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Rainfall variability and its impact on large mammal populations in a complex of semi-arid African savanna protected areas

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Abstract: We investigated the rainfall patterns and associated fluctuations of wild large herbivore species in the Great Limpopo Transfrontier Conservation Area (GLTFCA), southern Africa. The study objectives were to: (i) establish the synchrony in rainfall and drought occurrence patterns in Gonarezhou National Park, Zimbabwe, and four adjacent areas, and (ii) determine the responses of different large herbivore species' populations to droughts. We used annual rainfall data collected from the five sites within the GLTFCA and large herbivore population data collected from multispecies aerial surveys in Gonarezhou and Kruger National Park, South Africa. Our results showed that between 1970 and 2009, Gonarezhou recorded three wet years (1977, 1978 and 2000) and six drought years (1973, 1983, 1989, 1992, 1994 and 2005). However, there were some variations in the drought occurrences between Gonarezhou and the four adjacent areas indicating a weak synchrony in rainfall patterns. Furthermore, seven large herbivore species showed dips in their populations associated with the 1992 severe drought, with most of the species' populations recovering thereafter. Our study suggests that rainfall does have a strong influence on large herbivore population dynamics especially in really dry years in African savanna ecosystems. Our findings underscore the need for further detailed studies on bottom-up processes influencing large herbivore population trends in savanna ecosystems with high rainfall variability.

Key words: Annual rainfall, bottom-up process, conservation, drought, equilibrium systems, Great Limpopo Transfrontier Conservation Area, non-equilibrium systems.

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Introduction

African savannas harbour a high diversity of large herbivore species (Du Toit & Cumming 1999; Prins & Olff 1998), which have important ecological as well as economic value (Olff *et al.* 2002; Prins *et al.* 2000). The decline in large herbivore abundances in Africa has received

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considerable recent attention (Bouché *et al.* 2012; Craigie *et al.* 2010; Ogutu *et al.* 2011a). Large herbivore population dynamics are thought to be influenced by bottom-up processes (Gandiwa 2013a; Slobodkin 1960). Bottom-up processes include competition for forage resources which may be determined by rainfall amongst other forces (Grange & Duncan 2006; Kay 1998). The discussion of bottom-up processes in the regulation of mammalian herbivore populations has been prominent in ecology for over 50 years (e.g., MacArthur 1955; Smuts 1978) and has become an even more important research topic today (Fritz *et al.* 2011; Grange & Duncan 2006; Hopcraft *et al.* 2010).

According to a review by Saether (1997), population changes of large herbivores in predator-free environments are strongly influenced by a combination of variations in the environment and population density. Fluctuations in population size can be caused by climatic variation influencing resource availability (Illius & O'Connor 2000; Owen-Smith 1990; Saether 1997). Rainfall is a central climatic factor governing population dynamics in African savannas (Ogutu & Owen-Smith 2005; Ogutu *et al.* 2008) through its influence on primary production, particularly in semi-arid areas (Coe *et al.* 1976; Mduma *et al.* 1999; Prins 1988). Therefore, the population of African large herbivores decline during droughts because of reduced vegetation production (Illius & O'Connor 2000; Owen-Smith 1990; Voeten *et al.* 2009).

Arid and semi-arid ecosystems have highly variable rainfall and frequent droughts, and herbivore populations vary markedly (Boone & Wang 2007; Chamaille-Jammes *et al.* 2007). Ellis & Swift (1988) recorded large variations in livestock numbers in response to low and extremely variable rainfall in northern Kenya, although they emphasized that the system was persistent. Ellis & Swift (1988) hypothesized a non-equilibrium system in which livestock populations increased during years of ample rainfall, then crashed during droughts, with populations at other times rarely becoming high enough to be limited by primary production, or in turn to have significant effects upon vegetation. Vegetation and livestock dynamics were only weakly linked, competition for forage was low, and the system was dominated by abiotic factors (Boone & Wang 2007). In contrast, equilibrium systems are thought to be driven by the important role of biotic feedbacks such as density-dependent regulation of animal populations and the feedback of animal density on vegetation composition, cover and productivity, with resultant range management under this system focusing on carrying capacity, stocking rates and range condition assessment (Vetter 2005). Similar, mechanisms and patterns have been reported among wild herbivore population dynamics in arid and semi-arid ecosystems (Illius & O'Connor 2000).

Weak or non-synchronicity of droughts have been reported to occur in some regions (Vicente-Serrano & Cuadrat-Prats 2007), primarily as a result of geographic diversity and different atmospheric patterns, thus influencing the spatial availability for forage resources for large herbivores, their movements and population dynamics. Moreover, previous studies considering multiple species assemblages of large herbivores in African savannas have generally shown that large herbivore populations are variably influenced by rainfall, with large grazers being more negatively affected than large browsers following droughts (Drent & Prins 1987; Owen-Smith & Ogutu 2003; Shrader *et al.* 2010).

In this study we considered the influence of variable rainfall, a bottom-up process, on wild large herbivore populations in the semi-arid Gonarezhou National Park (hereafter, Gonarezhou), southeast Zimbabwe and four adjacent areas which forms the study region (i.e., rainfall in the study area lying within the Great Limpopo Transfrontier Conservation Area (GLTFCA)). We define the study region as constituting a geographical extent of ~700 km long and ~50 km wide. The study objectives were to: (i) establish the synchrony in rainfall and drought occurrence patterns in Gonarezhou and four adjacent areas, and (ii) determine the responses of different large herbivore species' populations to droughts. We expected the grazers to be more negatively affected than the browsers because grass production is likely to be highly negatively affected than the woody leaf production during severe droughts (i.e., drier than average droughts). In addition, we expected the large grazers to be more negatively affected than the small grazers, because the drought causes a low grass production where small grazers can still acquire some green leaves from the landscape, but large grazers will not acquire enough bulk food.

