

# Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population

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## Summary

1. An emerging perspective in the study of density dependence is the importance of the spatial and temporal heterogeneity of resources. Although this is well understood in temperate ungulates, few studies have been conducted in tropical environments where both food and water are limiting resources.
2. We studied the regulation of one of the world's largest elephant populations in Hwange National Park, Zimbabwe. The study period started in 1986 when the population was released from culling. Using census data we investigated changes in elephant abundance with respect to rainfall and density across the entire park and across waterholes.
3. The population more than doubled since culling stopped. The population increased continuously during the first 6 years, and then fluctuated widely at about 30 000 individuals. Immigration processes must have been involved in the increase of the population size.
4. Population growth rates were negatively related to previous population density by a convex relationship, and negatively related to the ratio of previous population density on annual rainfall by a linear relationship. However, only this latter model (i.e. assuming a fluctuating carrying capacity related to annual rainfall) produced realistic dynamics. Overall, population decreased during dry years when the elephant density was high.
5. During dry years there were fewer waterholes retaining water during the dry season and consequently elephant numbers at waterholes increased, while their aggregation level across waterholes decreased. On the long-run elephant numbers increased only at the less crowded waterholes.
6. We suggest that the interaction between population size and the available foraging range determined by the number of active waterholes during the dry season controls the park population.
7. Our results emphasize the need to understand how key-resource areas cause resource-based aggregation, which ultimately influences the strength of density dependence. More specifically, this study suggests that climate variability strongly affects local elephant population dynamics through changes in surface-water availability. Finally, as dispersal is likely to be an important driver of the dynamics of this population, our results support views that a metapopulation framework should be endorsed for elephant management in open contexts.

**Key-words:** Africa, megaherbivore, rainfall, resource heterogeneity, surface-water.

## Introduction

Intraspecific competition for common resources leads to a negative feedback between population size and population growth, expressed through reduced reproduction, increased mortality and/or dispersal. This type of density dependence is

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an important component of the regulation of populations in many systems, as for instance in ungulate populations (e.g. Fowler 1987; Gaillard *et al.* 2000; Sinclair 2003). Although resource depletion alone is sufficient to regulate population dynamics in homogeneous environments (May 1976), there is a growing recognition that resource heterogeneity, both in space and time, greatly matters (e.g. Sibly, Hone & Clutton-Brock 2003; Wang *et al.* 2006; see also Keeling, Wilson & Pacala 2000). For instance, interannual variability in the availability of some resources mediates the effects of density on demographic rates (e.g. for ungulates: Saether 1997), and enhances the crucial role of key-resource areas (*sensu* Illius & O'Connor 2000) on which animals depend to survive critical periods. Both the spatial arrangement and the extent of key-resource areas have the potential to affect population distribution and dynamics (e.g. Fryxell *et al.* 2005). In particular, interactions between the availability of resource patches and their accessibility can cause resource-based aggregation of individuals that creates heterogeneity in population density across landscapes. This 'crowding' effect (Lloyd 1967) increases intraspecific competition, which can in turn intensify the strength of density dependence (Taylor & Taylor 1977). Identifying interactions between resource variability, aggregation levels and population size is clearly a prerequisite to a better understanding of the mechanisms underlying density dependence (Sutherland 1996).

Large temperate ungulates in predator-free environments often build up to large populations and are then affected by an interplay between population density and climate-driven environmental stochasticity (Saether 1997; Sinclair 2003). How this applies to tropical ungulates living in highly variable environments remains poorly understood, as only few studies have actually been conducted in these ecosystems (Owen-Smith 1990; Mduma, Sinclair & Hilborn 1999; Georgiadis, Hack & Turpin 2003; Owen-Smith, Mason & Ogutu 2005). Most studies, however, pointed out that rainfall is a major driver of herbivore populations through its effect on food resource availability. The role of associated changes in surface-water availability, an obligatory, heterogeneously distributed resource in semi-arid ecosystems, remains poorly investigated (Redfern *et al.* 2003; Chamaillé-Jammes, Valeix & Fritz 2007). Ultimately, in these predator-rich environments, predation may obscure the interpretation of the observed relationships between resources and herbivore abundances (Sinclair, Mduma & Brashares 2003; Owen-Smith *et al.* 2005).

Here we studied the regulation of one of the world's largest African elephant *Loxodonta africana* (Blumenbach) populations, located in Hwange National Park (hereafter Hwange NP), Zimbabwe. Predation on elephants is anecdotal, therefore making this species a simplified model to study population regulation. Protected elephant populations in southern Africa have reached unprecedented levels of elephant densities due to successful conservation efforts or release from legal population control exercises (Blanc *et al.* 2005). The factors regulating elephant populations remain, however, unknown and are currently widely debated: across-site comparisons have shown that elephant biomass is related

to mean annual rainfall (Fritz *et al.* 2002), suggesting a tight link between elephants and their resources. Bulte *et al.* (2004) recently argued that elephant populations could rather be limited by density-independent catastrophic mortalities typical of a 'disequilibrium' dynamics, while Caughley's model (1976) of coupled cycles between vegetation and elephants is still favoured by many researchers (but see Duffy *et al.* 1999). The scale at which the regulation of elephant populations may occur also remains uncertain, as the species ranging ability is beyond the extent of most study areas, and populations may respond to changing environmental conditions primarily through dispersal movements (Laws, Parker & Johnstone 1975). It is only now that populations have recovered from being controlled by human intervention that regulatory factors may be identified by using long-term monitoring studies.

