Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-term data

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Abstract

In some African protected areas, elephant populations have reached high densities causing concern about their influence on other forms of biodiversity, and in particular, other large herbivores. This has led to a debate whether management of elephant populations might need to be implemented. Surprisingly, few studies have focused on the influence of elephants on other herbivores and the existing results are conflicting. We investigated such influence in Hwange National Park, Zimbabwe, where elephants were culled and maintained at low density up to 1986, and have more than doubled since then, thus providing the opportunity to explore their possible influence on other herbivore species. Trends of different herbivore populations were obtained using long-term waterhole census data, with these results also being correlated to changes in dry season rainfall, as another fundamental determinant of herbivore population fluctuations. While our study did not allow us to properly disentangle the role of elephants and rainfall, it provided valuable insights. For five out of the 13 herbivore species studied, the population increased between 1973 and 1986 (high dry season rainfall; relatively low elephant abundance), then decreased between 1987 and 1995 (extremely low dry season rainfall; increase in the elephant population), and finally have increased since 1996 (high dry season rainfall; high elephant abundance). These results are consistent with an important role of dry season rainfall on herbivore population dynamics. Additionally, for four other species, the population increased between 1973 and 1986 and has decreased since then. As most herbivore declines occurred simultaneously with increase in the elephant population in the 1987–1995 period, and with the recent increase in most populations happening at a lower rate than the 1973–1985 period, our results suggest the possible existence of a negative influence of high elephant densities on other herbivores. We discuss what the possible underlying mechanisms can be and how to investigate them.

Introduction

Many areas throughout southern Africa have experienced increases in their elephant *Loxodonta africana* populations due to successful conservation efforts or culling cessation, and consequently, some protected elephant populations have reached unprecedented levels of elephant densities (Blanc *et al.*, 2005). This situation is exacerbated by the compression of elephant population ranges due to human extension (Parker & Graham, 1989). In such areas, the potential impacts of elephants on other forms of biodiversity have been of great concern to managers and accordingly, the need to control their populations has been suggested and widely debated (e.g. Butler, 1998; Whyte, van Aarde & Pimm, 1998; van Aarde & Jackson, 2007).

Elephants are megaherbivores (herbivores weighting over 1000 kg) that need to harvest and process a large amount of vegetation (Owen-Smith, 1988), and consequently may impact on ecological niches of other animals through the modification of habitats and changes in the abundance and structure of the food resources. They have been considered as keystone competitors (Paine, 1969; Bond, 1993), and as ecological engineers, which by changing habitat structure, may directly or indirectly modulate the availability of resources to other organisms, and also mediate competition and predation relationships (Jones, Lawton & Shachak, 1994). Because of the potential strength of their interactions, elephants not only hold the key to play more fundamental roles than other species in the complex network of interspecific interactions (Paine, 1992), but strongly affect

community structure and abundance, hence ecosystem functions (Duffy *et al.*, 2007). It is therefore crucial to investigate the potential effect of elephants on other species, especially in ecosystems where they are very abundant and where management decisions might need to be taken.

Many studies have focused on the impact of elephants on vegetation (e.g. Cumming, 1982; Holdo, 2003; Baxter & Getz, 2005), but very few have studied their impact on animal biodiversity (e.g. Herremans, 1995; Cumming *et al.*, 1997; Fenton *et al.*, 1998). Studies investigating the influence of elephants on other large herbivores are few and provide contrasting results. Some have suggested a competitive influence of elephants on other herbivore species, and more specifically on browsers. For example, a negative correlation between the elephant biomass and the browser biomass seems to exist across ecosystems (Fritz *et al.*, 2002), and in Tsavo National Park, Kenya, the growth of elephant populations in the 1960s was followed by a decrease in browser populations (Parker, 1983). In Hluhluwe Game Reserve, South Africa, the growth in browser populations was attributed to the extermination of elephants (Owen-Smith, 1989). The suggested prime mechanism underlying the observed patterns was a change in habitat conditions. Conversely, some studies have suggested facilitation between elephants and browsers. In Chobe National Park, Botswana, the increase in the elephant population has been correlated to an increase in some populations for which medium-term facilitation has been suggested, as elephants may generate more browse resources through coppicing (Skarpe *et al.*, 2000; Rutina, Moe & Swenson, 2005; Makhabu, Skarpe & Hytteborn, 2006). The reasons why plants react differently to elephant herbivory are still not understood because of the diversity of factors that may affect elephant–plant interactions such as elephant foraging ecology, attributes of plants, tolerance to herbivory, and populations, and historical changes in ecosystems (Augustine & McNaughton, 1998; O'Connor, Goodman & Clegg, 2007). Understanding the role of elephants in their ecosystems is thus challenging and needs further investigation.

