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Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability

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Summary

1. Concerns over the ecological impacts of high African elephant *Loxodonta africana* densities suggest that it may be necessary to control their numbers locally, although the best management approach is still widely debated. Artificial water supply is believed to be a major cause of local overabundance, and could be used as a potential tool to regulate elephant distribution and impact across landscapes, but its effect on elephants at the population scale has never been studied.

2. We assessed how dry-season surface-water availability constrained the distribution of an entire elephant population, using aerial and waterhole census data from Hwange National Park, Zimbabwe. The study was initiated in 1986, when the population was released from culling. We studied how artificial waterholes, holding water throughout the dry season, and vegetation production, estimated from a normalized difference vegetation index (NDVI), influenced the long-term distribution of elephant densities. We also investigated how the elephant distribution responded to changes in population density and annual rainfall, a driver of surface-water availability.

3. Long-term dry-season elephant densities across the park tended to increase with vegetation production, and increased asymptotically with the density of artificial waterholes.

4. Since the culling stopped, dry-season elephant densities have increased in most areas of the park, except in areas of low vegetation production and low water availability. Interannual fluctuations in elephant distribution are linked to rainfall variability through its effect on surface-water availability. During dry years elephants concentrated in areas where artificial pumping maintained surface-water availability during the dry season.

5. During dry years elephant numbers at waterholes increased because of reduced surface-water availability, and elephants were distributed more evenly across waterholes, although active waterholes were unevenly distributed across the park.

6. *Synthesis and applications*. Surface-water availability drives the distribution and abundance of elephants within Hwange National Park, and therefore appears to be at the heart of the trade-off between elephant conservation and the extent of their impact on ecosystems. Artificial manipulation of surface water is one of the tools available for the management of elephant populations and should not be overlooked when considering options for controlling elephant numbers in places where they are considered to be overabundant.

Key-words: Africa, elephant impact, herbivore, landscape, *Loxodonta africana*, management, rainfall, waterholes

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Introduction

Large herbivores have a major impact on vegetation dynamics in both natural and pastoral ecosystems worldwide, ultimately influencing ecosystem processes (Hobbs 1996) and species diversity and composition (Olff & Ritchie 1998). The intensity and heterogeneity of these effects are determined by a spatiotemporal hierarchy of factors associated with behavioural decisions, from landscape use by herbivores to finer-scale intake mechanisms (Bailey *et al.* 1996; Adler, Raff & Lauenroth 2001). A clear example of spatial heterogeneity in environmental impact by herbivores is the development of utilization gradients around water sources in arid and semi-arid savannas, where grazing intensity (and trampling) increase with a decrease in distance to water. This phenomenon, known as a 'piosphere' effect (Lange 1969), has implications for nutrient cycling (Turner 1998), vegetation dynamics and composition (Weber *et al.* 1998; Todd 2006), animal diversity (James, Landsberg & Morton 1999) and feedback to herbivore population dynamics (Illius & O'Connor 2000; Derry 2004). Because water is a primary determinant of herbivore distribution, it constrains other mechanisms and processes that create heterogeneity at finer scales (Bailey *et al.* 1996).

The African elephant *Loxodonta africana* Blumenbach, a water-dependent species (Estes 1991), has a larger effect on savanna ecosystems than any other single herbivore, and is often referred to as an 'ecosystem engineer' (Jones, Lawton & Shachak 1994). Elephants at high densities strongly modify vegetation structure, converting woodland to shrubland (Ben-Shahar 1993; Styles & Skinner 2000; Mosulego *et al.* 2002; Augustine & McNaughton 2004), with subsequent modifications in plant and animal species composition (Herremans 1995; Cumming *et al.* 1997; Fenton *et al.* 1998). Elephants mainly affect vegetation structure during the dry season, when they are predominantly browsers (Williamson 1975b; Owen-Smith 1988), and these effects increase with increasing elephant densities (Ben-Shahar 1996). The effects have been found to be stronger in the vicinity of waterholes (Ben-Shahar 1993; de Beer *et al.* 2006), where aggregation of elephants occurs during the dry season (Stokke & du Toit 2002). Indeed, the primary environmental factor affecting local elephant density is distance to water (Western 1975; Stokke & du Toit 2002; Redfern *et al.* 2003; see also Verlinden & Gavor 1998; Grainger, van Aarde & Whyte 2005) although there are others, such as vegetation heterogeneity (Murwira & Skidmore 2005) and sodium availability (Weir 1972). Predicting the dry-season distribution of elephant densities across a given landscape should allow prediction of the severity and heterogeneity of elephant influence on the ecosystem.