The elephant population of Hwange NP was released from culling in 1986. Using data from aerial censuses, we first described the dynamics of the population and assessed the effects of population density and annual rainfall on population changes. Then, using waterhole census data, we studied elephant number and distribution at waterholes. We discussed how these results suggest (1) that surface-water availability and population size mediate elephant aggregation levels and ultimately drive the local regulation of the population, and (2) that population changes are likely to be caused by dispersal movements, although further research, and particularly investigation of population age structure, is needed.

## Materials and methods

### STUDY SITE

Hwange NP, located on the north-west border of Zimbabwe (19°00' S, 26°30' E), covers an unfenced area of c. 15 000 km<sup>2</sup>. Vegetation is typical of southern African dystrophic wooded savannahs with patches of grasslands (Rogers 1993; Chamaillé-Jammes, Fritz & Murindagomo 2006). Surface water becomes scarce in the dry season, as the river network and most natural pans dry up. In addition to the few natural waterholes retaining water throughout the dry season, up to 67 artificial waterholes can maintain water availability year-round through ground water pumping. Although the park hosts a wide variety of herbivores, elephants represent more than 85% of the total biomass of large herbivores. Since culling stopped in 1986 anthropogenic mortality has been limited to illegal off-take and official ration hunting, unlikely to affect population dynamics as most killed animals were males and both off-take were low (< 100 per year) compared with population estimates.

### RAINFALL DATA

Rainfall data were collected daily since 1928 at three different stations and rainfall over the park was estimated by the average of these stations. On average 98% of the annual rainfall occurs during the season extending from October to April (Chamaillé-Jammes *et al.* 2006). Annual rainfall for year *t* was therefore calculated as the integrated rainfall from October in year *t* - 1, to September in year *t*. Long-term mean annual rainfall is 606 mm (1928–2005).

## AERIAL CENSUSES

Aerial strip-transect censuses were conducted annually from 1980 to 2001 (except in 2000) at the end of the dry season (conducted by Zimbabwe Parks and Wildlife Management Authority from 1980 to 1992; Price Waterhouse Consultants 1996; conducted by the World Wildlife Fund (WWF) from 1993 to 2001: Working Papers available at the WWF Regional Office).

These censuses followed standard procedures recommended in Norton-Griffiths (1978) and were analysed using Jolly's (1969) method, producing population estimates as well as an estimation of the census errors (standard errors and 95% confidence intervals).

## WATERHOLE CENSUSES AND WATER AVAILABILITY

Twenty-four-hour animal censuses at waterholes (natural or artificial pans, seeps and springs) were conducted from 1967 to 2005 (except in 1968–71, 1976–81 and 1983). Once a year during late September–early October (end of the dry season) at full moon, the number of animals coming to drink from midday to midday the next day was recorded for all species. Data from 1986 and 1997 were not included in the analyses because rains occurred during the surveys, and animals were able to drink in the numerous ponds created. Contrary to other years, the number of animals counted in 1986 and 1997 were then very low and not representative of dry season abundances around waterholes.

Waterholes were visited 1 week before the census to note presence or absence of water. An index of water availability in the park was calculated for each year as the proportion of waterholes that had retained water during the dry season. Data were available from 1982 to 2005 (except 1983 and 1994).

## STATISTICAL ANALYSES

Our objective was to identify the natural factors of regulation and we restricted our analyses to data collected after the culling operations, i.e. we used data collected from 1986 onwards. Fifteen annual estimates of population size from aerial censuses and 18 years of waterhole censuses originating from 45 waterholes regularly monitored were analysed.

## POPULATION TRENDS AND GROWTH RATES

Population abundances  $N_t$  and population growth rates, calculated as  $\log_e(\lambda = N_t/N_{t-1})$ , were derived from the aerial census data. We investigated population dynamics (population trends and population growth rates) by primarily fitting concurrent models, then selecting the most likely model using information-theoretic approaches – Akaike Information Criteria corrected for small sample size: AICc; model a could be considered more likely to represent the true dynamics than model b when  $\Delta\text{AICc} (= \text{AICc}_b - \text{AICc}_a) > 2$  (Burnham & Anderson 2002). Relative strength of evidence of each model was assessed using Akaike weights (referred to as  $w$ ) and we used  $R^2$ , proportion of the variance explained by the model, as a general measure of goodness-of-fit. We combined a priori density-independent and density-dependent models emerging from theoretical studies of population dynamics in closed context (random walk, exponential, linear, logistic, Ricker and Gompertz models – see Jacobson *et al.* 2004 or Brook & Bradshaw 2006 for details), and also allowed for alternative dynamics by using more descriptive models (piecewise regression, generalized theta-logistic model – see Turchin 2003).

