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Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: Potential implication for herbivore dynamics

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Abstract In arid and semiarid environments surface-water strongly constrains the distribution and abundance of large herbivores during the dry season. Surprisingly, we know very little about its variability in natural ecosystems. Here we used long-term data on the dry-season occurrence of water at individual waterholes to model the surface-water availability across Hwange National Park, Zimbabwe, under contrasted climatic and management scenarios. Without artificial pumping only 19.6% of the park occurred within 5 km of water under average climatic conditions. However surface-water availability was strongly influenced by annual rainfall, and over 20 years the variability of the surface area of the park occurring within 5 km of water was slightly larger than the variability of rainfall. This contrasts with the usual buffered response of vegetation production to rainfall fluctuations, and suggests that the variability in dry-season foraging range determined by surface-water availability could be the main mechanism regulating the population dynamics of large herbivores in this environment. Artificial pumping increased surface-water availability and reduced its variability over time. Because changes in surface-water availability could cause the greatest changes in forage availability for large herbivores, we urge ecologists to investigate and report on the variability of surface-water in natural ecosystems, particularly where rapid climate changes are expected.

Key words: key resource, population regulation, rainfall, savanna, waterholes.

INTRODUCTION

Large herbivores can greatly affect vegetation and ecosystem processes, and understanding the factors underlying their distribution and abundance is a prerequisite to their sound management (Gordon *et al.* 2004). Unsurprisingly, forage availability during the critical season, often under climatic control, has been found to be a major factor affecting large herbivore abundance (e.g. Saether 1997). However in arid and semiarid ecosystems most large herbivores additionally require free dinking water to complement forage consumption. The regular need to access drinking water restrains the ability of animals to range far from water, and surface-water has actually been found to constrain the landscape distribution of large herbivores, the decrease of water dependent species density, or surrogates, with increasing distance-to-water being a typical feature of arid ecosystems worldwide (e.g. Africa: Western 1975; Redfern *et al.* 2003; Australia: Pringle & Landsberg 2004; North America: Rosenstock *et al.* 1999).

The quantity and the distribution of surface-water across landscapes thus affect the accessible foraging range of individuals, and, in conjunction with the heterogeneity of forage availability within this range, the total amount of forage available to herbivore populations. The extent to which animals can use the proportion of the landscape within a certain distance-to-water is dependent upon their water requirements, physiology and mobility (e.g. Western 1975; Kay 1997). Modelling exercises, assuming either homogeneous (Illius & O'Connor 2000) or heterogeneous (Derry 2004) distribution of forage, showed that the size of the dry season foraging range, determined by surface-water distribution, is a major determinant of large herbivore abundance. Artificial water provision in previously dry areas unused by herbivores has indeed long been a successful common practice to increase their abundances in both pastoral and protected areas (e.g. Africa: Livingstone & McPherson 1989; Owen-Smith 1996; Australia: James *et al.* 1999; North America: Rosenstock *et al.* 1999).

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However the increased abundance of herbivores in the vicinity of water creates strong utilisation gradients and radial trends in herbivore pressure, creating so-called 'piosphere' effects (Andrew 1988; Thrash & Derry 1999). Many ecosystem properties such as forage availability, vegetation structure and composition, or animal biodiversity have been found to be related to distance-to-water (James *et al.* 1999; Thrash & Derry 1999).

Overall, distribution of surface-water proximity across the landscape circumscribes the area in which herbivore foraging takes place, as well as determining the potential extent of the effects of herbivores. This is at the heart of the trade-off between herbivore abundance and the effect that this has on ecosystems. Characterizing the distribution of distance-to-water across landscapes, and understanding how it changes through time is therefore required to understand the functioning and the management of arid and semiarid lands.

Climatic conditions, particularly rainfall, influence the variability of surface-water availability across landscapes at the interannual time scale (e.g. Schumann 1997; Redfern *et al.* 2005). However, very few studies have actually quantified this effect. In particular, how climatic fluctuations translate into changes in the general vicinity of surface-water, and subsequently limit the potential foraging range of large herbivores remains poorly known. This lack of knowledge provides us with a biased picture of the functioning of large herbivore populations in arid and semiarid rangelands or protected areas, surface-water distribution being often considered as static over time. It also prevents us from fully understanding how these ecosystems will respond to the recent trends reported in climatic conditions (New *et al.* 2001), that are expected to persist over the course of the 21st century (IPCC 2001).