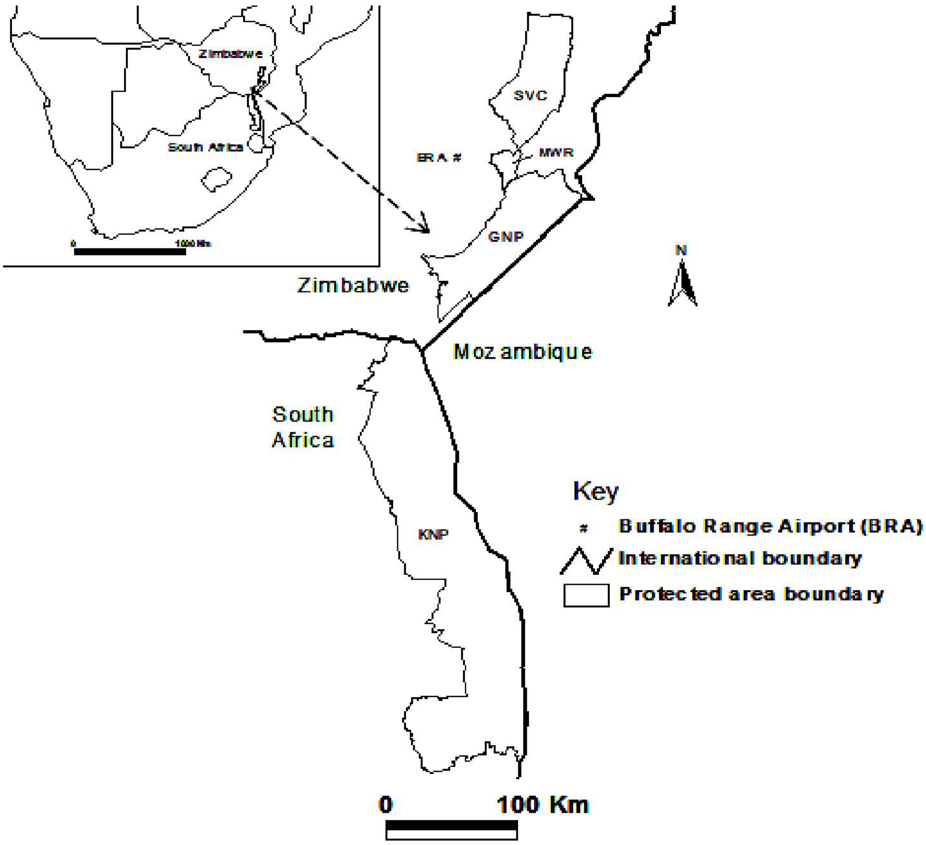

Fig. 1. Location of Gonarezhou National Park (GNP), Malilangwe Wildlife Reserve (MWR), Save Valley Conservancy (SVC) and Buffalo Range Airport (BRA) (in Zimbabwe), and Kruger National Park (KNP) (in South Africa), which forms the rainfall study area (or study region). Notes: The study region is ~700 km long and ~50 km wide, i.e., North - South "transect" and falls within the "same" rainfall zone. It gets wetter towards the north-east and south-east (FAO 2004).

Materials and methods

Study areas

We considered five rainfall study areas: Gonarezhou, Buffalo Range Airport, Malilangwe Wildlife Reserve, Save Valley Conservancy in Zimbabwe and Kruger National Park (hereafter, Kruger), South Africa. The five rainfall study areas lie within the GLTFCA. From those areas we collected data on annual rainfall between 1970 and 2009. We selected the period 1970 - 2009 so as to get a representative rainfall mean and associated rainfall variability for a sufficiently long period of approximately 40 years. Moreover, we collected data on large herbivore populations between 1984 and 2009 from Gonarezhou and Kruger (large mammal study area) since these were the wildlife areas with large herbivore population data before and after the 1992 severe drought. We limited our study period to between 1984 and 2009 since multispecies aerial surveys in Gonarezhou only commenced in 1984. Gonarezhou National Park is a state protected area that was established by the Parks and Wildlife Act of 1975. Gonarezhou has been part of the Great Limpopo Transfrontier Park since 2000. Covering an area of ~5,050 km^2, Gonarezhou is located in the southeast lowveld of Zimbabwe, between 21° 00' - 22° 15' S and 30° 15' - 32° 30' E (Kupika *et al.* 2014), and is the country's second biggest protected area. Gonarezhou has an altitudinal range of 165 - 575 m asl and shares over 100 km border with Mozambique to the east. On the Mozambiquean side adjacent to the Gonarezhou, the predominant land-use is wildlife conservation and the area consists of landscapes that are generally flat with similar vegetation to that of Gonarezhou. Gonarezhou also borders the fenced Malilangwe Wildlife Reserve in the northwest (Fig. 1), and communal lands in the north, south and west. Gonarezhou is partly fenced on the northern border with Malilangwe

Table 1. Background information on large herbivore aerial surveys in Gonarezhou National Park, southeast Zimbabwe, between 1984 and 2009.