Surface-water management has been suggested as a tool to manage elephant-induced heterogeneity efficiently in ecosystems (Owen-Smith 1996) to avoid highly controversial culling operations. Manipulation of surface-water supply should allow managers to shape the landscape, and create, maintain and regulate heterogeneity in herbivore impact on an ecosystem. Such management options clearly fit the new paradigm of managing heterogeneity for biodiversity conservation (Rogers 2003; Gordon, Hester & Festa-Bianchet 2004). However, managers have limited information from which to predict the effects of changing water management policies on elephant-induced heterogeneity, because most available information is at the individual elephant level or summarized as average densities related to distance to water (Western 1975; Stokke & du Toit 2002; Redfern *et al.* 2003; Cushman, Chase & Griffin 2005; Grainger, van Aarde & Whyte 2005). A comprehensive description of the effect of water availability and distribution on an elephant population is lacking. Surface-water management will be successful only if it restrains the distribution of the whole population. It is also unclear how the relationships between elephant distribution and surface water will change in response to changes in elephant density, which limits our ability to predict the efficiency of surface-water management because most elephant populations are increasing (Blanc *et al.* 2005) as they recover from previous legal population reduction exercises (culling) and poaching outbreaks.

We addressed these issues using aerial and waterhole census data for the elephant population of Hwange National Park (Hwange NP), Zimbabwe, which was released from culling 20 years ago. We studied the relationships between long-term dry-season elephant densities and both dry-season surface-water availability, estimated from the density of artificial waterholes, and vegetation production. We also investigated how the elephant distribution responded across the whole park as well as across surface-water sources to changes in population density and annual rainfall, a driver of surface-water availability. We discuss our results within the framework of active management of elephant distribution, and highlight how surface-water management appears to be an efficient tool for reaching the objectives of maintaining heterogeneity in elephant impacts across landscapes.

Materials and methods

STUDY AREA

Hwange NP (*c.* 15 000 km^2) is located on the north-west border of Zimbabwe (19°00′S, 26°30′E). The vegetation is typical of southern African dystrophic wooded savannas, with patches of grasslands (Rogers 1993). The park is divided into nine management units (blocks; Fig. 1). Mopane trees *Colophospermun mopane* (Kirk ex Benth.) Kirk ex J. Léonard dominate the Robins, Sinamatella and Josivanini blocks, with clay-type soils, while mixed woodlands and bushlands (*Combretum* spp., *Acacia* spp., *Terminalia sericea* Burch ex DC., *Baikiaea plurijuga* Harms) develop on Kalahari sands

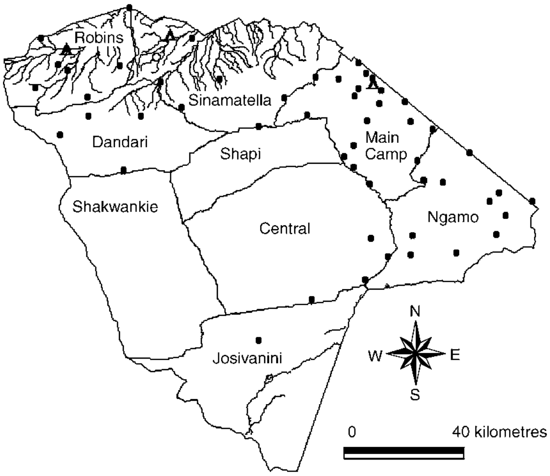

Fig. 1. Map of Hwange National Park showing the nine management blocks. Artificial waterholes (black dots) are mainly distributed in the northern and eastern blocks. In the Sinamatella block a large dam provides permanent water supply (open dot). The wet season river network that dries up during the dry season, apart from a few pools in the Robins block, is also shown. Tent symbols: rainfall collecting stations.

in the other blocks (Rogers 1993; Chamaillé-Jammes, Fritz & Murindagomo 2006).