In this article we contribute a study investigating the influence of annual rainfall fluctuations and artificial pumping efforts on surface-water availability, estimated as the distribution of distance-to-water across the landscape in an African protected area, Hwange National Park (hereafter Hwange NP), Zimbabwe. We studied how annual rainfall affected the likelihood of waterholes to retain water during the dry season using long-term data of presence or absence of water from individual waterholes. We then used this information to model surface-water availability across the whole park under contrasted climatic and management scenarios. We also investigated the variability of surface-water availability over 20-year periods under a natural level of rainfall variability and different artificial water supply efforts. We discussed how a better knowledge of the variability in surface-water availability can improve our understanding of the functioning of herbivore populations and of their effects on ecosystems.

METHODS

Study site

Hwange NP is located on the north-west border of Zimbabwe (19°00′S, 26°30′E) and covers approximately 15 000 km^2. Vegetation is typical of dystrophic semiarid wooded savannas with patches of grassland (Rogers 1993). Surface-water is naturally provided by pans, springs and seeps, most of which dry up during the dry season. Perennial water sources are limited to a few pools of the river situated at the extreme north-west of the park, and to a large dam, also located in the northern part of the park. Locations of the 139 surface-water sources that may retain water during the dry season are shown in Figure 1. In the present manuscript surface-water sources are referred to as waterholes, and are classified either as pans (a natural depression filled by rainfall) or as being of another type such as river pool, spring or seep. Before the study period 67 boreholes had been installed at natural waterholes allowing for artificial pumping of ground water and maintenance of surface-water availability year-round (Anonymous 1999). These waterholes are referred to as artificial waterholes in the manuscript (63 were initially pans, and four were of other types).

Surface-water availability data

From 1982 to 2005 (except in 1983 and 1994) waterholes were monitored once a year at the end of the dry

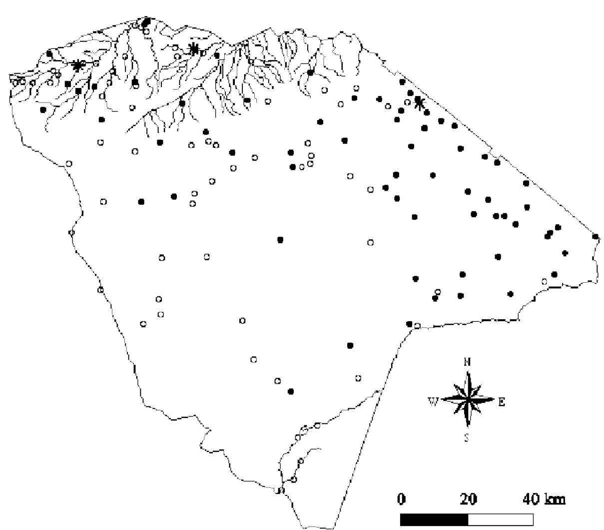

Fig. 1. Map of Hwange National Park showing natural (open symbols) and artificial waterholes (filled symbols). Rainfall-fed pans (circles) are distinguished from springs, seeps or river pools (squares). The river network dries up during the dry season. Asterisks indicate rainfall-collecting stations.

season (September or October) and the presence or absence of water was recorded. Not all waterholes were monitored every year. No systematic records on pumping efforts were available, (i.e. we did not know when artificial waterholes were actually pumped).

Rainfall data

Rainfall data were collected daily from 1928 at three stations located in the northern part of the park (Fig. 1). Hwange NP experiences only one rainy season starting in October, and on average 98% of the precipitation falls between October and April (Chamaillé-Jammes *et al*. 2006). For each station we calculated annual rainfall in year *t* as the sum of precipitation from October in year *t-1* to September in year *t*, and annual rainfall over the park was calculated as the average of the three stations. Long-term annual rainfall is approximately 600 mm (1928–2005) and inter-annual variability is 25% (coefficient of variation; Chamaillé-Jammes *et al*. 2006).