Year	Survey period	Sampling intensity (%)	Source
1984	September	11	Sharp (1984)
1986	August	17	Sharp (1986)
1987	May	10	Sharp (1987)
1989	August - October	10	Gibson (1989)
1991	September	10	Jones (1991)
1993	September	14	Bowler (1993)
1995	July - November	11	Davies *et al.* (1995)
1996	August - September	11	Davies (1996)
1998	August	14	Mackie (1999)
2001	August	14	Dunham (2002)
2007	September - October	12	Dunham *et al.* (2007)
2009	September	20	Dunham *et al.* (2010)

Wildlife Reserve (Gandiwa *et al.* 2013a) and adjacent communal areas for a distance of ~80 km.

Malilangwe Wildlife Reserve (20° 58′ - 21° 15′ S, 31° 47′ - 32° 01′ E) covers ~400 km² and borders the northern Gonarezhou with an altitudinal range of 300 - 510 m above sea level. The reserve was established in 1994 with ecotourism as the primary land use form (Clegg & O'Connor 2012). Save Valley Conservancy (20° 05' S, 32°00' E) covers ~3,400 km² and is located north of Malilangwe Wildlife Reserve with an altitudinal range of 480 - 620 m above sea level. The conservancy which is a cooperatively managed wildlife area was established in 1992 with ecotourism being the primary land use (Williams 2011). Buffalo Range Airport (21° 00' S, 31° 34' E) has an altitude of ~430 m above sea level and is located close to the three wildlife areas in Zimbabwe (Fig. 1). The Kruger National Park (22° 25′ - 25°32′ S, 30° 50′ - 32° 2′ E) is situated in north-eastern South Africa and covers ~20,000 km² with an altitudinal range of 260 - 840 m above sea level. The park was established in 1926 (Kennedy *et al.* 2003; Seydack *et al.* 2012). Malilangwe Wildlife Reserve, Save Valley Conservancy and Kruger are largely fenced, but this does not stop the movement of some animal species to and/or from the adjacent areas and also across the country boundaries.

Three seasons can be distinguished for the five rainfall study areas: hot and wet (November to March), cool and dry (April to August), and hot and dry (September to October). The study area is characterised by highly variable rainfall with a coefficient of variation (CV) ≥ 33 % and is prone to frequent droughts. The study area forms part of arid and semi-arid deciduous African savanna biome, with *Colophospermum mopane* woodland a dominant vegetation type (Clegg & O'Connor 2012; Seydack *et al.* 2012). There is a wide variety of wild large herbivore species in Gonarezhou, Malilangwe Wildlife Reserve, Save Valley Conservancy and Kruger, and these include buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*), wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), eland (*Taurotragus oryx*), greater kudu (hereafter, kudu; *Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), roan antelope (*Hippotragus equinus*), sable (*Hippotragus niger*), waterbuck (*Kobus ellipsiprymnus*) and warthog (*Phacochoerus aethiopicus*).

Data collection

Rainfall

Monthly total rainfall data for the period 1970 to 2009, from five rainfall study areas, namely, Gonarezhou (three rain stations), Buffalo Range Airport (one rain station), Malilangwe Wildlife Reserve (one rain station), Save Valley Conservancy (two rain stations) and Kruger (between 20 and 30 rain stations) were collected from the properties' management and South African National Parks.

Animal data

Data on long-term population sizes of wild large herbivores in Gonarezhou were obtained from the Zimbabwe Parks and Wildlife Management Authority (formerly Department of National Parks and Wildlife Management) as were aerial survey reports (Table 1). All past aerial surveys in Gonarezhou used the repeated systematic reconnaissance flight method (Norton-Griffiths 1978). Aerial census procedures have been described fully elsewhere (Norton-Griffiths 1978; Ottichilo *et al.* 2001). Briefly, in Gonarezhou, 12 aerial surveys were conducted between 1984 and 2009 and these surveys had a mean sampling intensity (i.e., area covered with transects) of 13 %, and were mostly conducted in the dry season between August and September. Most of the aerial surveys used Cessna 182, 185, or Cessna 210J centurion aircrafts fitted with a radar altimeter. The population estimates for each species and their 95 % confidence intervals for every census were calculated using the Jolly's No. 2 method for unequal size sample units (Jolly 1969).

We also used data on large herbivore population estimates in Kruger for the period 1984 and 2006 from published articles (Ogutu & Owen-Smith 2003; Seydack *et al.* 2012; Van Aarde *et al.* 1999; Young *et al.* 2009). In this study, we only used large herbivore data up to 2006, as these were the data readily available from the published reports from Kruger. In Kruger, population counts for large herbivores throughout the entire park were undertaken annually between 1980 and 1993 using fixed-wing aircraft which comprised of a pilot, a recorder and four observers. Surveys were conducted between May and August when visibility was best. However, after 1998, surveys were conducted at relatively low sampling intensities using the distance sampling method. Moreover, buffalo and elephant counts in Kruger have been conducted separately using a helicopter to split herds into smaller groups which were then photographed with animals on the photographs being later counted with visual aids (Owen-Smith *et al.* 2012; Seydack *et al.* 2012). More details about aerial surveys in Kruger are provided by Viljoen (1996).