For natural large mammal communities, experiments are very difficult to carry out, and documented drastic population changes over time can be used to investigate competition or facilitation (see Sinclair, 1995). In protected areas, management interventions on populations of perceived 'over-abundant species' have often been justified by the possible negative effects on other species or on fundamental ecological processes. However, the scientific ecological basis for these interventions has not always been clearly understood nor taken into account (Chase, 1986; Gordon, Hester & Festa-Bianchet, 2004). Nevertheless, these interventions have facilitated better understanding of ecosystem functioning, and in particular, ecological processes that determine the structure and functioning of communities, so crucial to ecology, conservation and management. Consequently, where elephant numbers have experienced radical change, the hypothesis that elephant abundance can change the structure of herbivore communities can be investigated using long-term data on the abundance of different herbi-

vore populations at the same site. Few places allow such long-term trends analyses, and even fewer where elephants have experienced major changes in numbers or distribution. In this paper, we test for the influence of African elephants on the structure of herbivore communities in a southern African savanna using a long-term dataset from Hwange National Park (HNP), Zimbabwe. The elephant population of HNP was culled and maintained stable up to 1986 and no management action has been taken since then resulting in a major increase of the population, from *c.* 15 000 to over 30 000 elephants, that is from one to over two individuals per km^2 (Chamaillé-Jammes *et al.*, 2008). This created a unique opportunity to assess the influence of elephants on other herbivores.

As fluctuations in population abundance can be driven by climatic variation influencing resource availability (Saether, 1997; Post & Stenseth, 1999), assessing the influence of elephants on other herbivore populations cannot be done without taking into account rainfall variability. In particular, dry season rainfall variability seems to have a fundamental influence on the dynamics of herbivore populations in semi-arid savannas (Mduma, Sinclair & Hilborn, 1999; Ogutu & Owen-Smith, 2003; Dunham, Robertson & Grant, 2004). To rigorously tease apart the independent and interacting effects of elephants and dry season rainfall in driving herbivore population dynamics would require designed experiments that are logistically not possible. Consequently, through the investigation of long-term trends, the present study aims to provide valuable insights into the influence of elephant numbers and rainfall patterns on herbivore population trends. If herbivore population size increases in periods of high rainfall and decreases in periods of low rainfall, rainfall will be interpreted as the main factor driving large herbivore populations. If herbivore population size increases or is stable in periods of low elephant abundance and decreases in periods of high elephant abundance, elephant abundance will be interpreted as the main factor influencing herbivore populations negatively (i.e. competition suggested). Conversely, if herbivore population size decreases or is stable in periods of low elephant abundance and increases in periods of high elephant abundance, elephant abundance will be interpreted as the main factor influencing herbivore populations positively (i.e. facilitation suggested). If herbivore populations exhibit a continuous long-term trend, unaffected by the change in elephant numbers or rainfall, none of these two factors can be interpreted as a driver of herbivore populations.

Materials and methods

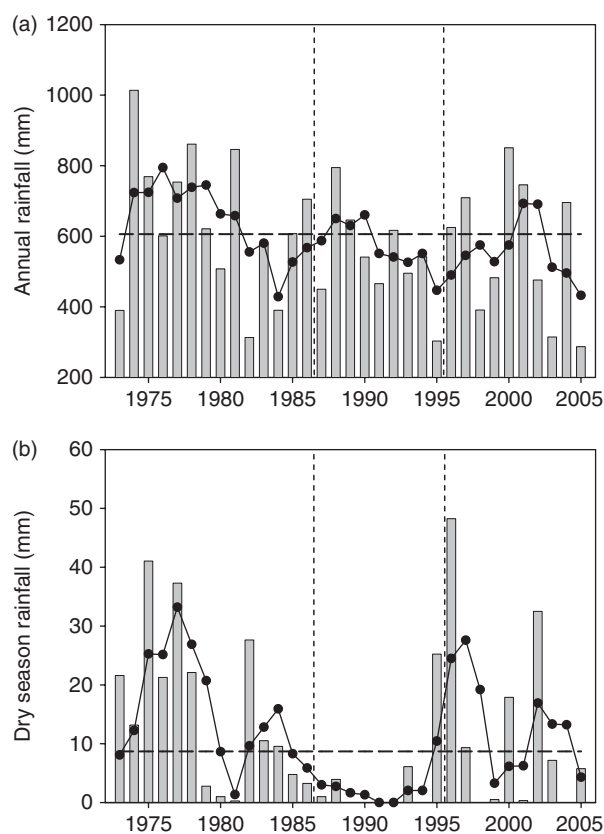### Study area and environmental data

HNP covers *c.* 15 000 km^2 of semi-arid savanna in the northwestern Zimbabwe (19°00′S, 26°30′E). Altitude varies from 800 to 1100 m. The vegetation of HNP is primarily woodland savanna. Most rain falling between October and April, the annual rainfall is defined as the sum of the rainfall from October to September and the dry season rainfall as the sum