Analyses

Landscape-scale measure of surface-water availability

Various measures can be used to describe surface-water availability across large areas, ranging from the simple measure of waterhole densities to more complex estimations using Thiessen polygons (Ryan & Getz 2005). However, because many ecosystem processes, vegetation characteristics and animal abundances have been shown to be functions of distance-to-water (Andrew 1988; Thrash & Derry 1999), it appears useful to study the distribution of the surface area of the park occurring at varying distances to water. In this study we calculated the percentage of the park's surface area in five classes: 0–2, 2–5, 5–10, 10–20 and >20 km from water. These distances were chosen because they were relevant to the distribution of herbivores and allow for comparisons with other studies (e.g. Western 1975; Redfern *et al*. 2003; Redfern *et al*. 2005). However, because herbivores use the whole range available to them rather than a portion of the landscape in some specific distance-to-water classes, we also reported the cumulative surface area of the park (in percentage) occurring within 2, 5, 10 and 20 km of any waterholes.

Assessing the relationship between rainfall and water occurrence at individual waterholes

The relationship between annual rainfall and the likelihood of waterholes retaining water during the dry season was studied using logistic regressions (Sokal & Rohlf 1995). Analyses were conducted for each waterhole that was surveyed for at least 10 years (24 pans and 18 waterholes of other types), and artificial waterholes were excluded from the analyses as the relationship between annual rainfall and the occurrence of water could have been disrupted by the pumping of ground water. Pans and waterholes of other types were on average monitored for the same number of years (respectively 19.6 ± 4.3 and 19.5 ± 5.3 years; Mann–Whitney test: $W = 210.5$; $P = 0.896$). For both types of waterhole the logistic regressions were also carried out on data pooled over all waterholes of all types to build general relationships between annual rainfall and the probability of waterholes retaining water during the dry season.

Modelling the effects of rainfall fluctuations and pumping at the landscape scale

We studied the respective influences of annual rainfall fluctuations and pumping on surface-water availability across the park. Each measure of surface-water availability was conditioned to (i) a given rainfall; and (ii) a given number of pumped artificial waterholes. All our investigations were based on the same methodological framework:

For each waterhole we used the fitted logistic regressions to estimate the likelihood that it had retained water in the dry season at the given level of rainfall. For the 42 waterholes that were monitored for more than 10 years we used the regressions based on their own data, while for the other waterholes we used the regressions based on the data pooled over all waterholes of their type. Artificial waterholes were considered either pumped and had a probability of retaining water equal to one, or were considered not pumped and had a probability associated with their original type. For each waterhole a random number between 0 and 1 was then drawn from a uniform distribution. If this number was lower than the probability of the waterhole retaining water, it was considered as having water; if the number was higher, the waterhole was considered dry. The area of the park occurring within 2, 2–5, 5–10, 10–20 and >20 km from water was calculated, as well as the cumulative area occurring at a distance lower than 2, 5, 10 and 20 km from water.

Using this framework we carried out two sets of simulations:

1. Annual rainfall was varied from 200 to 1000 mm with either all artificial waterholes pumped or none of the artificial waterholes pumped. We tested these two extremely contrasting scenarios in order to provide information on the range of situations that might be experienced in Hwange NP.

2. We investigated how rainfall variability over time translated into variability of surface-water availability, and how increasing pumping efforts buffered this variability. Surface-water availability was measured over 20 consecutive years, with annual rainfall drawn each year from a normal distribution of the mean 600 mm and variance chosen so that the coefficient of variation was 25%. The number of waterholes actively pumped (0, 5, 10, 20, 30, 40, 50, 60 or 67) was maintained constant inside each 20-year period.

All simulations were carried out on a grid (resolution 500 × 500 m; n = 58 408 cells) using the R *spatstat* library (Baddeley & Turner 2005) and replicated 100 times for each scenario. We compared scenarios using the Pearson χ^2 test of independence (Sokal & Rohlf 1995) on the number of cells in each distance-to-water class, averaged over all replications. The sensitivity of each distance-to-water class to changes in rainfall was estimated by the slope of linear regressions between rainfall and the number of cells in each class, averaged over all replications and standardized to correct for the difference in cell number between classes.