Natural surface water becomes scarce in the dry season, as most waterholes dry up. Rivers also dry up during the dry season, although a few river pools can retain water throughout the year in the Robins block (Fig. 1). Between the 1930s and the early 1980s, artificial waterholes were developed by pumping groundwater during the dry season to create a year-round water supply and increase herbivore populations. Artificial waterholes are unevenly distributed across the park, with most located in the northern and eastern blocks (Fig. 1).

The elephant population responded to the increased water availability and increased from *c.* 1000 individuals in the 1920s (Davidson 1967) to almost 8000 in 1968 (Williamson 1975a). A culling programme was initiated in 1966 and in 1974 the park adopted a policy of maintaining a population level of 13 000 elephants (Cumming 1981), until culling was abandoned in 1986. Since the culling stopped, the population has more than doubled. The last aerial census, conducted in 2001, reported a population estimate of 44 492 elephants (i.e. 2·92 individuals km^{-2}; Dunham & Mackie 2002), one of the highest densities observed world-wide over a large area (Blanc *et al.* 2005).

RAINFALL DATA

Rainfall data have been collected daily since 1928 at three different stations in the northern blocks (Fig. 1). Rainfall over the park was estimated as the average of these stations. Hwange NP has one rainy season (October–April), when an average of 98% of the rainfall occurs (Chamaillé-Jammes, Fritz & Murindagomo 2006). Annual rainfall for year t was calculated as the integrated rainfall from October in year $t - 1$ to September in year t. The long-term mean annual rainfall is 606 mm (1928–2005).

VEGETATION PRODUCTION DATA

We used the satellite-derived normalized difference vegetation index (NDVI) as a proxy for vegetation production. NDVI combines the reflectance of the earth's objects in the red (RED) and near-infrared (NIR) spectrum: $\text{NDVI} = (\text{NIR} - \text{RED})/(\text{NIR} + \text{RED})$. It is strongly related to the fraction of absorbed photosynthetically active radiation (Tucker & Sellers 1986). When integrated over time, it is an effective estimate of vegetation productivity and standing biomass in semi-arid systems (du Plessis 1999; Milich & Weiss 2000; Schmidt & Karnieli 2000). NDVI has been used successfully to explain population dynamics and distributions of herbivores (reviewed by Pettorelli *et al.* 2005). Elephants eat a wide range of plant species and plant parts, particularly when food resources are limited (Owen-Smith 1988; Stokke & du Toit 2000), so a coarse index of vegetation biomass such as NDVI is likely to be a good index of forage availability (Rasmussen, Wittemyer & Douglas-Hamilton 2006).

We used 10-day NDVI images (resolution 8 × 8 km) derived from 1982 to 2002 from Advanced Very High Resolution Radiometer/National Oceanographic and Atmospheric Agency satellites. The NDVI images were provided by the Famine Early Warning System of the US Agency for International Development (USAID 2006). More information on image production and corrections can be found at http://igskmncnwb015.cr.usgs.gov/adds/ (accessed January 2003). We integrated NDVI images annually by summing them from October to September, and then for each year we extracted the average NDVI value over each block.

AERIAL CENSUS DATA

Aerial stratified strip-transect game counts were conducted annually (except in 2000) at the end of the dry season, from 1980 to 2001 [conducted by the National Parks and Wildlife Management Authority from 1980 to 1992 (Price Waterhouse Consultants (1996) and the World Wildlife Fund (WWF) from 1993 to 2001 (Working Papers available at the WWF Regional Office, Harare, Zimbabwe)]. These censuses followed standard procedures as recommended in Norton-Griffiths (1978) and were then analysed using Jolly's (1969) method. A breakdown of population size by block was available for all years except 1985.