from May to September. Rainfall data have been recorded daily since 1928 in three climatic stations located in the northern part of the park. From these data, we represented the annual and the dry season rainfall averaged over the three climatic stations for the past 30 years (Fig. 1). The long-term (1928–2005) annual average is 606 mm (Fig. 1a) and the long-term dry season average is 8.7 mm (Fig. 1b). Annual and dry season rainfall are characterized by a very high variability (CV ≈ 30 and 170%, respectively). The surface water available to animals is largely dependent on rainwater, collected in natural depressions that are generally dry at the end of the dry season, and artificial permanent dams or waterholes, which are pumped during the dry season. In this paper, we studied the northern part of the park, which covers *c*. 4000 km^2 and hosts most herbivores in the dry season because artificial waterholes are located in this area.

Long-term dataset

In HNP, information from both aerial censuses and waterhole censuses were available. Aerial census was conducted


Figure 1 Trends in (a) annual rainfall and (b) dry season rainfall over 32 years in the northern part of Hwange National Park. Bars indicate annual records and solid lines the 3-year running means of the preceding conditions. The horizontal dotted line represents the long-term average. The vertical dotted lines separate the three study periods (see text for details).

yearly from 1980 to 2001, except in 2000, and data were obtained from National Parks and WWF aerial survey reports. These censuses followed standard procedures recommended in Norton-Griffiths (1978) and were analysed using Jolly's method (1969). Information from waterhole censuses were obtained from the Wildlife Environment Zimbabwe that has monitored herbivore populations from waterholes since 1973, with missing data for 1974, 1976–1981 and 1983. The 1997 data from waterhole census were not included in the analyses because exceptional rain fell during the count, which provided an abnormal situation where only few animals came to drink. The waterhole monitoring consisted of recording the number of animals coming to drink in yearly 24-h counts that occurred at the end of the dry season during the full moon. Although aerial census is a standard technique to monitor wildlife, and waterhole census is less common, the specific characteristic of water distribution in HNP provides a unique opportunity to count animals around artificial waterholes. In addition, aerial technique is biased towards larger species (Jachmann, 2002) with waterhole censuses providing data on even the smallest herbivores. The waterhole monitoring also presents the advantage of being the longest dataset available.

Relevance of waterhole count data to assess population trends

With waterhole counts, the effect of rainfall on surface water availability can affect numbers of animal drinking, thus creating inter-year variance. Individuals could vary both the number of waterholes visited and visitation rates, which may affect waterhole count accuracy. However, these specific biases are likely to be the same each year. Hence if waterhole counts cannot be considered as total counts, long-term trends are very likely to reflect the actual patterns of abundance changes in herbivore populations. To test whether the trends stemmed from waterhole censuses were similar to those stemmed from aerial censuses, while accounting for the effect of rainfall on variation in animal counts at waterholes, we focused on elephants for which aerial census data are considered reliable (Jachmann, 2002) and regressed the number of elephants counted at waterholes on the number of elephants counted during aerial censuses for the northern part of HNP, with *yrain* (*yrain* was calculated as the log$_{10}$ transformation of the annual rainfall in millimetres for the closest climatic station) as a covariate.

Description of three contrasted periods

Because elephants and other species disperse as water availability increases, and thus present similar responses to annual rainfall variability (i.e. the drier a year, the more elephants are counted at waterholes and the more other herbivores are also counted), it prevented us from using the number of elephants counted at waterholes as an explanatory variable for the trends in other species. In addition, the methodological bias linked to the fact that animals disperse as annual rainfall increases is too important to take rainfall
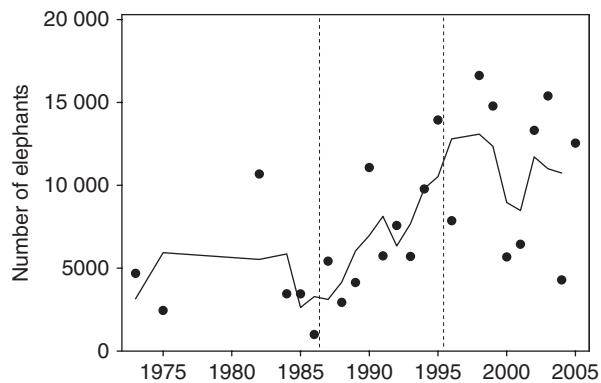
Figure 2 Trends in the total number of elephants counted at waterholes in the northern part of Hwange National Park. The line represents the changes in the 3-year running means (mean of years $n-1$, n and $n+1$). The vertical dotted lines separate the three study periods (see text for details).