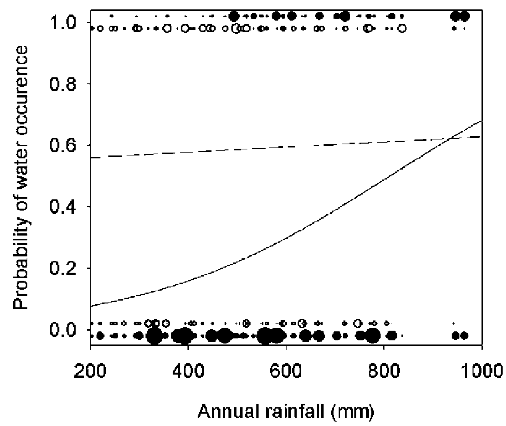

Fig. 2. The relationship between annual rainfall and the likelihood of occurrence of water during the dry season in both rainfall-fed pans (solid line) and waterholes of other types (spring, seeps, river pools – dashed line). The relationship is significant for pans only ($P < 0.0001$). Dot size is proportional to the number of rainfall-fed pans (closed dots) or waterholes of other types (open dots) that retained water (1) or were dry (0) at a given annual rainfall.

RESULTS

Relationship between rainfall and water availability at individual waterholes

The relationship between annual rainfall and the likelihood of waterholes of retaining water during the dry season differed between pans and waterholes of other types. This relationship was positive in 23 out of 24 pans and significant for 12 of them ($P < 0.05$). Conversely, the relationship was positive for 10 out of 18 waterholes of other types, significant ($P < 0.05$) only for three (and among them two were *negative* relationships).

The relationships based on the pooled data were significant for pans ($F_{1,469} = 52.166$; $P < 0.0001$) but not for waterholes of other types ($F_{1,347} = 0.342$; $P = 0.559$) (Fig. 2). Generally pans had a lower probability of retaining water during the dry season than waterholes of other types, except during the wettest years (Fig. 2).

Effects of rainfall fluctuations and pumping at the landscape scale

Under average climatic conditions (rainfall of 600 mm) and without any pumping, 3.8, 15.8, 31.2, 34.8 and 14.2% of the park occurred in the <2, 2–5, 5–10, 10–20 and >20 km distance-to-water classes, respectively (Fig. 3a). However when no artificial pumping was undertaken these proportions varied greatly with annual rainfall (Fig. 3a; $\chi^2 = 24973$, d.f. = 8, $P < 0.0001$). The sensitivity of the <2, 2–5, 5–10, 10–20 and >20 km distance-to-water classes were 4.1, 15.0, 17.9, –7.3 and –29.8 respectively, showing that increases in rainfall mainly reduced the area of the park occurring the furthest from water and increased the area of the park occurring within 2 to 10 km from water (Fig. 3a,c). Modelling a situation where all artificial waterholes were pumped significantly modified the distribution of distance-to-water across the landscape (Fig. 3b; $\chi^2 = 5075$, d.f. = 4, $P < 0.0001$). Although rainfall still had a significant effect on the distribution into distance-to-water classes ($\chi^2 = 3187$, d.f. = 8, $P < 0.0001$), its effect was greatly reduced because pumping was independent of rainfall: the sensitivity of the <2, 2–5, 5–10, 10–20 and >20 km distance-to-water classes were, respectively, 1.8, 5.3, 3.7, –3.7 and –0.1 (Fig. 3b,d). Whatever the actual annual rainfall, the vicinity of surface-water when all artificial waterholes were pumped was similar to one without any pumping in a year of extremely high annual rainfall (compare Fig. 3c with d). Overall, increasing the number of pumped waterholes only slightly increased the absolute long-term surface-water availability experienced over a 20-year period (Figs 4a and 5a,b) compared to the effect of rainfall under a natural situation (Fig. 3c). Conversely, over the same length of time pumping has a drastic effect on the variability of surface-water availability (Figs 4b and 5c,d), particularly on the surface area occurring close to water (<10 km). Over a 20-year period and without