Data analyses

The data were analysed in six steps. First, we analysed the occurrence of unusually wet and drought periods for the five rainfall study areas over the period 1970 and 2009. Annual rainfall was based on the July - June calendar so as to cover the rainfall which is important ecologically (i.e., for plant growth given that most of the rainfall falls between November and March) for southern Africa savannas. We calculated the following: (i) mean annual rainfall; (ii) standard deviation (SD) from the mean annual rainfall; (iii) annual rainfall deviation from the mean (i.e., difference between the annual mean and the recorded annual rainfall); and (iv) coefficient of rainfall variation for each of the five areas. Wet or drought year determination was based on the following formulae: mean annual rainfall ± 1SD, where years with annual rainfall greater than mean annual rainfall +1SD were classified as wet and years with annual rainfall less than mean annual rainfall –1SD were classified as drought (Prins 1996). By using mean ± 1SD we assumed that the distribution of annual rainfall is symmetric, and hence we regarded the mean as a good estimator of the central location of the distribution, and also that mean ± 1SD is sensitive to extreme observations such as severe droughts or floods (Ottichilo *et al.* 2001; Prins 1996).

Second, we determined whether mean annual rainfall for the five areas was significantly different from each other using a one-way analysis of variance and Tukey's Honestly Significant Difference (HSD) *post-hoc* tests using SPSS version 19 (SPSS Inc., Chicago, IL, USA) in order to test whether there was variability of rainfall among study areas which would influence the variation of forage resources during droughts, hence important for animal movements across landscapes. Third, we tested whether annual rainfall increased, decreased or remained the same for each of the five rainfall study areas for the period 1970 - 2009, using simple linear regression models with year as the independent variable and annual rainfall as the dependent variable. This is important in order to show whether the study region is getting wetter or drier thus also influencing availability of forage resources.

Fourth, we analysed long-term trends in large herbivore population estimates within Gonarezhou using a flexible nonparametric model with square root transformed data in R software version 2.13.1 (R Development Core Team 2011). We used the flexible nonparametric model because population counts are generally non-normally distributed, hence, a suitable model for the trends should allow for the non-normality and non-linearity of the counts and the varying frequency of surveys (Ogutu *et al.* 2011a). For this study, only the large herbivores that are most visible from the air were considered and population estimate data from the multispecies aerial surveys were used in the analyses. We focused on nine wild large herbivores which were counted frequently over the study period, and these included one browser (giraffe), three mixed feeders (elephant, eland, and kudu) and five grazers (wildebeest, buffalo, zebra, sable, and waterbuck). We used a smoothing model using B-splines (Eilers & Marx 1996) with a break-point (or jump) associated with the 1992 severe drought (identified from preliminary data analysis) to determine the impact of the 1992 severe drought on the selected large herbivore populations. A B-spline consists of polynomial pieces, connected at certain values of x (x referring to the knots). B-splines are attractive as base functions for ("nonparametric") univariate regression (Eilers & Marx 1996), and have been successfully applied in analysing long-term animal population estimate data (see Ogutu *et al.* 2011a). The expected response to the 1992 severe drought would be a decline of some large herbivore species population estimates followed by a recovery thereafter whereas some large herbivore species populations would be not or less affected by the drought. We used the 1992 severe drought as the break point due to the relatively small data set of surveys conducted between 1984 and 2009. The 1992 drought (annual rainfall = 93 mm) was the driest compared to the 1989 (annual rainfall = 277 mm), 1994 (annual rainfall = 298 mm) and 2005 (annual rainfall = 290 mm) droughts. Moreover, a total of 10 rainy days were recorded at Chipinda Pools rain station in northern Gonarezhou in the 1992 rain season. The smoothing model produces a smoothed curve of animal numbers over time. Similar to any nonparametric smoother, B-spline approaches need a smoothing parameter (lambda, λ) to control the smoothness of the fitting curve. A linear combination of third-degree B-splines gives a smooth curve. Too many knots lead to over-fitting of the data; too few knots lead to under-fitting. To prevent over-fitting, a penalty on the second derivative restricts the flexibility of the fitted curve (see Eilers & Marx 1996). In our case, we smoothed the population estimates data of nine wild large herbivore species in Gonarezhou, either side of the period 1984 - 1991 and 1993 - 2009, using B-splines of degree 3, a second-order penalty, and 20 intervals. We used a k-fold cross-validation method to find the optimal value of λ.

Fifth, we presented and qualitatively analysed the trends of large herbivore populations in Kruger between 1984 and 2006 in order to establish the influence of wet and drought years on the population size of nine large herbivores. Sixth, we compared the response to rainfall variations of the nine large herbivore species yearly total population sizes for Gonarezhou and Kruger between 1984 and 1993. We covered only the period 1984 and 1993 to primarily show the influence of the 1992 severe drought in the large mammal study area. We used the total populations of nine large herbivores in 1984 as the reference points, i.e., 100 %, in order to establish the similarities in patterns of the total populations of the subsequent years.