data into account in the analyses for demographic purposes. Consequently, it was impossible to carry out a multiple regression approach with elephant abundance and rainfall as independent variables. We therefore chose to explore the possible influence of elephants and rainfall indirectly through the study of three contrasting periods: period 1 (1973–1986), period 2 (1987–1995) and period 3 (1996–2005). The periods were defined based on the changes in elephant abundance (Fig. 2) and on the rainfall patterns (Fig. 1). We first contrasted a period up to 1986 when elephant population was regulated and remained stable, from a period when no elephant population reduction was undertaken and therefore when elephant population increased (Fig. 2). This increase can be divided into two phases: a period between 1987 and 1995 when the number of elephants increased continuously and a period from 1996 when the population seems to have stabilized (Fig. 2). These trends are similar to those showed in another study based on aerial data only (Chamaillé-Jammes *et al.*, 2008). The three periods therefore correspond to three different elephant abundance levels (mean elephant number $\pm$ SE $= 3911 \pm 1865$ for period 1; 7362 ± 1809 for period 2; $10\,767 \pm 1279$ for period 3; Kruskall–Wallis: $\chi^2_{1,2} = 11.18$; $P = 0.0037$). Regarding rainfall patterns, annual rainfall does not show any particular trend (Fig. 1a; mean annual rainfall $\pm$ SE $= 640.1 \pm 76.1$ for period 1; 539.4 ± 84.5 for period 2; 557.8 ± 58.2 for period 3; Kruskall–Wallis: $\chi^2_{1,2} = 1.64$; $P = 0.44$), but period 2 contrasts with the other two by its low dry season rainfall (Fig. 1b; mean dry season rainfall $\pm$ SE $= 15.5 \pm 5.5$ for period 1; 4.0 ± 6.1 for period 2; 12.2 ± 4.2 for period 3; Kruskall–Wallis: $\chi^2_{1,2} = 7.26$; $P = 0.0265$). The 1995/1996 break between period 2 and 3 was chosen because 1996 is the first year following this long dry spell with above average dry season rainfall as well as with a good annual rainfall (Fig. 1). If annual rainfall influences herbivore population dynamics, we expected no major change in trends over the study period as annual rainfall did not differ significantly between the three periods.

If dry season rainfall has an overwhelming influence on herbivore population dynamics, we expected populations to increase during period 1 and period 3, both of which presented high dry season rainfall, and to decrease during period 2 which presented low dry season rainfall. If elephant abundance strongly influences herbivore population dynamics, we expected populations to decrease (if elephants affect negatively other herbivores) or to increase (if elephants affect positively other herbivores) in periods 2 and 3 when elephant abundance was increasing and reaching high level.

Trends study

We studied the trends of 13 herbivore species among which five are browsers or mixed-feeders (giraffe *Giraffa camelopardalis*, greater kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus*, steenbok *Raphicerus campestris* and common duiker *Sylvicapra grimmia*) and eight are grazers (African buffalo *Syncerus caffer*, roan antelope *Hippotragus equinus*, reedbuck *Redunca arundinum*, sable *Hippotragus niger*, warthog *Phacochoerus aethiopicus*, waterbuck *Kobus ellipsiprymnus*, blue wildebeest *Connochaetes taurinus* and Burchell's zebra *Equus burchelli*). Because of the unpredictable and potentially high variability between waterholes (e.g. surrounding vegetation, local weather conditions, local disturbance, sampling intensity), we studied changes in population abundance by using mixed models. Because not all waterholes had water every year and consequently were not counted every year, we used only the 23 waterholes most regularly surveyed and we assumed that no animal was counted in the few years when these waterholes were dry. For each species, we performed a covariance analysis on the number of animals counted at waterholes with waterhole identity as random effect and with three fixed effects: *period* as a factor, *year* and *yrain* as covariates. Annual rainfall had to be controlled to account for its effect on waterhole attendance by animals so we used a Type I error approach and *yrain* was the first covariate to be entered in the covariance analyses to control for its effect before testing for the other variables. As temporal serial autocorrelation often affects time series counts, we checked whether autocorrelation was present and accounted for it using a first-order autoregressive covariance structure. If the interaction *year × period* was significant once rainfall effects were accounted for, it indicated that population trends differed between the three periods of contrasted elephant population dynamics and rainfall patterns. When only *year* was significant once rainfall effects were accounted for, we considered that species exhibited a continuous long-term trend, unaffected by the change in elephant numbers or rainfall. All statistical analyses were performed with SAS software (version 8.2) (SAS Institute Inc. 1999). It has become standard practice to consider a Poisson distribution for count data, but it often goes under appreciated that such analyses are not robust to minor departures from Poisson distribution. Conversely, there is evidence that analysis of variance models, based on normal distributional