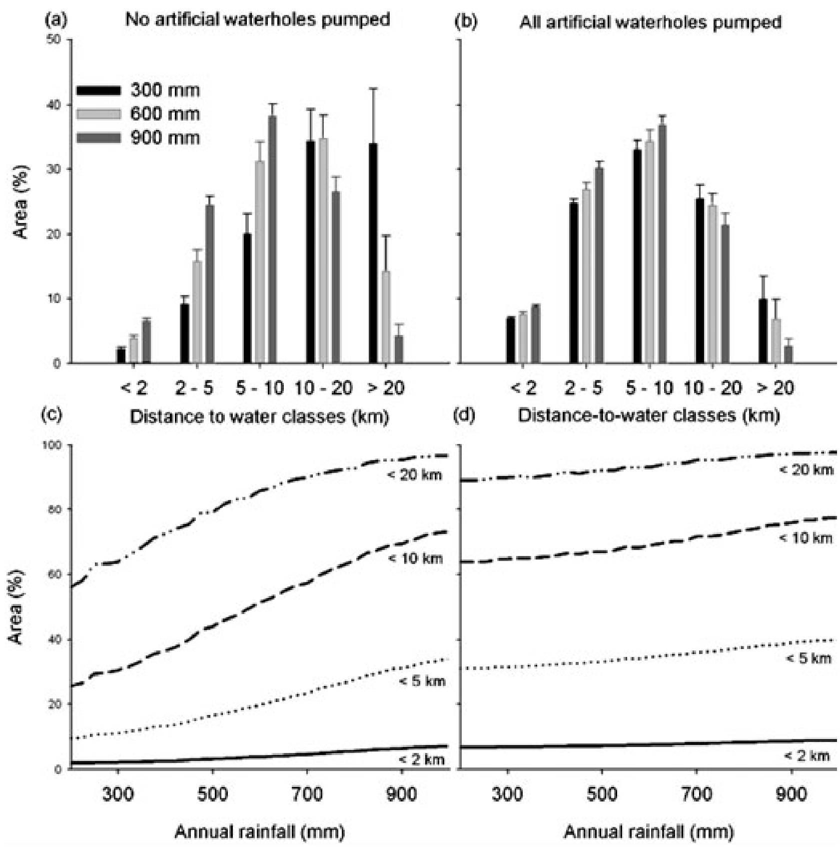

Fig. 3. The percentage of the area of the park in five distance-to-water classes under three contrasted rainfall conditions (a,b) and the relationship between annual rainfall and the cumulative percentage of the area of the park in four distance-to-water classes (c,d) when no artificial waterholes were pumped (a–c) or when all artificial waterholes were pumped (b–d).

pumping the variability of the surface area of the park occurring within <2 km, 2–5, 5–10, 10–20 and >20 km of water varied, respectively, by 29.6, 27.1, 18.4, 14.5 and 11.4%, indicating that over time the surface area of the park occurring within 2 and 5 km of water varied naturally in an extent similar to the one of annual rainfall (CV = 25%).

DISCUSSION

Surface-water exerts a strong constraint on herbivore distribution in arid and semiarid systems, and assessing the availability and the dynamics of surface-water is therefore required to reach a full understanding of these ecosystems. Redfern *et al.* (2005) suggested that surface-water availability at any site can be represented along a gradient of increasing contribution of the ephemeral water sources to the overall surface-water availability. In that respect, Hwange NP clearly lies close to the end of the gradient where ephemeral water sources have a dominant influence when no management action is undertaken. Only 4% and 20% of the Hwange NP occurs, respectively, within 2 and 5 km to water, whereas it is approximately 20 and 80% in the nearby Kruger National Park, South Africa, due to more numerous permanent water sources (Redfern *et al.* 2005). Our results however, suggest that different types of ephemeral water sources should be distinguished. Rainfall-fed pans were, as expected, sensitive to climatic fluctuations, while ground water-based water sources (springs, seeps) did not respond to rainfall changes and generally had a much higher probability of retaining water during the dry season. Taking these differences into account, as well as further waterhole properties, should allow one to improve the accuracy of surface-water availability assessments.

In the absence of any surface-water management, fluctuations in annual rainfall strongly affect surface-water availability in Hwange NP, and the surface area occurring close to water varied at a level similar to rainfall variability. This strongly contrasts with the effect of rainfall on vegetation production that is commonly lower (e.g. Hwange NP: Chamaillé-Jammes *et al.* 2006; Australia: Holm *et al.* 2003; North