Seven competing models were fitted to determine the most likely population trend since culling stopped: no trend (stochastic fluctuations around the mean), an exponential increase, a linear increase, a logistic increase, two asymptotic increases allowing to model the shape of abundance changes of population experiencing Ricker and Gompertz dynamics (respectively  $N_t = a - b * \exp(-c * t)$  and  $N_t = a * \exp(-b * \exp(-c * t))$ , with  $a, b, c$  constants and  $t$  an index of time). We also allowed for a two-phase dynamics by fitting a piecewise regression with one breakpoint (Toms & Lesperance 2003; each year tested as a breakpoint, and the best model was selected using AICc).

Rate of population changes and density dependence were investigated by fitting variants of the generalized theta-logistic equation commonly used to describe population dynamics (Getz 1996; Turchin 2003; Brook & Bradshaw 2006) and consistent with life-history theory predicting various shapes of density dependence (Fowler 1981, 1988; Owen-Smith 2006):

$$\log_e(\lambda) = r_m [1 - (N_t/K)^\theta] + \epsilon \quad \text{eqn 1}$$

with  $r_m$  the maximal intrinsic population growth rate,  $K$  the ecosystem's carrying capacity,  $\theta$  the shape parameter, and  $\epsilon$  a stochastic error with a mean of zero.

Measurement errors in population estimates can produce spurious density dependence (Shenk, White & Burnham 1998; Freckleton *et al.* 2006). The potential confounding effect of errors in population estimates in our data set was assessed as follows: we reproduced random measurement errors by simulating time series of population estimates from a time-invariant population. For year  $t$  of a simulated time series, a population estimate was drawn from a normal distribution of mean  $\mu = 30\,000$  and variance  $\sigma = (\text{SE})^2$  where SE was the estimated standard error of the original population estimate in year  $t$ . Ten thousand simulated time series were produced. We fitted density-independent random walk and density-dependent Ricker and Gompertz models to each of them and extracted the AICc-related statistics to assess if the observed level of measurement errors may produce spurious density dependence. It is ultimately expected that a pure census errors process should produce log-linear ( $\theta = 0$ ) shape of density dependence (Freckleton *et al.* 2006). We therefore also fitted a theta-logistic model with a fixed shape parameter corresponding to the best theta-logistic model fitted to the original data set to assess if measurement errors alone may reproduce the observed shape of density dependence.

However, the assumption of a fixed carrying capacity underlying the theta-logistic model has been challenged, particularly in highly variable environments. In African savannahs rainfall is the main driver of herbivore food production and is commonly used in carrying capacity models (e.g. Pascual, Kareiva & Hilborn 1997; Georgiadis *et al.* 2003). We therefore also fitted a variant of eqn 1 allowing for the carrying capacity to be fluctuating as a function of annual rainfall:

$$\log_e(\lambda) = r_m [1 - (N_t/\alpha * \text{AR})] + \epsilon \quad \text{eqn 2}$$

with AR the annual rainfall and  $\alpha$  a constant giving the number of elephants that can be sustained per mm of rainfall. The site-specific rainfall–vegetation production relationship is often linear in semi-arid lands (e.g. Le Houérou 1984), and this model is therefore an analogue of the ratio-dependent models of predator dynamics (Arditi & Ginzburg 1989; for recent use of this equation in ungulate demography see Hone & Clutton-Brock 2007). Although this model is usually modelled as linear, it can be seen from eqns 1 and 2 that eqn 2 could be fitted as a nonlinear equation:

$$\log_e(\lambda) = r_m[1 - (N_t/\alpha * AR)^\theta] + \epsilon \quad \text{eqn 3}$$

where  $\theta$  retains the meaning of the abruptness of population response to the ratio of population abundance on present carrying-capacity.

#### SURFACE-WATER AVAILABILITY, WATERHOLE ATTENDANCE AND AGGREGATION

The annual proportions of the surveyed waterholes that retained water during the dry season were normalized using the arcsine transformation before analyses. The mean elephant number coming to drink per waterhole per 24 h was studied in relation to total population size assessed via aerial census and to annual rainfall. We also investigated patterns of elephant aggregation across waterholes in relation to elephant numbers. Aggregation can be modelled in many ways, but the negative binomial distribution with parameters mean  $m$  and dispersion  $k$  is the most commonly used, allowing us to model a wide range of distribution as it asymptotically ( $k \rightarrow \infty$ ) approximates a random Poisson distribution (Krebs 1989).  $k$  alone can be used as an index of aggregation only when  $m$  remains constant. Since in our study  $m$  varied between years, the coefficient of variation of the negative binomial,  $CV = \sqrt{(1/m + 1/k)}$  was used as an aggregation index (Grear & Schmitz 2005). Lower CV will indicate a more even distribution of elephants across waterholes.