Table 1 Results from mixed models (for normally distributed data) testing for changes of slope in herbivore populations

| Species | Change in slope | | Slope up to 1986 | Slope from 1987 to 1995 | Slope from 1996 |
	In 1986/1987	In 1995/1996			
Elephant	$t_{1,523}=-3.06$ $P=0.0023$	$t_{1,523}=-1.71$ $P=0.0870$	−5.67	15.40	1.73
Browsers and mixed feeders					
Common duiker	$t_{1,523}=3.04$ $P=0.0025$	$t_{1,523}=2.42$ $P=0.0159$	0.02	−0.24	0.01
Impala	$t_{1,523}=4.97$ $P<0.0001$	$t_{1,523}=3.50$ $P=0.0005$	4.47	−13.65	0.96
Greater kudu	$t_{1,523}=5.18$ $P<0.0001$	$t_{1,523}=3.52$ $P=0.0005$	0.79	−2.86	−0.04
Steenbok	$t_{1,523}=2.40$ $P=0.0167$	$t_{1,523}=2.32$ $P=0.0209$	0.00	−0.09	0.01
Giraffe	$t_{1,523}=-0.32$ $P=0.7475$	$t_{1,523}=-0.22$ $P=0.8241$	0.04	0.15	0.02
Grazers					
Buffalo	$t_{1,523}=3.14$ $P=0.0018$	$t_{1,523}=0.24$ $P=0.8127$	8.43	−11.97	−10.22
Reedbuck	$t_{1,523}=2.30$ $P=0.0217$	$t_{1,523}=0.82$ $P=0.4101$	0.19	−0.30	−0.09
Roan	$t_{1,523}=1.84$ $P=0.0661$	$t_{1,523}=1.56$ $P=0.1200$	0.15	−0.33	0.14
Sable	$t_{1,523}=0.88$ $P=0.3770$	$t_{1,523}=0.76$ $P=0.4478$	0.13	−0.22	0.12
Warthog	$t_{1,523}=5.28$ $P<0.0001$	$t_{1,523}=2.60$ $P=0.0095$	0.83	−1.07	0.02
Waterbuck	$t_{1,523}=2.13$ $P=0.0332$	$t_{1,523}=1.04$ $P=0.2974$	0.38	−0.24	0.13
Wildebeest	$t_{1,523}=-0.66$ $P=0.5090$	$t_{1,523}=-1.19$ $P=0.2360$	−0.18	0.26	−0.66
Zebra	$t_{1,523}=1.05$ $P=0.2930$	$t_{1,523}=0.23$ $P=0.8181$	0.93	−0.69	−0.28

Estimates of slopes are given for the three periods. Significant changes are indicated in bold.

assumptions are robust to severe departures from normality, and that these models are more robust than Poisson regression models (even with correction for overdispersion) with data from discrete distributions (White & Bennetts, 1996). We preliminarily performed analyses for both (1) normally distributed data (MIXED procedure) and (2) Poisson distributed data (MIXED procedure with the GLIMMIX macro) using a log link function and a quasi-likelihood correction for over-dispersion (scaling function: deviance^{-1}). As the results were similar, we present only the results from analyses for normally distributed data here, and the results from analyses for Poisson distributed data are provided in (Supplementary Material Appendix S1).

Results

Population trends of elephants stemmed from waterhole censuses were similar to those stemmed from aerial surveys, with the numbers estimated by both methods being highly correlated (number of elephants counted at waterholes = 11 115 + 0.902 × number of elephants counted from

the air-21.0 × *yrain*; $P<0.0001$; $r^2 = 0.72$). Breaks in elephant population trend were detected from mixed-models covariance analyses on waterhole counts data: once controlled for *yrain*, the *year* × *period* interaction was significant in 1986/1987 and very close to significance in 1995/1996 (Table 1). As expected, the elephant population decreased before 1986, increased after the culling stopped and stabilized after 1995 (Table 1). This confirmed that the period factor used allowed us to distinguish between the three distinct periods of elephant dynamics.