WATERHOLE ANIMAL CENSUSES AND WATER AVAILABILITY

Twenty-four-hour game counts at waterholes (natural or artificial pans, seeps and springs) were conducted from 1967 to 2005 (except in 1968–71, 1976–81 and

1983). Data from 45 waterholes monitored regularly were used for the analyses. In late September–early October (the hot dry season), at full moon, the number of animals coming to drink from midday to midday the next day was recorded for all species. In contrast with other years, it rained during the 1986 and 1997 surveys, and animals were able to drink in the numerous ponds created. Because of the increased availability of water, the number of animals counted was very low and not representative of dry season abundances. Therefore data from 1986 and 1997 were not included in the analyses. Potential waterholes were visited 1 week before the game count to note the presence or absence of water. Data were available from 1982 to 2005 (except for 1983 and 1994) and on average 121 ± 8 (SD) potential water sources were visited. From these data an index of water availability in the park was created and calculated for each year as the proportion of waterholes that retain water during the dry season.

STATISTICAL ANALYSES

To avoid the bias of culling in our analyses of elephant distribution (van Aarde, Whyte & Pimm 1999), we restricted our study to the post-culling period (from 1986 onwards). We investigated elephant distribution at two scales: (i) we compared the determinants of elephant densities between blocks over the entire park, and (ii) we studied changes in elephant abundance and distribution at waterholes.

Between-block comparisons

Elephant densities were calculated annually per block and normalized using $\log_{10}(\text{density} + 1)$ for statistical analyses. We first assessed the similarity in temporal dynamics among blocks with a hierarchical cluster analysis. The dendrogram was based on the Euclidean distance matrix and Ward minimum variance method (Legendre & Legendre 1998). We compared the long-term elephant densities in each group and studied their relationships with the mean NDVI and the density of artificial waterholes in the blocks. A very large dam providing permanent water in the Sinamatella block (Fig. 1) was considered as an artificial waterhole for the analyses. We investigated which factors caused the clusters by studying the relationships between the interannual changes in elephant densities per block and the total elephant population size and annual rainfall. We did not test the effect of the NDVI because it responded to rainfall variations similarly in all blocks (rain effect $F_{1,171} = 83\,650$, $P < 0{\cdot}0001$; block effect $F_{8,171} = 2{\cdot}596$, $P = 0{\cdot}011$; interaction $F_{8,171} = 0{\cdot}300$, $P = 0{\cdot}965$).

Waterhole attendance

We calculated the annual mean number of elephants coming to drink at a waterhole in 24 h per waterhole. We also characterized the distribution of the population among waterholes using the Lloyd's index of mean crowding, *J* (Lloyd 1967). This index measures the evenness of the distribution of a population across sites. Because we wanted to measure evenness across all available sites (including sites with no elephants), we added one individual to all sites (Payne *et al.* 2005). We also rescaled this index between 0 and 1, following Payne *et al.* (2005). Values closer to 1 indicated a more even distribution of elephants among waterholes.

Results

BETWEEN-BLOCK COMPARISONS

The hierarchical cluster analysis classified the temporal dynamics of blocks into three main groups (Fig. 2). Elephant densities, NDVI and densities of artificial waterholes were generally higher in group 1, followed by group 2 and group 3 (Fig. 3a,b).

The relationship between mean NDVI per block and mean elephant densities was close to significance (Fig. 3a; $F_{1,7} = 4{\cdot}951$, $P = 0{\cdot}061$). Mean elephant density in each block was positively related to the density of artificial waterholes in the block ($F_{1,7} = 7{\cdot}849$, $P = 0{\cdot}026$) and an asymptotic model provided a better fit than linear regression (Fig. 3b; $F_{1,7} = 18{\cdot}714$, $P = 0{\cdot}003$).

Dry-season elephant densities in blocks varied with the total population size as well as with annual rainfall, although not evenly across blocks (Table 1). Elephant densities per block increased with total population size in all blocks, except in two blocks of group 3 with low vegetation production and low water availability (Fig. 4).