Results

Rainfall patterns and trends

Between 1970 and 2009, Gonarezhou recorded three wet years (1977, 1978 and 2000) and six drought years (1973, 1983, 1989, 1992, 1994 and 2005) (Table 2). The recorded number of wet and drought years in Gonarezhou was almost similar to those recorded in the four adjacent areas. Overall, there was a weak synchrony in the occurrence of wet and drought periods across the five areas, with only the year 2000 being the common wettest period whereas 1973, 1983 and 1992 were the common droughts recorded across the five areas. For instance, the number of years between two consecutive droughts in Gonarezhou was recorded as 10, 6, 3, 2, and 11, giving an average of 6.4 years. Mean annual rainfall for Gonarezhou was 499 mm with a standard deviation (SD) of 195 and a CV of 39 %. Mean annual rainfall for the period from 1970 to 2009 did not differ significantly across the five areas (one way ANOVA, $F_{4,195}$ = 1.02, P = 0.398). Moreover, there was no indication that annual rainfall declined or increased at all in the five areas: Gonarezhou (t = -0.28, P = 0.780, slope (beta, β) = -0.003, 95 % confidence limits [CL] for β = -0.02 to 0.02), Kruger (t = -0.27, P = 0.689, β = -0.003, 95 % CL for β = -0.02 to 0.02), Malilangwe Wildlife Reserve (t = 0.45, P = 0.652, β = 0.004, 95 % CL for β = -0.02 to 0.02), Save Valley Conservancy (t = 0.06, P = 0.956, β = 0.001, 95 % CL for β = -0.02 to 0.02) and Buffalo Range Airport (t = -1.02, P = 0.312, β = -0.01, 95% CL for β = -0.03 to 0.01) (Fig. 2). Thus, not a single slope deviated significantly from zero.

Table 2. Annual rainfall (AR) and its deviation from the mean (Dev.) (difference between the annual mean and the recorded annual rainfall) recorded in five rainfall study areas between 1970 and 2009. Wet (Wt) and drought (Dt) years were defined as having a rainfall one standard deviation (SD) below or above mean annual rainfall respectively. The wet and drought years that are common to all five areas are shown in bold.

Year	Zimbabwe												South Africa		
	Buffalo Range Airport			Gonarezhou National Park			Malilangwe Wildlife Reserve			Save Valley Conservancy			Kruger National Park		
	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt
1970	523	-61		537	38		481	-81		401	-149		412	-118	
1971	355	-229	Dt	381	-118		439	-124		346	-204	Dt	501	-29	
1972	773	189		601	102		627	65		879	329	Wt	849	320	Wt
1973	**302**	**-282**	**Dt**	**177**	**-322**	**Dt**	**213**	**-349**	**Dt**	**281**	**-269**	**Dt**	**316**	**-214**	**Dt**
1974	973	389	Wt	658	159		722	159		512	-38		741	212	Wt
1975	647	63		672	173		789	227	Wt	670	120		667	137	
1976	820	236	Wt	670	171		602	39		749	199	Wt	623	93	
1977	753	169		801	302	Wt	719	157		683	133		687	157	
1978	1120	536	Wt	834	335	Wt	751	189		850	300	Wt	726	196	
1979	734	150		611	112		575	12		552	2		453	-77	
1980	706	122		378	-121		669	107		520	-30		536	7	
1981	762	178		590	91		643	81		681	131		522	-8	
1982	455	-129		387	-112		513	-50		397	-153		354	-176	
1983	**336**	**-248**	**Dt**	**227**	**-272**	**Dt**	**217**	**-346**	**Dt**	**206**	**-344**	**Dt**	**259**	**-271**	**Dt**
1984	424	-160		478	-21		488	-75		492	-58		480	-49	
1985	672	88		566	67		647	85		640	90		761	232	Wt
1986	688	104		567	68		611	48		603	53		424	-105	
1987	287	-297	Dt	318	-181		314	-248	Dt	405	-145		332	-198	Dt
1988	590	6		471	-28		735	173		616	66		585	55	
1989	350	-234	Dt	277	-222	Dt	388	-175		578	28		399	-130	
1990	431	-153		320	-179		424	-139		500	-50		523	-6	
1991	499	-85		467	-32		357	-205	Dt	295	-255	Dt	391	-139	
1992	**127**	**-457**	**Dt**	**93**	**-406**	**Dt**	**72**	**-490**	**Dt**	**157**	**-393**	**Dt**	**238**	**-291**	**Dt**
1993	806	222		511	12		601	38		556	6		520	-10	
1994	556	-28		298	-201	Dt	416	-146		485	-65		339	-191	
1995	479	-105		499	0		607	45		442	-108		511	-19	
1996	609	25		508	9		746	184		584	34		704	174	
1997	576	-8		594	95		573	10		698	148		461	-69	
1998	378	-206		333	-166		415	-148		846	296	Wt	350	-180	
1999	822	238	Wt	575	76		846	284	Wt	843	293	Wt	887	357	Wt
2000	**1177**	**593**	**Wt**	**1118**	**619**	**Wt**	**1213**	**651**	**Wt**	**999**	**449**	**Wt**	**1230**	**700**	**Wt**
2001	543	-41		528	29		624	62		586	36		559	29	
2002	401	-183		330	-169		357	-205	Dt	419	-131		451	-78	
2003	715	131		675	176		737	175		726	176		333	-197	Dt
2004	643	59		647	148		756	193		491	-59		694	164	
2005	289	-295	Dt	290	-209	Dt	374	-188		342	-208	Dt	384	-146	

Contd...

Table 2. Continued.