For other herbivores, examination of the 3-year running means on total numbers counted at waterholes suggested that many species decreased between 1986 and 1995, and seem to have stabilized since 1996 (Fig. 3). The results from mixed-models covariance analyses tend to corroborate these trends. For all the browsers except giraffe and for one grazer (warthog), the *year* × *period* interaction was significant both in 1986/1987 and in 1995/1996 (Table 1). Generally, these species showed an increase in the first period, a decrease in the second period and an increase or stabilization in the third period (Table 1). For impala and warthog, the increase
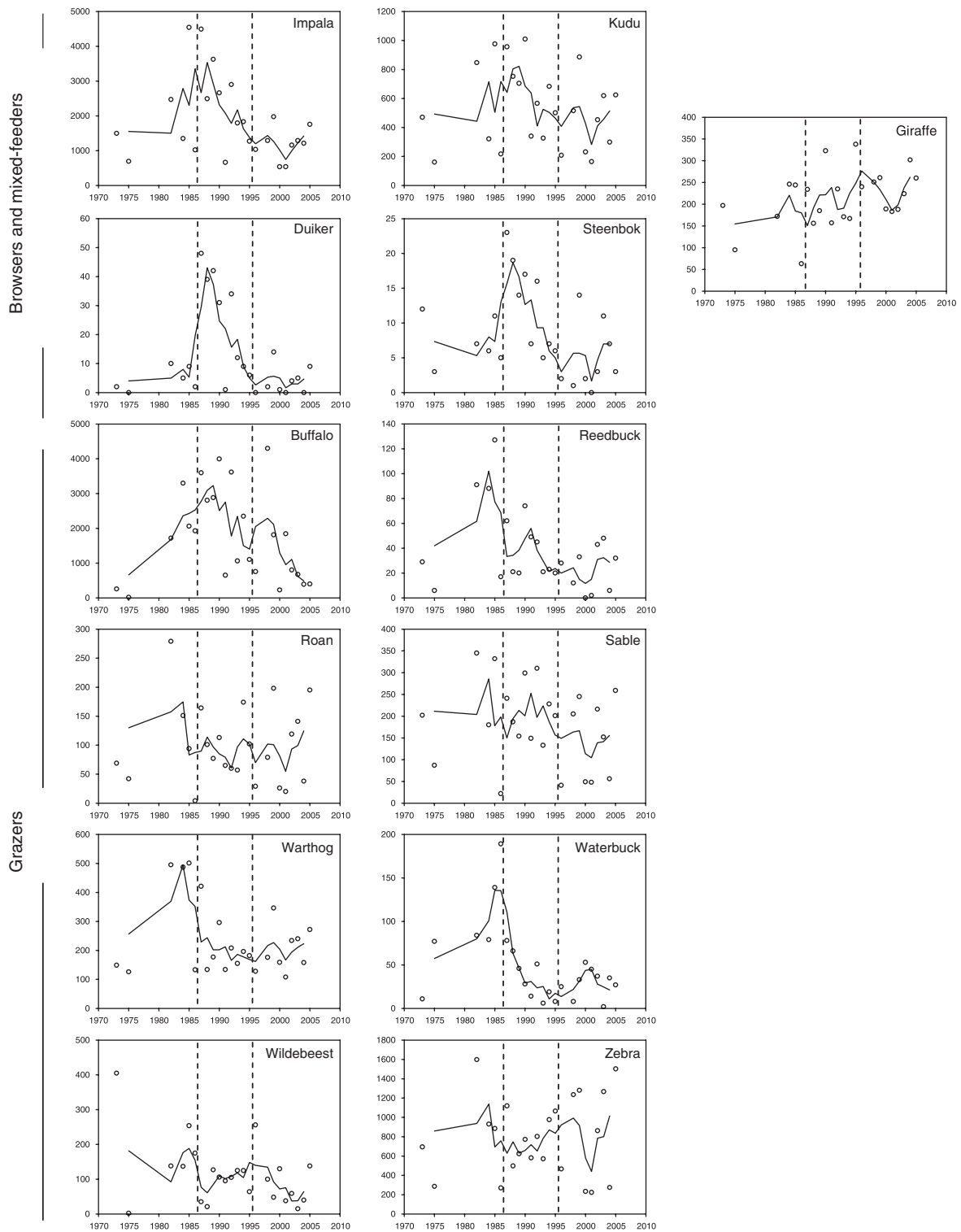
Figure 3 Trends in the total number of animals counted at waterholes in the northern part of Hwange National Park per species. The lines represent the changes in the 3-year running means (mean of years $n-1$, n and $n+1$). The vertical dotted lines separate the three study periods (see text for details). The species are grouped according to their diet.