The proportion of waterholes surveyed that retained water during the dry season increased with increasing rainfall ($F_{1,18} = 8{\cdot}299$, $P = 0{\cdot}010$). Elephant densities per block also changed significantly with annual rainfall (Table 1) and during dry years elephants concentrated in blocks with the highest surface-water availability, i.e. blocks of group 1 (Robins, Ngamo and Main Camp;

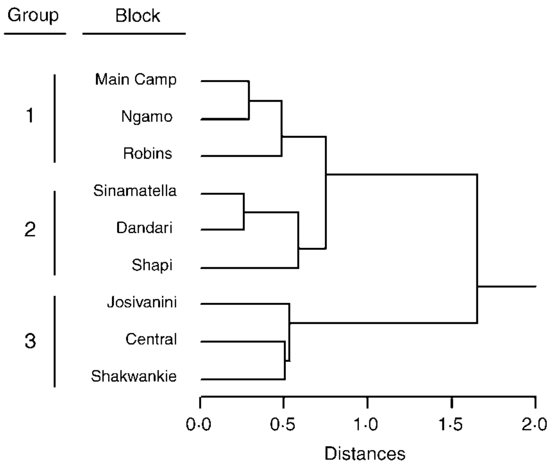

Fig. 2. Ward's dendrogram of a hierarchical cluster analysis conducted on times series of elephant densities in management blocks. Three main clusters, i.e. groups, were identified.

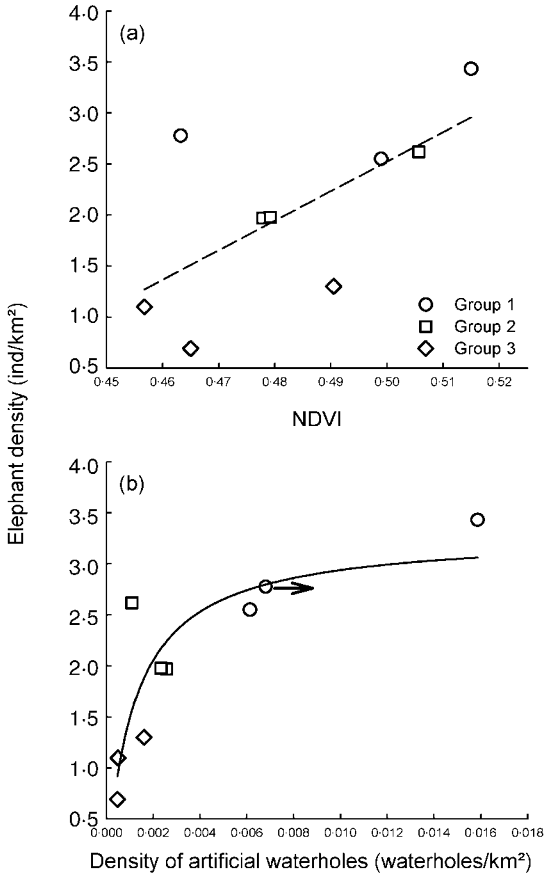

Fig. 3. Mean elephant density per block in relation to (a) mean NDVI (P = 0·061) and (b) density of artificial waterholes (P = 0·003). Surface-water availability in the Robins block is actually slightly higher (black arrow) as some river pools retain water during the dry season. In both panels different symbols identify distinct groups produced by the hierarchical cluster analysis.

Table 1. Effects of total population size, annual rainfall and block and their interactions on elephant densities per block

	d.f.	F	P
Population size	1	52·198	< 0·0001
Annual rainfall	1	0·004	0·949
Block	8	4·141	< 0·001
Block × population size	8	2·575	0·013
Block × annual rainfall	8	4·895	< 0·0001
Residuals	99		

Annual rainfall × population size P = 0·772.
Densities were normalized with a $\log_{10}$(density + 1) transformation.

Fig. 5). Conversely, densities increased during wet years in the block with the lowest density of pumped waterholes, i.e. the Shakwankie block.

WATERHOLE ATTENDANCE

Mean elephant number per waterhole was not directly related to total population size as estimated from aerial census data ($F_{1,11}$ = 0·739, P = 0·408) but increased with decreasing rainfall ($F_{1,16}$ = 17·100, P < 0·001). There was, however, a large spatial variability, as indicated by the large coefficients of variation (CV; range 46–109%). Once corrected for this rainfall effect, the mean elephant number at waterholes increased with total population size ($F_{1,10}$ = 5·777, P = 0·037).

