structural measurements; triangles represent the calculated rates for growth, recruitment, mortality, and primary productivity; and stars represent diversity and species richness indices.

perceptions on the impact that elephants may have on woody plants in African savannas.

Elephant management is contentious and often fueled by interpretation of studies designed to assess elephant impact on woody vegetation (van Aarde et al. 2006, van Aarde and Jackson 2007). There are several reasons why impact is difficult to assess. From the literature we know that elephants can induce structural changes in woody vegetation, and it is not surprising that some authors characterize such changes as unacceptable (Pienaar et al. 1966, Astle 1971, Cumming et al. 1997). However, we also know that climatic and edaphic factors may influence elephant impact and that savannas are dynamic (Gillson 2004). Managing elephants to limit impact is not a universal recommendation (see Gillson and Lindsay 2003, van Aarde and Jackson 2007).

Formal interest on the impact of elephants on other species has been increasing since 1960. For the last 45 years, a few publications on elephant impact (20 of 238) dominated interpretation of research findings; 50% of scientific papers on elephant impact that were published between 1960 and 2005 refer to these 20 papers. Continual reference to these 20 papers may have introduced a bias towards concluding that elephants have a negative impact on woody vegetation, especially when considering that 15 of the 20 frequently referred to papers shared this conclusion. Citation bias is not unknown in science and may be explained by direction and extent of differences between control and treatment values, significance in their findings, journal quality, article length, number of authors per article, and institutional prestige (Møller and Jennions 2001, Gates 2002, Murtaugh 2002, Leimu and Koricheva 2005). Based on our analyses it seems that citation bias and author opinion may have influenced interpretation of elephant impact when based on inferences from vegetation response variables. Moreover, studies on elephant impact are also more likely to be conducted at sites where researchers can show that elephants have an impact or may focus on variables that are likely to respond to such impact.

Most authors in our database did not express an opinion on elephant management. Wildlife agencies often separate their science and management departments, or people that conduct studies from outside these agencies are reluctant to jeopardize future research opportunities by publishing management opinions. In addition, most studies have little success in separating elephant impact from those caused by other herbivores and events such as fire, soil characteristics, and drought and, therefore, confine interpretation of →