Long-term changes in elephant crowding were also assessed. Elephant numbers at waterholes were subject to strong interannual fluctuations associated to annual rainfall (see the Results section) and, therefore, temporal trends were not readily available. However, 20 waterholes were surveyed for at least 3 years both at the start and at the end of the study period, allowing us to accurately assess long-term changes in elephant attendance at these waterholes. The annual rate of increase  $R$  (in percentage) was calculated as:

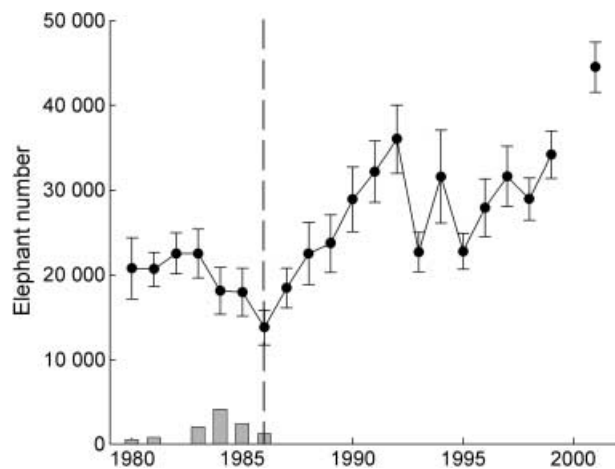
$$R = ((N_t/N_0)^{1/t} - 1) \times 100$$

(Caughley 1977) with  $N_0$  being the initial elephant attendance (calculated as the average elephant number seen in 1987, 1988 and 1989),  $N_t$  the final elephant attendance (calculated as the average elephant number seen in 2003, 2004 and 2005), and  $t$  the time elapsed between these two observations (16 years). Using AICc-related statistics we compared three alternative models: no relationship, linear or nonlinear relationship between  $R$  and the initial elephant attendance.

## Results

### POPULATION TRENDS

The population increased dramatically after culling stopped in 1986 (Fig. 1), reaching an average density of more than two



**Fig. 1.** Estimated elephant numbers ( $\pm$  SE) in Hwange NP from 1980 to 2001. Bars indicate the number of culled elephants. Culling stopped in 1986 before the annual census.

elephants per km<sup>2</sup> over the whole park. The confrontation of alternative models clearly showed that the observed dynamics was most likely to be described by the best two-phase, piecewise regression model (relative support of 97.9%), rather than by any a priori model designed for closed context dynamics (Table 1). This piecewise regression identified a breakpoint in the population dynamics in 1992. The population increased continuously up to 1992 at a mean annual rate of 17.7% ( $\pm$  10.2 SE), and then fluctuated widely around 30 000 individuals (Fig. 1).

### POPULATION CHANGES

It was very likely that the study population experienced some form of density dependence, as the overall relative support for density dependence models was 98% (Table 2a). The raw relationship between population growth rates and population abundances was actually likely to be convex (Fig. 2a; theta-logistic shape parameter  $\theta = 6.55 \pm 2.51$  SE), and predicted negative population growth rates above 30 608 elephants, i.e. above an average density of *c.* 2 individuals per km<sup>2</sup> over the whole park. Measurement errors alone were far more likely to produce a linear or log-linear density dependence (overall relative support = 79%) than this particular shape, although this possibility could not be fully rejected (Table 3).

A model with a fluctuating carrying capacity linked to annual rainfall was more parsimonious when assumed to be

	k	AICc	$\Delta$ AICc	w	R <sup>2</sup>
Stochastic	2	314.771	18.143	0.000	0.000
Exponential	3	306.143	9.515	0.008	0.541
Linear	3	306.021	9.392	0.009	0.547
Logistic	4	310.203	13.575	0.001	0.530
Asymptotic (Ricker-type)	4	309.624	12.996	0.001	0.555
Asymptotic (Gompertz-type)	4	310.012	13.384	0.001	0.531
Two-phase (piecewise)	5	296.628	0.000	0.979	0.863

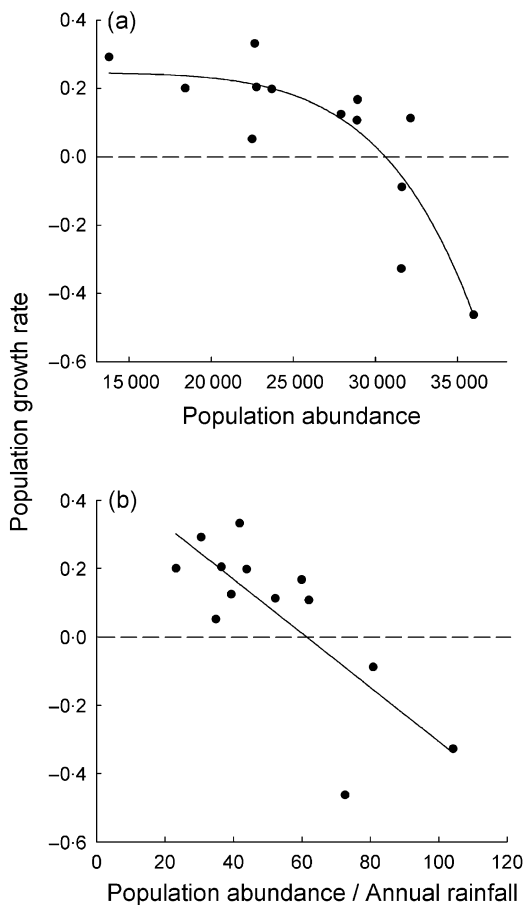
**Table 1.** Alternative models of population dynamics since culling stopped in 1986. Number of parameters (k), AICc,  $\Delta$ AICc, Akaike weights ( $w$ ) and R<sup>2</sup> are shown