The index of mean crowding was not directly related to total population size ($F_{1,11}$ = 0·226, P = 0·644) but decreased significantly with increasing rainfall ($F_{1,16}$ = 9·831, P = 0·006). Once corrected for the rainfall effect, the index of mean crowding tended to increase with total population size ($F_{1,10}$ = 3·545, P = 0·089). The index increased with the mean number of elephant at waterholes (Fig. 6; $F_{1,16}$ = 26·430, P < 0·0001), indicating that the population was more evenly distributed across waterholes when elephant aggregation at waterholes was high, although elephants remained more abundant in the northern and eastern sections of the park where waterholes were concentrated.

Discussion

We conducted a comprehensive study of the heterogeneity in elephant distribution at a population scale over a large area and an extended period of time, and described the changes in elephant distribution at varying population sizes and environmental conditions.

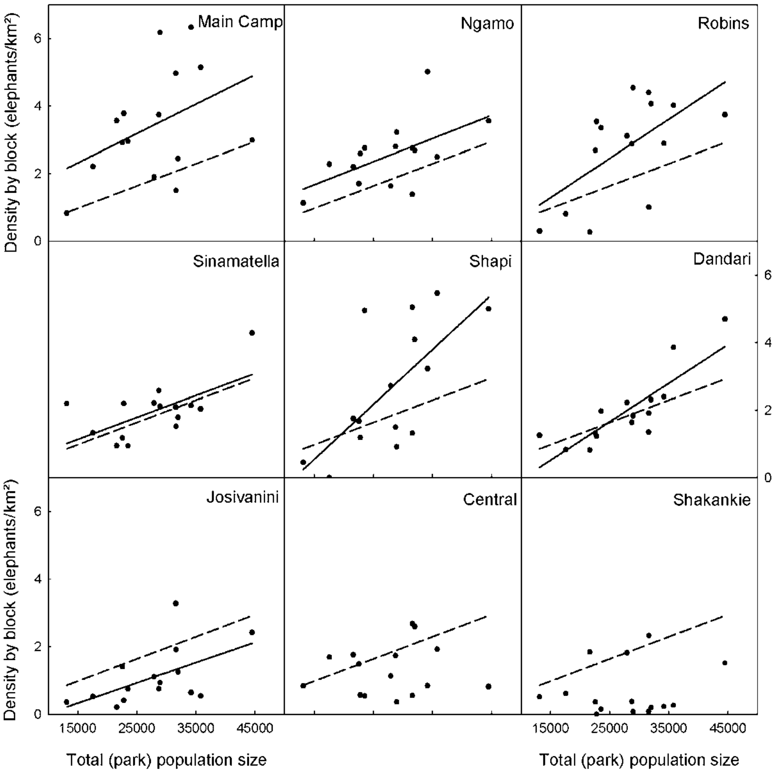

Fig. 4. The relationships between total (park) population size and elephant density for each management block. Each row was identified as a distinct group by the hierarchical cluster analysis. Solid lines show the significant relationships (P < 0·05). Dotted lines show the expected densities under the assumption of an even distribution of the population across blocks.