Year	Zimbabwe												South Africa		
	Buffalo Range Airport			Gonarezhou National Park			Malilangwe Wildlife Reserve			Save Valley Conservancy			Kruger National Park		
	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt	AR	Dev.	Wt/Dt
2006	384	-200		323	-176		568	6		544	-6		665	136	
2007	615	31		655	156		547	-16		473	-77		357	-173	
2008	553	-31		539	40		641	79		613	63		495	-35	
2009	480	–104		461	-38		475	-88		343	-207	Dt	469	-61	
Annual mean	584			499			562			550			530		
SD of mean	225			195			203			189			197		
Variability (%)	39			39			36			34			37		

Animal population trends

The population trends for nine wild large herbivore species in Gonarezhou between 1984 and 2009 are shown in Fig. 3. Populations for six species (elephant, buffalo, giraffe, zebra, waterbuck and wildebeest) increased between 1984 and 1991 whereas populations of three other species (eland, kudu and sable) declined during the same period (Fig. 3). With the exception of the small (N< 300) giraffe populations and small (N< 300) sable populations, populations for seven species (elephant, buffalo, eland, zebra, kudu, wildebeest and waterbuck) show a dip associated with the 1992 drought. Thereafter, populations for these seven species increased in Gonarezhou. However, based on the modeled trend, only populations of five species (elephant, giraffe, zebra, wildebeest and kudu) increased to above the abundance levels recorded prior to 1992 whereas the populations for two species (buffalo and sable) were slightly lower than those recorded before 1992. Only kudu and waterbuck show a slight dip around 2005 possibly associated with the 2005 drought recorded in Gonarezhou and the species' population increased thereafter.

In the adjacent Kruger, populations for seven species (buffalo, eland, kudu, sable, waterbuck, wildebeest and zebra) declined following the 1992 drought (Fig. 4a, b). Only elephant population increased whereas giraffe population was slightly negatively affected by the 1992 drought. Increases in animal abundances after the 1992 drought were recorded for buffalo, waterbuck and zebra. In contrast, eland and sable populations continued to decline after the 1992 drought. Overall, an almost similar response to bottom-up processes in the nine large herbivore species' total population sizes between 1984 and 1993 was evident between Gonarezhou and Kruger (Fig. 5).

Influence of (above) average rainfall on large herbivore populations in Gonarezhou

Abundances for six species (elephant, buffalo, giraffe, kudu, zebra and waterbuck) slightly increased following the wet year, i.e., 2000, whereas populations of eland and sable slightly declined after 2000. Overall, abundances for five species (elephant, buffalo, giraffe, wildebeest and zebra) slightly increased following average and above average annual rainfall years, i.e., 1985, 1986, 1996 and 2007, whereas kudu and waterbuck abundances were almost similar whilst eland and sable abundances slightly declined during the same years.

Discussion

Our study showed that the mean annual rainfall for the five rainfall study areas between 1970 and 2009 was similar with only the peak wet and drought periods overlapping to some extent despite the 700 km length of the entire study region. However, we also recorded variations in the occurrence, in particular, of other less severe droughts across the five rainfall study areas, translating to a weak synchrony of drought and