in the 1996–2005 period has occurred at a lower rate than the increase in the 1973–1986 period, whereas for the others (duiker, kudu, steenbok) the population appears to have stabilized in the 1996–2005 period (Table 1). For buffalo, reedbuck, roan and waterbuck the 1986/1987 break was significant with the population increasing before and decreasing after. The *year × period* interaction was not significant for four species: giraffe, sable, wildebeest and zebra (Table 1). *year* was significant for giraffe ($P = 0.036$) for which a continuous increase for the whole study period is indicated, and *year* was nearly significant for wildebeest ($P = 0.067$), for which a continuous decrease for the whole study period is indicated. The sable and zebra did not show any particular trend ($P = 0.12$ and 0.44 respectively).

Discussion

To investigate long-term trends in different herbivore populations, we have used a census database spanning over 32 years. The trends detected here are consistent with those from population density estimates using road transect counts (Valeix *et al.*, 2007b). Our findings that most herbivore populations increased in periods of high dry season rainfall and decreased in the decade of low dry season rainfall, are consistent with other studies highlighting that dry season rainfall is a major driver of herbivore population dynamics in semi-arid savannas (Mduma *et al.*, 1999; Ogutu & Owen-Smith, 2003; Dunham et al., 2004). The synchrony in declines of herbivore populations in both Kruger National Park, South Africa (Ogutu & Owen-Smith, 2003), and HNP substantiates the fact that some regional influence affects herbivore population dynamics. A deeper understanding of the mechanisms by which dry season rainfall influences herbivore population dynamics is clearly needed in a context where drought frequency and severity are increasing in southern Africa (Richard *et al.*, 2001; Chamaillé-Jammes, Fritz & Murindagomo, 2007a).

Though our results are consistent with a fundamental influence of dry season rainfall, they also strongly suggest that high elephant numbers may have a negative influence on some other herbivores for five reasons. Firstly, we cannot reject the hypothesis that some herbivore population decreases could be due, at least partly, to the increase in the elephant population during the 1987–1995 period as they occurred simultaneously. Secondly, since 1986, some species have declined in HNP (e.g. impala) while they have been stable in Kruger where elephant culling has occurred (Ogutu & Owen-Smith, 2003). Thirdly, some herbivore populations showed a lower rate of increase in 1996–2005 than in 1973–1986. If high elephant numbers would have a neutral or beneficial effect on other herbivores (e.g. facilitation mechanisms suggested by Skarpe *et al.*, 2000; Rutina *et al.*, 2005; Makhabu *et al.*, 2006), we would have expected herbivore populations to grow in the 1996–2005 period (both high dry season rainfall and high elephant numbers) either at a similar rate (if neutral effect) or at a higher rate (if beneficial effect) than in the 1973–1986 period (high dry season rainfall and lower elephant numbers). Hence no

medium-term facilitation can be deemed to have occurred in HNP. Fourthly, if dry season rainfall was the only driver of herbivore populations, it is unexpected that the *year × period* interaction in 1995/1996 was not significant for more herbivore species. Finally, if rainfall was the only major driver, grazers should be more affected by rainfall variability than browsers, because the herbaceous layer responds more strongly to precipitation than does the woody component of savanna vegetation (Rutherford, 1980). However, this was not the case in HNP where browsers showed some of the most dramatic declines yet some grazers (wildebeest, zebra) were not affected by these changes. While our study does not allow us to properly disentangle the role of elephant abundance and dry season rainfall, these considerations strongly suggest that high elephant densities have played a role in the declines of some herbivore populations.