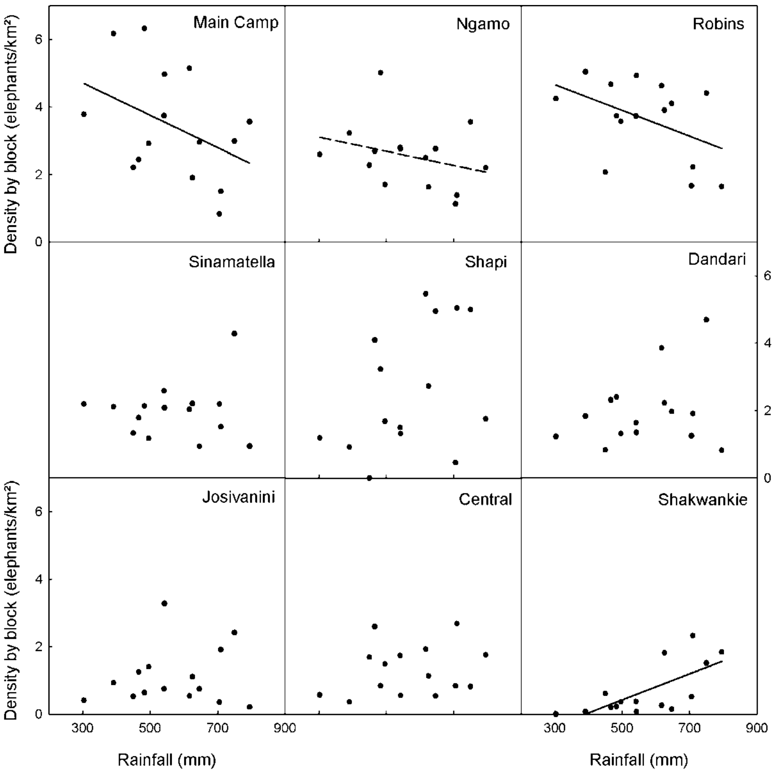

Fig. 5. The relationships between annual rainfall and elephant density for each management block. Each row was identified as a distinct group by the hierarchical cluster analysis. Solid lines show the significant relationships ($P < 0{\cdot}05$). Ngamo block, $P = 0{\cdot}067$.

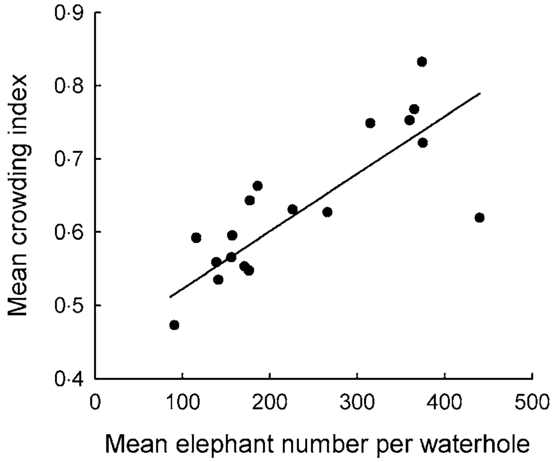

Fig. 6. The relationship between scaled Lloyd's mean crowding index and the mean number of elephants per waterhole. Values closer to 1 indicate a more even distribution of elephants among waterholes.

DISTRIBUTION CHANGES IN RELATION TO SURFACE WATER, ELEPHANT DENSITY AND ANNUAL RAINFALL

The elephant population was not distributed evenly within Hwange NP during the dry season. Surface-water availability, measured by the density of artificial waterholes, was the best predictor of elephant densities per block. However, the asymptotic shape of this relationship showed that another factor limited elephant densities at *c.* 3 individuals/km^2. The close-to-significance relationship between NDVI and elephant densities suggested that vegetation production, i.e. food resources, could be a valid candidate for such a limitation. At a continental scale, elephant abundances are positively correlated with mean annual precipitation (Fritz *et al.* 2002), a good proxy for vegetation production, although the importance of surface-water availability at such a scale has not been investigated.

Over time, elephant densities in blocks varied with total population size and annual rainfall, although differently between blocks. The most striking result was that in blocks with few artificial waterholes elephant densities were not related to total population size. This result showed that population increase was strongly constrained in space by the distribution of surface water, as expected because, although elephant can roam over large areas, individuals rarely occur far from water during the dry season (Stokke & du Toit 2002; Redfern *et al.* 2003).

Annual rainfall also influenced the distribution of the elephant population. During dry years, a lower proportion of the waterholes retained water across the dry season, and water was available mainly through the artificial waterholes, mostly located in the northern and eastern sections of the park. Consistently during dry years, elephant densities increased in the three blocks with the highest densities of artificial waterholes. Because of the reduction in the number of active waterholes, mean elephant numbers at waterholes also increased. However, this increase differed between waterholes, and elephant numbers shifted towards a more even distribution across waterholes, probably caused by a saturation process occurring at crowded waterholes (S. Chamaillé-Jammes, H. Fritz, M. Valeix & F. Murindagomo, unpublished data).