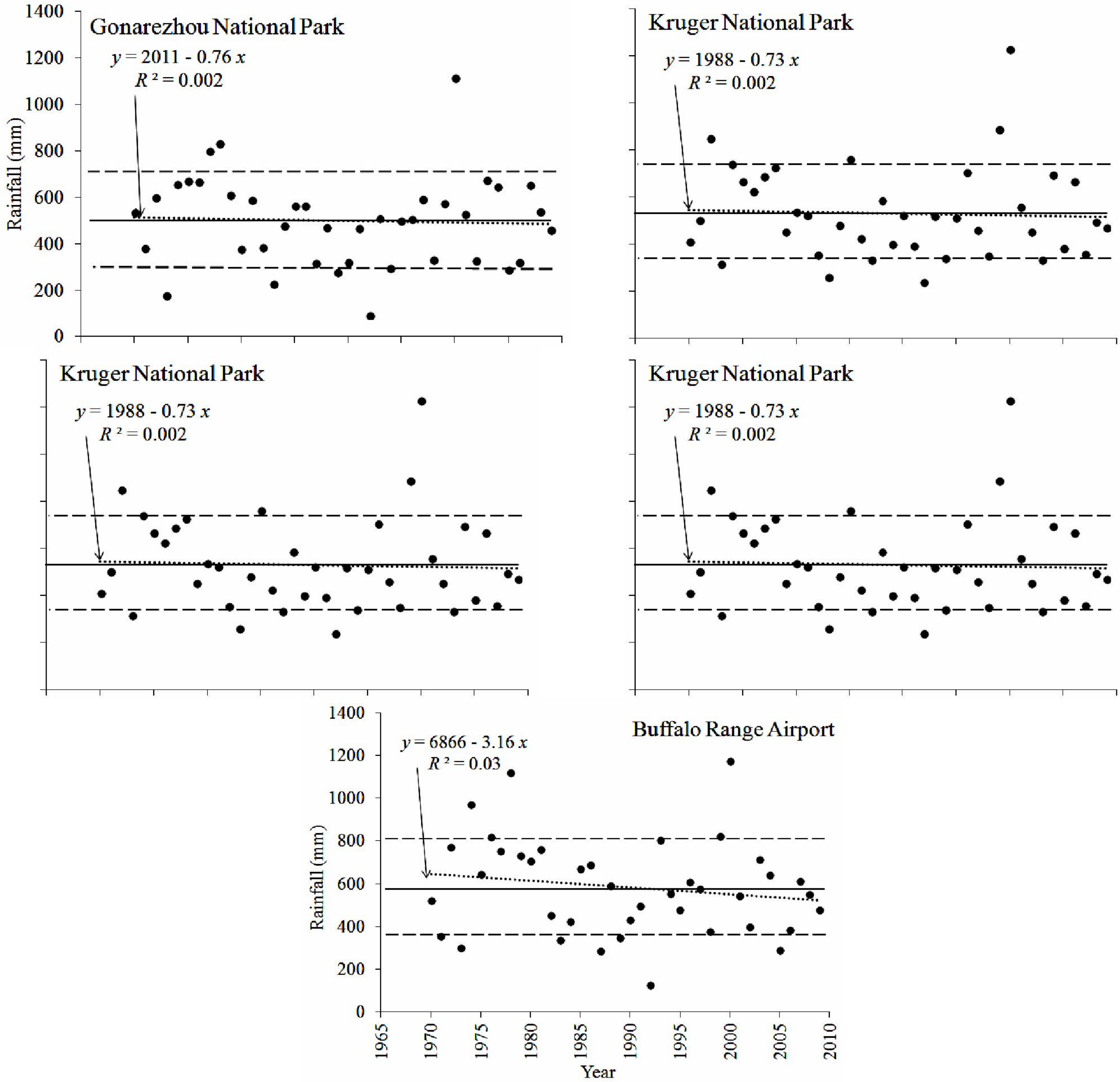

Fig. 2. Patterns and trends of rainfall for Gonarezhou National Park, Malilangwe Wildlife Reserve, Save Valley Conservancy and Buffalo Range Airport (in Zimbabwe), and Kruger National Park (in South Africa) between 1970 and 2009. Notes: The solid lines represent the annual mean rainfall and the two broken lines represents ±1SD (standard deviation) of the annual mean rainfall. Dotted lines represent the long-term trends of annual rainfall.

also wet years. The weak synchrony, particularly, of droughts have been reported to occur in some ecosystems with geographic, hydrographic diversity and different atmospheric patterns that control precipitation across landscapes being attributed as causes of the weak synchronicity (Prins & Loth 1988; Vicente-Serrano & Cuadrat-Prats 2007). Because of the temporal heterogeneity that may be caused by large variations in rainstorm effects across wildlife areas during drought periods in semi-arid areas, the spatial heterogeneity can be crucial for the survival of local herbivores through influencing the animal feeding patterns and their distribution (Drent & Prins 1987). Therefore, we deduce that animals can move to areas which are slightly less bad and