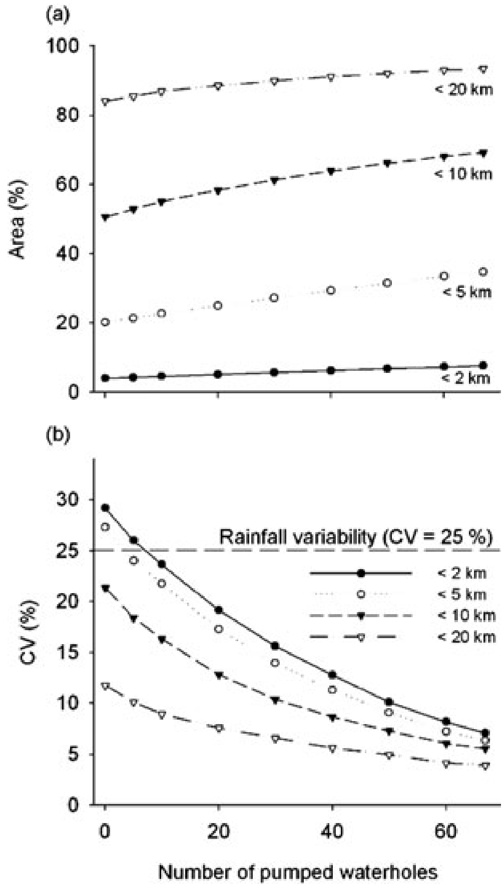

Fig. 4. The relationship between the number of pumped artificial waterholes and (a) the mean and (b) the coefficient of variation over 20 years of the cumulative percentage of the area of the park in four distance-to-water classes. Mean annual rainfall was 600 mm and its coefficient of variation was 25%.

America: Paruelo & Lauenroth 1998), rainfall variability being buffered by soil and plant processes. Decreased sensitivity of vegetation production becomes even higher on heavily grazed, degraded lands (Pickup & Chewings 1994). If such contrast between vegetation and surface-water response to rainfall variability proved to be general, variability in food resources available to herbivores in arid and semiarid systems is likely to be more strongly coupled to rainfall variability through changes in the surface area of the foraging range determined by surface water availability, rather than through the direct effect of rainfall changes on vegetation production, as is usually found in systems with a non-limiting water supply (e.g. Saether 1997). Actually, these are likely to be interactive effects making global forage availability in natural conditions more variable than previously thought, although being finally dependent upon the underlying spatial heterogeneity of forage in the landscape. Of particular relevance is the piosphere development around heavily used waterholes. It creates radial gradients of decreasing forage availability at the vicinity of water (Thrash & Derry 1999; see also Adler & Hall 2005), and the resulting usage gradients can affect individual intake of foraging herbivores and their subsequent survival (Derry 2004). The strength and the persistence of these gradients should thus be taken into account to successfully predict the effects of surface-water variability on herbivore abundance.

Due to their slow demography, variability will tend to lower large herbivore abundances (see Davis *et al.* 2002), and our findings question whether herbivore increase following artificial water provision has arisen more from the buffering of natural variability than from the absolute increase in accessible range. Although it has long been recognized that surface-water strongly constrains the distribution of herbivores in arid and semiarid lands (Rosenstock *et al.* 1999; de Leeuw *et al.* 2001; Redfern *et al.* 2003; Pringle & Landsberg 2004), its effects on population dynamics has so far been neglected (but see Illius & O'Connor 2000 and Derry 2004). Prospective studies of the effect of climatic changes have also ignored surface water availability (e.g. Thuiller *et al.* 2006), so we urge ecologists to investigate its variability in other natural ecosystems.

Surface-water creates focal points in the landscape that concentrate herbivore activity, from which piosphere effects emerge (Andrew 1988; Thrash & Derry 1999). Variability in the distribution and number of waterholes therefore mediates large-scale herbivore effects on ecosystems, not only affecting total herbivore abundance, but also distributing grazing pressure more or less evenly at scales larger than the piosphere. Within the piosphere area, smaller-scale heterogeneity and particularly radial piospheric gradients will also affect herbivore distribution and effects, the interaction between the pre-existing pattern of vegetation heterogeneity and herbivore distribution ultimately influencing vegetation patterns (Weber *et al.* 1998; Adler *et al.* 2001). Variability in surface-water also maintains pulse-type dynamics of grazing pressure at non-permanent waterholes, and it is assumed to allow vegetation to recover when waterholes are dry and grazing pressure is low (but see Thrash 1998).