Generally, we found that large-scale elephant distribution was linked to surface-water distribution. This did not hold true at a small scale with low elephant densities, as elephant aggregated at some favoured waterholes, maybe linked to water quality or nutrient availability (e.g. sodium; Weir 1972). However, as elephant numbers at waterholes increased (as a result of an increase in the population or a reduction in the number of waterholes), elephant distribution came closer to an even distribution among available waterholes. Therefore, distribution of surface water was ultimately the driver of elephant distribution at all scales at high elephant densities, when concerns about elephant impact on the ecosystem are highest.

A KEY FOR THE MANAGEMENT OF LANDSCAPE HETEROGENEITY AND ELEPHANT POPULATIONS?

Manipulation of surface water to manage herbivore distributions and their effects on ecosystems has been proposed previously (Owen-Smith 1996; Redfern *et al.* 2005). We have shown that this may be possible even for a large, long-distance free-ranging animal that is a key modifier of the ecosystem. However, our results show that heterogeneity in elephant densities in the ecosystem may change in opposite directions at different scales in response to changes in surface-water distribution. For instance, concentrating water sources in a small portion of the landscape will increase heterogeneity at the largest scale, with some areas being either unvisited or heavily used by elephants. At finer scales, the heterogeneity will decrease as either no elephant will be present or, where elephants are present, their distribution across waterholes will be more even. Creating and maintaining heterogeneity will help to preserve a wide variety of habitats to enhance biodiversity (Rogers 2003). However, our results illustrate that we need to understand not only how heterogeneity affects biodiversity and ecological processes but also at which scale heterogeneity is most relevant.

This study also suggests that surface-water management may allow balancing elephant population size and elephant impact on ecosystems. Maintaining a homogeneous, low-density elephant distribution across the whole landscape while still supporting a large population is unlikely to be either feasible (waterholes acting as attractors causing heterogeneity) or desirable. Large elephant populations are beneficial for elephant conservation, species favouring elephant-modified ecosystems and tourism, and potentially increase the profits from sport hunting if animals are allowed to disperse outside protected areas (Cumming 1989). However, as high elephant densities threaten some specific components of biodiversity (Herremans 1995; Cumming *et al.* 1997; Fenton *et al.* 1998) and increase the risk of human–elephant conflict in neighbouring areas (Hoare 1999), the largest elephant population may need to be maintained while controlling its distribution. Finding a balance between elephant population size and its effect on the ecosystem probably lies in the creation of some ‘sacrificed’ areas of high elephant densities while making other areas inaccessible to elephants during the dry season, by closing, or not opening, artificial waterholes. This would also maximize heterogeneity in elephant distribution across the landscape. Our results suggest that surface-water management is a prerequisite for increasing elephant numbers while still allowing control to be exercised regarding elephant distribution and impacts on ecosystems.

Although it is increasingly recognized that some large elephant populations may need to be reduced and managed, no uncontroversial option has yet been found. The two most commonly proposed management options, culling and contraception, are usually rejected as being unethical, for the former (e.g. Butler 1998), or impractical for large populations, for the latter (Pimm & van Aarde 2001). Surface-water management does not suffer from these weaknesses and, although it has other drawbacks (e.g. it is restricted to water-limited environments and affects other species), it offers an additional, usually overlooked, opportunity for the context-specific regulation of elephant populations. Recently, it has been advocated that regional elephant management (range expansion and metapopulation management with corridors) could solve problems of locally high elephant abundances. In the light of our results, we urge scientists, managers and conservationists to consider first surface-water availability to assess the suitability of landscape measures for elephant management.

We have shown that surface-water drives the distribution of a whole elephant population during the dry season and constrains the spatial pattern of population increase. Elephant distribution across waterholes was explained by a density-dependent pattern of aggregation. Such results allow predictions to be made regarding the future distribution across the landscape of elephant populations released from culling or recovering from poaching.

Our study also provides empirical evidence supporting previous suggestions that surface-water management allows the distribution and abundance of elephants in ecosystems to be controlled, and can ultimately be used as a tool to create, maintain and regulate landscape heterogeneity at multiple scales. Overall, surface-water variability is likely to be the only ecological mechanism able to maintain spatial heterogeneity in ecosystems facing high elephant densities.

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