Our results did not show any guild effect, which differs from what could have been expected from previous studies (Parker, 1983; Owen-Smith, 1989; Fritz *et al.*, 2002). In fact, most browser populations and five grazer populations decreased between 1986 and 1995. Therefore our results do not support an elephant scenario based exclusively on alteration of habitats for browsers. Indeed, elephants do not seem to alter habitats for browsers at the landscape scale in HNP (Valeix *et al.*, 2007b), and other mechanisms need to be sought. For example, even though the giraffe is a strict browser, it was not impacted by the increase in the elephant population, which was also the case in Fritz *et al.* (2002). This gives potential support to a food competition hypothesis as only giraffes may escape competition by feeding higher than elephants (du Toit, 1990). Additionally, declines in grazer populations could be due to a change in composition and density of grass layer associated with elephant presence (Young, Palmer & Gadd, 2005). Because waterholes become scarcer as the dry season progresses, with elephants and other herbivores aggregating at the same waterholes, and vegetation becoming depleted around these waterholes, the interaction in the dry season between surface water distribution and resource depletion can be a limiting factor for herbivore populations in HNP (see also Chamaillé-Jammes *et al.*, 2008 for elephants). We feel that it is possible to sketch a scenario of food depletion competition between elephants and other herbivore species in key-resource areas (*sensu* Illius & O'Connor, 2000) surrounding the few dry season waterholes. Consequently, in key-resource areas, it will be important to quantify resource depletion induced by elephants in the dry season, and measure diet overlap between elephants and other species. Furthermore, assessing distances that herbivores can travel from waterholes will add valuable information to define the key-resource areas relevant for each herbivore species. It is possible that the increase in the elephant population coupled with the increased severity of droughts in HNP (Chamaillé-Jammes *et al.*, 2007a) has led to dry season conditions extremely critical for herbivores, and could explain the declines observed. Because elephants gather in high densities and could monopolize the few available waterholes in the

dry season, competition for water could also be a mechanism responsible for the decrease in many species in HNP. However, no major negative effect of elephants on other herbivores at waterholes has been reported (Valeix, Chamaillé-Jammes & Fritz, 2007a).

When trying to detect competition effects, predation can represent a confusing factor, which could explain here the declines not only in browsers but also in grazers. It is possible that we may only detect an apparent competition (*sensu* Holt, 1977), which intervenes through indirect inter-actions via a shared predator. Predation has long been recognized as possibly having direct and indirect effects on species coexistence and diversity (e.g. Holt, 1984; Abrams, 1999). For large herbivores, predation has a direct impact on the dynamics of their prey (lethal effects, particularly below 150 kg: Sinclair, Mduma & Brashares, 2003). Nevertheless, no massive increase in predator populations has been documented over the last 20 years in HNP (see Loveridge, 2002 for lions; Rasmussen, 1997 for painted dogs). Major indirect effects of predation (nonlethal behavioural effects, Lima, 1998) have been documented as well, but have been so far overlooked. In HNP, where most medium to small size herbivores have declined, it is possible that elephant-induced vegetation changes have modified the vulnerability of herbivores to their predators. Research priorities should be put on understanding the fine-scale habitat selection of herbivores, which will allow us to investigate whether herbivores select or avoid sites modified by elephants, and studying kill sites characteristics, which will allow us to define the habitat characteristics, and particularly the degree of elephant impact, where prey are vulnerable to their predators. Individual-based approaches will be crucial in the future to test whether behavioural adjustments induced by elephant abundance can lead to costs that are likely to affect individual fitness and consequently to be the cause of the population declines observed.

Many debates have arisen on the necessity of controlling elephant populations and on the means to reach such a goal. Culling operations are controversial (Butler, 1998) and other alternatives have been suggested (e.g. see Chamaillé-Jammes, Valeix & Fritz, 2007b for surface water management; see van Aarde & Jackson, 2007 for megaparks). The reasons usually advanced to justify the control of elephant populations rely on the impact of elephants on vegetation and on the concerns about the potential associated consequences on other forms of biodiversity. However, this study stresses a general lack of knowledge, particularly about the influence of elephants on other herbivore species. Given the declines in most herbivore populations reported in this study and the possibility of an elephant influence suggested here, but considering that (1) our results do not allow us to properly disentangle the role of elephants and rainfall; (2) the ethical and socio-economical implications of elephant management; (3) the stabilization of most populations since 1996, we consider that, without further evidence, our study does not demonstrate the necessity to directly control the Hwange elephant population (e.g. through culling operations). We consider that only the identification of the mechanism(s) through which elephants may influence other herbivores (see mechanisms suggested above) will allow us to demonstrate clearly an effect of elephants. More generally, this study underlines the need to better understand the role of keystone species in structuring communities. If it has been suggested that conserving keystone species presence in ecosystems is necessary for the maintenance of ecosystem integrity (Soulé *et al.*, 2005), it is also crucial to be able to predict ecosystem responses to changes in keystone species abundance. Further, by underlining the complexity of ecological interactions, this study emphasizes the need for a clearer understanding of the ecological rationale before management decisions might be undertaken.

Acknowledgments

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Supplementary material

The following supplementary material for this article is available online:

Appendix S1. Results from mixed models (for Poisson distributed data) testing for changes of slope in herbivore populations. Estimates of slopes are given for the three periods. Significant changes are indicated in bold.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-1795.2008.00194.x

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