The framework of this study can valuably be used to investigate opportunities and efficiency of water management practices. Climate-driven fluctuations in surface-water availability can be assessed to estimate the reliability of water provision in the long-term (Schumann 1997). The effects of changing the number and the location of active artificial waterholes can also be tested and compared to management objectives. Interestingly, we showed that the maximum artificial pumping effort presently possible in Hwange NP provides a surface-water availability similar to the one observed under natural conditions in the wettest years

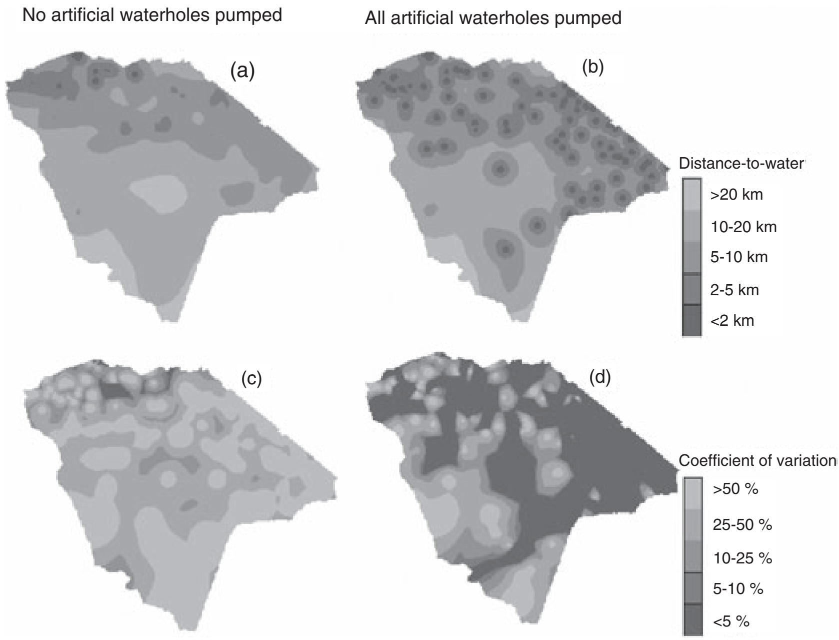

Fig. 5. The spatial distribution of (a,b) five distance-to-water classes and (c,d) the coefficient of variation of distance-to-water over 20 years when no artificial waterholes were pumped (a–c) or when all artificial waterholes were pumped (b–d). Mean annual rainfall was 600 mm and its coefficient of variation was 25%.

of the rainfall range. The most intensive effort of management therefore does not create an unnatural situation, regarding average proximity of surface-water only, but rather simulates and maintains a surface-water availability that would be much rarer under natural conditions. Actually in Hwange NP the most noticeable effect of active artificial pumping on surface-water availability is a reduction in the temporal, climate-induced, variability. In the long-term it significantly increases only the extent of the park occurring close (<5 km) to water. This arises because, compared to a fully natural situation, artificial pumping greatly increases surface-water vicinity only during dry years, and because of the large spatial overlap between areas defined by these artificial waterholes (2.4, 20.6, 52.8, 79.5% for the <2, <5, <10 and <20 km cumulative distance classes, respectively). Artificially supplying water therefore reduces the likely major cause of fluctuations in the abundance of herbivore populations. Populations are allowed to build up to levels where they become limited by forage available within the maximum dry season foraging range, and it can negatively feedback on herbivore populations during droughts, causing large mortalities, as no reserve forage is available (e.g. Walker *et al.* 1984). Artificial waterholes also reduce the spatial variability in herbivore distribution as populations become sedentary around artificial waterholes, and vegetation finds itself under permanent high herbivore pressure. Ultimately this situation often leads to over use and drastic changes in the vegetation around waterholes (e.g. Africa: Parker & Witkowski 1999; Australia: Landsberg *et al.* 2003; North America: Washington-Allen *et al.* 2004), and rangeland degradation has become a major issue worldwide where water provision has been used to increase livestock or wildlife abundance (Milton *et al.* 1994). Generally, although artificial water provision is commonly implemented to increase permanent accessibility of the landscape to herbivores, it could be that these effects should be traded against overlooked adverse consequences of reducing the natural variability of grazing processes.

In this study we showed that the variability of the surface area of Hwange NP accessible to large herbivores was of a similar magnitude to that of annual rainfall when no pumping was undertaken. Because the direct response of vegetation production to rainfall fluctuations is buffered, even in arid lands, variability in the size of the foraging range of herbivores determined by surface-water availability could be an important mechanism of the natural regulation of large herbivores if such a situation proved to be general. Artificial water provision that stabilizes surface-water availability is presently under much criticism, and our findings contribute to the understanding of ecological mechanisms underlying alternative management practices. Given the implications for the management and conservation of rangelands and wildlife-rich tropical lands, we call for further investigation of surface-water availability in natural ecosystems.

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