**Table 2.** Alternative models of population growth rates since culling stopped in 1986. (a) Variants of theta-logistic models with fixed carrying capacity (c.c.) when estimated. (b) Variants of theta-logistic models with c.c. either fixed or simple function of rainfall. Number of parameters ( $k$ ), AICc,  $\Delta$ AICc, Akaike weights ( $w$ ) and  $R^2$  are shown. See text for details

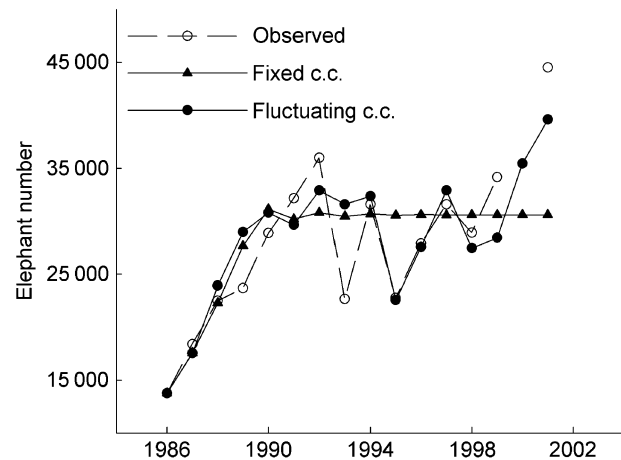
	$k$	AICc	$\Delta$ AICc	$w$	$R^2$
(a) Random walk	1	1.544	7.989	0.013	0.000
Exponential	2	3.170	9.615	0.006	0.000
Ricker	3	-3.684	2.760	0.185	0.548
Gompertz	3	-1.460	4.985	0.061	0.464
Theta-logistic	4	-6.445	0.000	0.735	0.738
(b) Fixed c.c., estimated $\theta$	4	-6.445	0.000	0.592	0.738
Rainfall-associated c.c., estimated $\theta$	4	-1.457	4.988	0.049	0.616
Rainfall-associated c.c., $\theta = 1$	3	-5.447	0.999	0.359	0.605

**Table 3.** Alternative models of spurious density dependence produced by measurement errors alone. Number of parameters ( $k$ ), mean AICc over 10 000 runs of density independent simulations,  $\Delta$ AICc and Akaike weights ( $w$ ) are shown

	$k$	Mean AICc	$\Delta$ AICc	$w$
Random walk	1	-9.581	4.238	0.048
Ricker	3	-13.769	0.050	0.391
Gompertz	3	-13.818	0.000	0.401
Theta-logistic (fixed $\theta = 6.55$ )	3	-11.990	1.829	0.161



**Fig. 2.** The relationships between population growth rates and (a) population abundance (b) ratio of population abundance on annual rainfall.



**Fig. 3.** Observed vs. predicted elephant populations dynamics since culling stopped. Predicted dynamics were deterministic runs (seeded with the observed 1986 census) of theta-logistic models of population growth rates assuming either fixed or fluctuating, rainfall associated, carrying capacity (c.c.). See text for details.

linear (Table 2b). Indeed, assuming a nonlinear shape for this relationship produced a similar fit and the shape parameter of the relationship did not differ significantly from 1 ( $\theta = 1.55 \pm 1.29$  SE). There was therefore virtually no support for this nonlinear model (Table 2b), and the usual ratio-dependent model assuming a priori a linear relationship was the second best model (Table 2a,b), receiving only slightly less support than the simple theta-logistic density-dependent model (Table 2b; Fig. 2b). However, these two models produced highly different deterministic dynamics when seeded with the initial 1986 census (Fig. 3). The density-dependent only model produced an almost stable dynamics once the population approached the equilibrium density, as the abruptness (i.e.  $\theta$ ) of density dependence was too low to produce population fluctuations given the low maximum population growth rate (Fig. 3). The linear ratio-dependent model produced a far more realistic dynamics remarkably similar to the observed one (Fig. 3). In this model, the estimated number of elephants that can be sustained per mm of rainfall was  $61.280 \pm 5.776$  SE, therefore long-term average carrying capacity of the park could be estimated to be  $61.280 \times 606 \text{ mm} = 37\,136$  elephants. The population has been below this level most of the time since 1992 probably because five of the nine census years were below-average

**Table 4.** Alternative models of changes in mean elephant number per waterhole. Density refers to total elephant population size over the Park. Number of parameters ( $k$ ), AICc,  $\Delta$ AICc, Akaike weights ( $w$ ) and  $R^2$  are shown

	$k$	AICc	$\Delta$ AICc	$w$	$R^2$
Stochastic	2	223.592	68.907	0.000	0.000
Density	3	161.847	7.162	0.024	0.063
Rainfall	3	213.404	58.718	0.000	0.517
Density + rainfall	4	154.685	0.000	0.856	0.613
Density $\times$ rainfall	5	158.603	3.917	0.121	0.659

rainfall years (with for instance only 50% of the long-term average received in 1995).