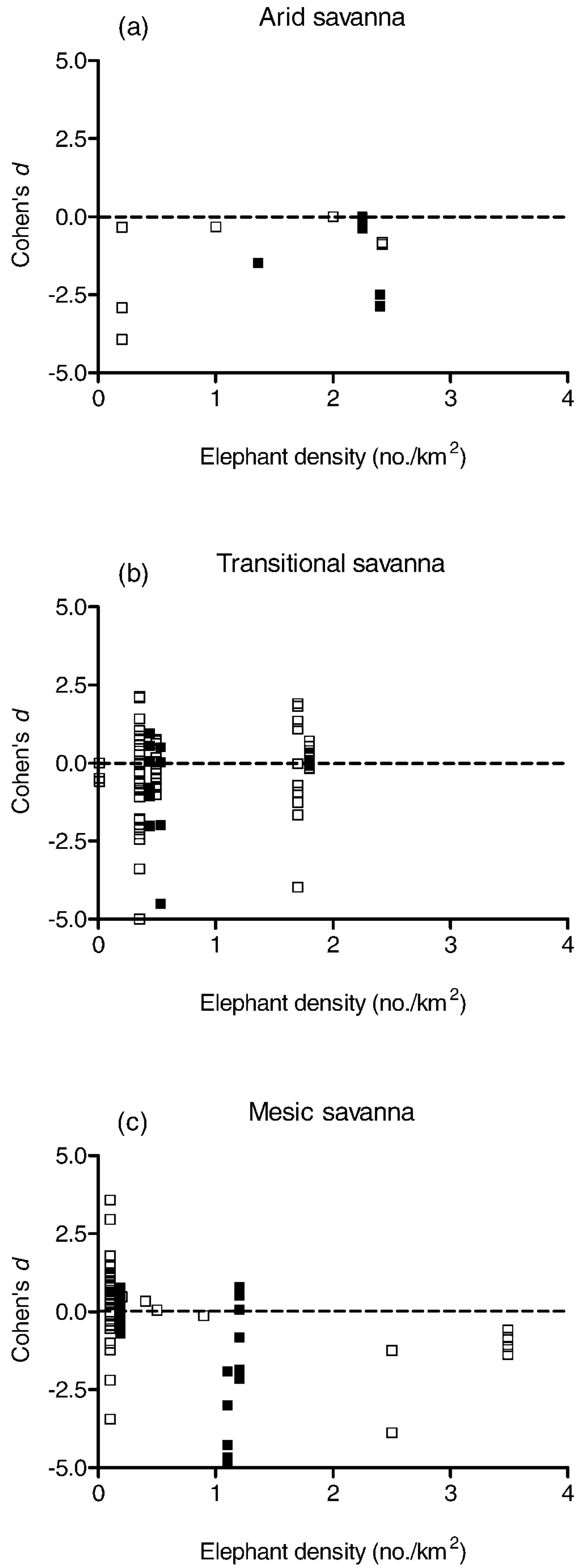

Figure 4. Cohen's *d* (an expression of effect of elephants on woody vegetation) as a function of elephant density for unfenced elephant populations (open symbols) and fenced populations (closed symbols) in (a) arid, (b) transitional, and (c) mesic savannas. Symbols below dashed lines represent cases where elephants had a negative effect, whereas symbols above lines denote positive effects.

research results and impact of elephants on savannas (Rutina et al. 2005, Guldemond and van Aarde 2007).

Only 21 of the studies in our database met the criteria for inclusion in the meta-analysis. These 21 studies came from 14 sites across sub-Saharan Africa but were conducted independently and published by different authorities (refer to Table 2). These studies supported the notion that elephants have an effect on woody vegetation and predictably, at relatively high elephant densities the negative effect was noted more often than at low densities.

Study duration explained little variation in effect sizes for short-term studies. However, long-term studies (>20 yr) from unfenced areas yielded both positive and negative vegetation responses. At sites where elephant movements were constrained by fences, most vegetation responses were negative. This may have consequences for evaluation of impact because long-term variation in elephant numbers may negate their impact on vegetation in unfenced areas (Caughley 1976, Dublin 1991, Lock 1993, Leuthold 1996, van Aarde and Jackson 2007).

Our analysis also provides support for the argument that rainfall may be a determinant of herbivore impacts on vegetation (Sankaran et al. 2005). For example, vegetation response to elephants was negative at all densities in arid savannas, but in transitional savannas elephant density played no distinct role. In mesic savannas negative vegetation responses increased with elephant density. Our analysis, therefore, supports the conclusion of Illius and O'Connor (1999) that herbivores influence arid savannas, although Sankaran et al. (2005) maintained that prevailing environmental conditions, rather than herbivores, shape arid woodlands. For mesic savannas, our assessment agrees with Sankaran et al. (2005) that disturbances, such as fire and herbivory, influence woodlands.

What does all of this mean? We aimed to summarize and evaluate the present literature on the impact of elephants on vegetation. We are somewhat clearer on the apparent impact that elephants have for vegetation based on covariates of measured responses of vegetation, elephant densities, and aspects of management. Much of the apparent impact relates to the short-term influence that elephant browsing has for individual plants, which happens to be the focus of most research. This does not say that elephants as such are responsible for higher scale effects on vegetation, and such effects seem to be modulated by rainfall and driven by local elephant densities and their confinement by fences (Baxter and Getz 2005). However, our analyses were based on too few studies to make broad generalizations on impact of elephants on vegetation, simply because only a few studies met our criteria for inclusion in a meta-analysis. The lack of sufficient published information is not unique to elephant studies, as many papers published in foremost journals do not meet criteria for later reanalyses (Anderson et al. 2001).

MANAGEMENT IMPLICATIONS

Response of vegetation to elephants in transitional savannas, where most of sub-Saharan elephants live and where need to manage seems most intense, ranged from negative to positive at different elephant densities. Our analysis also suggested that fencing influenced vegetation responses, even at relatively low elephant densities. Management that aims at reducing these responses may, therefore, have to focus on altering elephant confinement rather than density. We further suggest that impact studies should be planned and reported in such a way that evidence-based management decisions (e.g., Pullin et al. 2004, Newton et al. 2007) can be driven by an unbiased assessment and rigorous experimental protocols (such as in Young et al. 1998).

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