#### AGGREGATION AND WATERHOLE ATTENDANCE

There was a strong support for an increase in the proportion of waterholes that retained water during the dry season with increasing rainfall (AICc = -16.032,  $w$  = 0.921,  $R^2$  = 0.37 compared with stochastic variation around the mean: AICc = -11.112,  $w$  = 0.079).

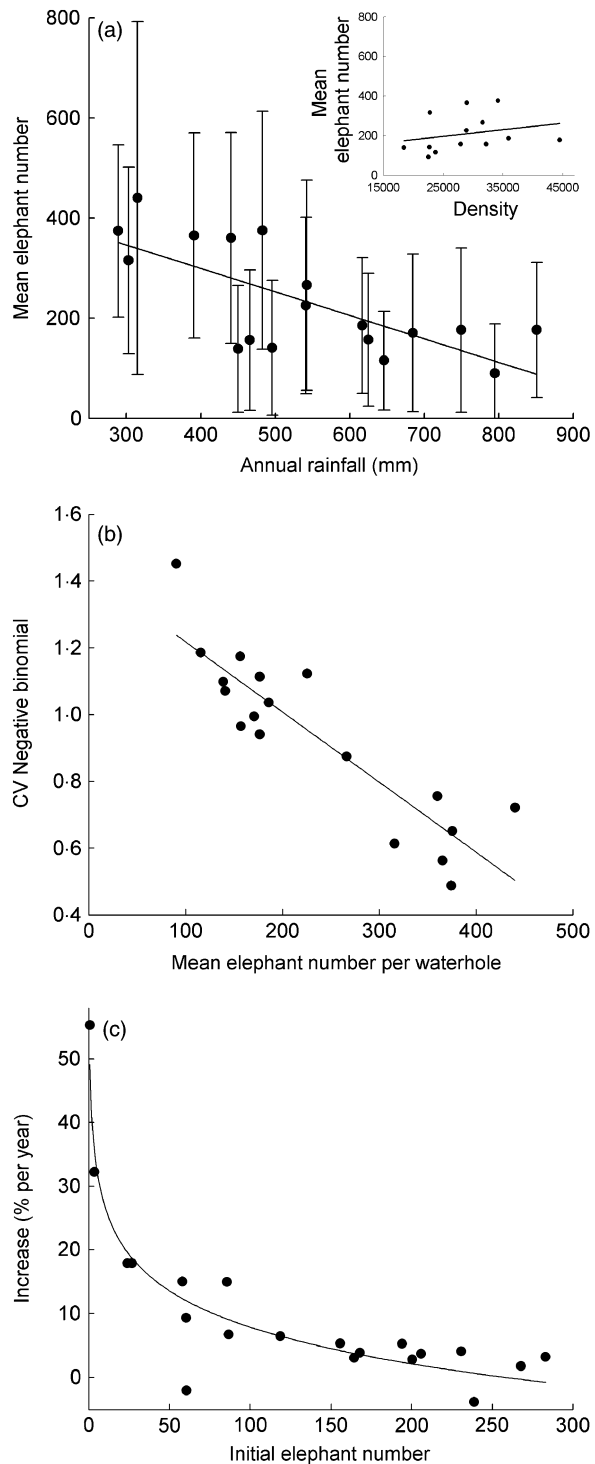
A relationship between mean elephant number per waterhole and population abundance only or rainfall only had a low support (respectively 0.024 and < 0.001; Table 4) compared with the model integrating additive effects of these two variables, found to be the most parsimonious model (Table 4). Overall, annual rainfall had a negative effect with a strong explanatory power, whereas population density a weak positive effect on the mean elephant number per waterhole (Table 4, Fig. 4a).

It was likely that aggregation of elephants across waterholes decreased with increasing elephant number at waterholes (compared with stochastic variation around the mean:  $\Delta$ AICc = 25.13,  $w$  = 0.999%,  $R^2$  = 0.789; Fig. 4b). In the long-run elephant numbers increased more rapidly at waterholes where initial elephant numbers were low (relative support for an absence of relationship was virtually zero), and a non-linear model was far more likely than a linear one (respectively AICc = 122.562,  $w$  = 0.999 and AICc = 154.388,  $w$  < 0.001), predicting no increase in elephant numbers at waterholes having an initial elephant attendance above 258 individuals (Fig. 4c).

## Discussion

#### POPULATION TRENDS

The elephant population of Hwange NP more than doubled since culling stopped in 1986. Most of the increase happened during the first 6 years, when the population increased continuously at a mean annual rate (17.7%) much greater than any theoretical calculus (e.g. 7% in Calef 1988) or field observation (11.28% in Moss 2001) of maximum population growth rate. Clearly, the population recovery was not only due to a demographic increase but immigration played a major part in the building up of the population. This is also supported by the observation that no a priori model of closed population



**Fig. 4.** (a) The relationship between mean elephant number ( $\pm$  SD) per waterhole and annual rainfall; inset: the relationship between mean elephant number per waterhole and population density, SD not shown for clarity. (b) The relationship between an aggregation index (the coefficient of variation of the fitted negative binomial distribution) and the mean elephant number per waterhole. Lower values of the index indicate a more even distribution. (c) The relationship between long-term annual rate of increase in elephant numbers at waterholes and the initial elephant numbers.

dynamics performed as well as a purely phenomenological two-phase (immigration/stabilization) model. It also supports previous suggestions that culling has an indirect effect on population abundance via a disturbance effect, elephants avoiding culling areas in spite of increased resource availability due to reduced intraspecific competition (van Aarde, Whyte & Pimm 1999). Since 1992 the population has been fluctuating around 30 000 elephants (i.e. around an average density of two individuals per km<sup>2</sup> over the whole park), although inside the park local densities during the dry season can be as high as nine elephants per km<sup>2</sup> (over areas about 1/10th of the park; Chamaillé-Jammes *et al.* unpublished data). This is presently one of the highest densities observed in elephant populations, and probably one of the first large elephant populations showing signs of local regulation (Blanc *et al.* 2005). By local, we mean that we are aware that the observed population changes have partly arisen from immigration/emigration processes in addition to demographic responses (mortality/fecundity). There is evidence that the Hwange elephant population is part of a larger metapopulation also covering south-west Zambia and northern Botswana where high elephant densities are also found (Hoare 2004; Blanc *et al.* 2007). Recent theoretical studies on metapopulations have highlighted the importance of local population dynamics to understand and predict dynamics at the metapopulation scale (Freckleton *et al.* 2005), and our study provides a first step towards such modelling. Our results therefore also support views suggesting that a metapopulation approach should be favoured when managing elephants in open, locally overabundant, populations (van Aarde & Jackson 2007).

#### POPULATION CHANGES

We showed that the raw relationship between population growth rates and density was negative and convex (for a similar relationship for the Serengeti elephant population, see Sinclair 2003). Detection of density dependence from census data has been widely debated (Shenk *et al.* 1998; Freckleton *et al.* 2006), as measurement errors alone can induce spurious density dependence. In many censuses the extent of measurement error is not known, which precludes the statistical testing of such effect. Here the sampling methodology (sample counts rather than 'total' counts) provided an estimate of census errors and allowed us to show that these errors were unlikely to have produced the observed convex pattern. This is also consistent with the simulation results of Freckleton *et al.* (2006) showing that the likelihood of detecting spurious density dependence is low when times series are short and with relatively low measurement error rates, as in our study where the confidence interval was on average 24% of the population estimate. It gives confidence in the fact that our results revealed ecological mechanisms rather than spurious statistical effects, and highlights that census methods estimating census errors should be favoured, while a variety of techniques are developing quickly to account for census errors in the detection of density dependence (see Freckleton *et al.* 2006).

However, the interpretation of the convex density-dependent relationship should be made with caution. First, we showed that this model, although providing a good fit of population growth rates, was unable to correctly mimic the observed highly variable population dynamics. Secondly, the estimated value of  $\theta$  was low compared with the expectations associated with elephant life history. Indeed, Fowler (1988) reported that the inflection of the population growth rate curve should occur at 85% of the equilibrium density for elephants, results that could be obtained only by theta values higher than 9 in the theta-logistic equation fitted to our data set. Clearly, simple models assuming fixed carrying capacity and reproduction/survival responses only do not correctly represent this complex system. It has been recognized that density dependence processes cannot be fully encompassed without taking into account the spatial and temporal heterogeneity in resources. For instance many studies of large herbivores have found that density effects were stronger during harsh conditions (e.g. Saether 1997) or in homogeneous environments (e.g. Wang *et al.* 2006). Here we showed that assuming a rainfall-associated carrying capacity provided a good fit model and allowed to simulate realistic dynamics, although the additional parameter needed to investigate nonlinearity would cause such a model to be rejected. Lima & Berryman (2006) recently also found that the carrying capacity of theta logistic models of an Ibex population could be related to climatic conditions (without making it an a priori model assumption), and additionally emphasized how the ability of predicting realistic dynamics should be part of the model selection process, although validation against independent *out-of-sample* data should be preferred when possible. Overall, these results call for further investigations of ratio-dependent models (as well as of the meaning of their potential shapes) where herbivore numerical responses depends on relative, rather than absolute, abundance of food (Arditi & Ginzburg 1989; Hone & Clutton-Brock 2007).

#### SKETCHING A CONSISTENT SURFACE-WATER-BASED SCENARIO

Rainfall positively influences vegetation productivity in Hwange NP (Chamaillé-Jammes *et al.* 2006) and a decrease in food resources alone could have been called for to explain the interacting effects of density and rainfall on population growth rates. However, our results suggested more complex processes where both density and spatio-temporal variability in resources interact to shape the local regulation of populations. Indeed, decreases in rainfall reduce local food availability as well as the number of waterholes that retain water throughout the dry season (this study; see also Chamaillé-Jammes, Fritz & Murindagomo *et al.*, in press). Elephant number at the remaining waterholes increases because individuals need to remain no more than a few kilometres away from water sources in the dry season (Stokke & du Toit 2002; Redfern *et al.* 2003; see also Cushman, Chase & Griffin 2005; Grainger, van Aarde & Whyte 2005). Additionally to an increased competition for water, a larger number of elephants

at waterholes increases browsing pressure and food depletion and should increase costs associated to the aggregation at waterholes, particularly those associated to the distance travelled between water and foraging areas. Although no data were available to investigate the availability of food resources around waterholes, gradients of food availability with increasing distance to water are a common feature of heavily used waterholes in semi-arid systems (Thrash & Derry 1999). Our study revealed a long-term saturation process occurring at waterholes, supporting previous results demonstrating the limitation of local, within-park, elephant density by surface-water availability (Chamaillé-Jammes *et al.* 2007). Such a saturation process, associated to the finite number of waterholes, is an appealing candidate for the mechanism determining the carrying capacity of this ecosystem. Our results thus support the theoretical model of Illius & O'Connor (2000) where surface-water actually defines key-resource areas by shaping the seasonal restriction of the foraging range and as a consequence determines the carrying capacity of the ecosystem. The very large elephant abundance recorded in 2001 is, for instance, likely to be linked to two consecutive years of high rainfall (2000 and 2001, respectively, 53% and 35% above average annual rainfall) providing exceptional conditions of food and surface-water availability. We showed elsewhere that population redistribution related to surface-water occurs within the park (Chamaillé-Jammes *et al.* 2007). Because the observed population changes could not arise only from reproduction/survival processes, the present study suggests that density-dependent responses to fluctuations in the carrying-capacity of the park could also occur through dispersal at a larger, regional scale, highlighting the importance of these processes for the regulation of elephant populations.

#### UNRAVELLING THE MECHANISMS BEHIND THE OBSERVED POPULATIONS CHANGES

Negative relationship between population growth rates and density is usually considered in the theoretical context of closed population and attributed to changes in reproduction and/or survival (Gaillard *et al.* 2000). In large herbivores it is now well established that the response of these demographic parameters occurs sequentially (Eberhardt 2002), affecting primarily the ones for which the population growth rate is the less sensitive (Gaillard *et al.* 2000). The shape of density dependence is ultimately an outcome of the intrinsic responses of all demographics parameters to changes in density (Owen-Smith 2006). Although density-dependent habitat selection can mediate the strength of density dependence (Morris 2003), the scale of potential animal movement is often much smaller than the extent of large-scale, climate-based, changing resource availability. However, for large ranging animals, and particularly for elephants, dispersal could be an efficient strategy to mediate both density and resource variability (Clobert *et al.* 2001). We could therefore expect the response of elephant populations to changing environmental conditions to occur primarily through dispersal, with reproduction and survival responding more slowly, as originally suggested by Laws *et al.* (1975). We are not aware of any

theoretical background suggesting that density-dependent dispersal or reproduction/survival processes only should produce a similar shape of density dependence, and dispersal may explain the low values of  $\theta$  found in our analyses, compared with expectations from elephant life history (Fowler 1988). Unfortunately our data do not allow the estimation of either demographic rates or migration fluxes, and we therefore could not disentangle the relative contribution of these processes in the dynamics of this local population. Although it is unlikely that this kind of information can really be gathered for such large populations, investigation of population age structure could shed some light on the processes underlying the observed density-dependent response. Similarly to most other herbivores, we expect elephant demographic responses to be initiated by reduced reproduction, juvenile and, maybe senescent, survival (Gaillard *et al.* 2000; Eberhardt 2002). Although no reliable age structure was available from our data, previous studies have reported high juvenile mortality in Hwange NP during droughts (Haynes 1987, 1988; Dudley *et al.* 2001). There are also suggestions that reproduction rates could respond to changes in population density (Laws *et al.* 1975) and, given the long gestation period, could also cause delayed effects in density dependence and age structure not investigated here. However, the simultaneous development of new techniques to quickly assess the age structure of elephant populations (Shrader *et al.* 2006) and of statistical methods estimating the general demographic strength of density dependence from time series of population age structure (Lande *et al.* 2006) could greatly help in improving our understanding of density-dependent processes in elephant populations.

Ultimately, our study highlights the limits of our knowledge of the link between spatial processes and density dependence. There is still no theoretical background allowing us to predict how spatial arrangement of populations and sampling of subpopulations can influence the detection and estimation of density dependence (Freckleton *et al.* 2006). Similarly although the study of population regulation has greatly benefited from studies in closed systems, the contribution of dispersal to the regulation of populations (e.g. Bonenfant *et al.* 2002; Clobert, Ims & Rousset 2004), and by extension the operating scales of density dependence, have been overlooked. Because many systems are spatially open, we believe it is where the contemporary challenges of integrating both density and environmental heterogeneity effects on large herbivore population dynamics lie.

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