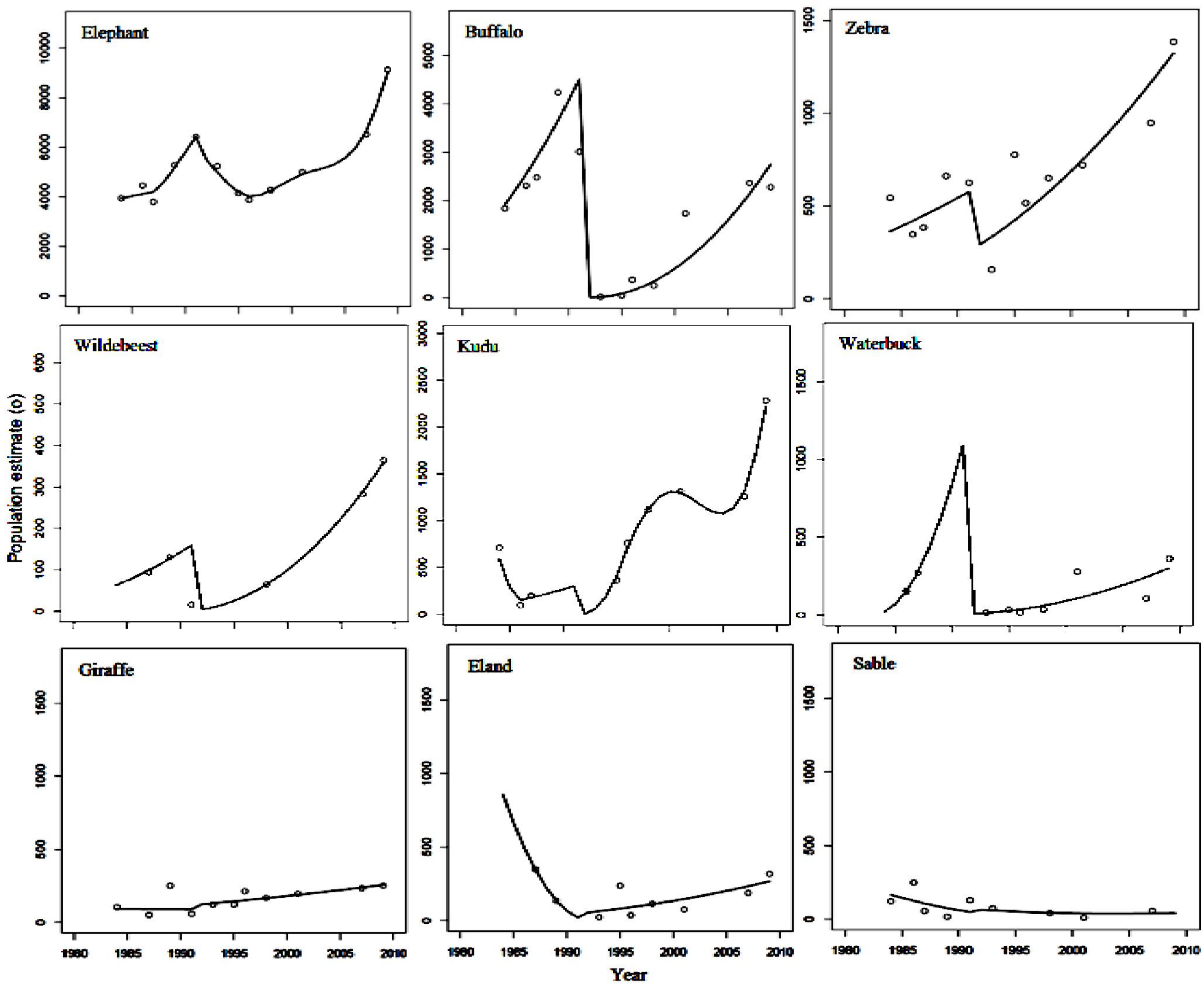

Fig. 3. Temporal trends in the population size of nine large herbivores in Gonarezhou National Park, Zimbabwe, from 1984 to 2009. Notes: The 95 % confidence limits have been omitted for clarity, but see Dunham *et al.* (2010). The lines represent the fitted trends according to a smoothing model using B-splines (Eilers & Marx 1996; see Material and methods).

more likely to be containing important forage and surface water resources and hence, soften the fall in food production during drought periods.

Gonarezhou is largely an open system, since the park is partly fenced, unlike the Kruger which is largely fenced. The large fluctuations and variability of population estimates particularly between 1991 and 1993, suggests that some animals could have moved in and out of Gonarezhou, particularly to the adjacent communal areas, game farms in Mozambique or even to adjacent areas in South Africa, particulalry Kruger, in a search for suitable forage resources. Recent evidence suggests that elephants move between Gonarezhou and Kruger (Save the Elephants, South Africa, unpublished data), and between Gonarezhou and Mozambique (Gonarezhou Conservation Project, unpublished data). In Kenya, elephants migrated out of the Mpala Ranch to adjacent ranches within the Laikipia-Samburu ecosystem following the 2000 drought and only returned during the wet seasons (Augustine 2010). Furthermore, movement of large herbivores across ecosystems following droughts in the 1980s have been documented in southern Africa (Walker *et al.* 1987). This, therefore, points for the importance of managing large herbivore populations at scales larger than individual protected areas

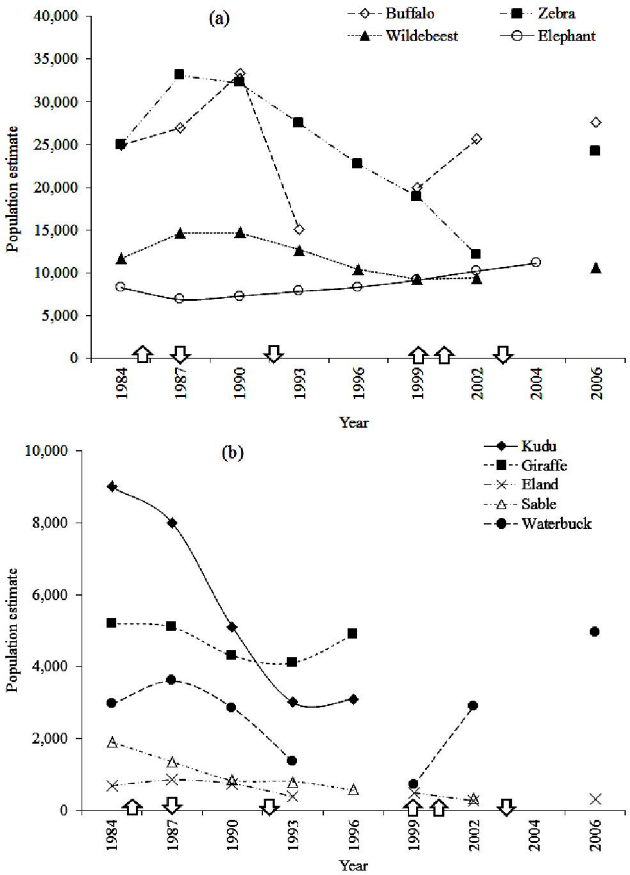

Fig. 4. Large herbivore population estimates in Kruger National Park, South Africa, between 1984 and 2006. Notes: For clarity, the figure is divided into (a) and (b). Data were only readily available for the period 1984 and 2006. Up arrow represents wet year and down arrow represents drought year. Population numbers orkudu and giraffe were unavailable after 1996. B-splines were not used for these figures. Source: Ogutu & Owen-Smith (2003), Seydack *et al.* (2012), Van Aarde *et al.* (1999) and Young *et al.* (2009).

(Augustine 2010), and in our case,we suggest that focus should be on managing wild large herbivores at the GLTFCA level (Van Aarde & Jackson 2007). Accordingly, it has been suggested that the removal of fences whenever practical should be encouraged to allow for animal movements, particularly, during the drought periods (Shrader *et al.* 2010).

Our results show that large herbivore species' response to the 1992 severe drought in Gonarezhou was not identical. A short-term decline in seven large herbivore species, namely elephant, buffalo, eland, zebra, kudu, wildebeest and waterbuck, associated with the 1992 severe drought and their subsequent recovery between 1984 and 2009 was recorded in Gonarezhou. Specifically, zebra appeared to be reacting differently from the other species, not to be explained by death and recovery but possible emigration and immigration. A largely similar trend in large herbivore species' population response to bottom-up processes was recorded in

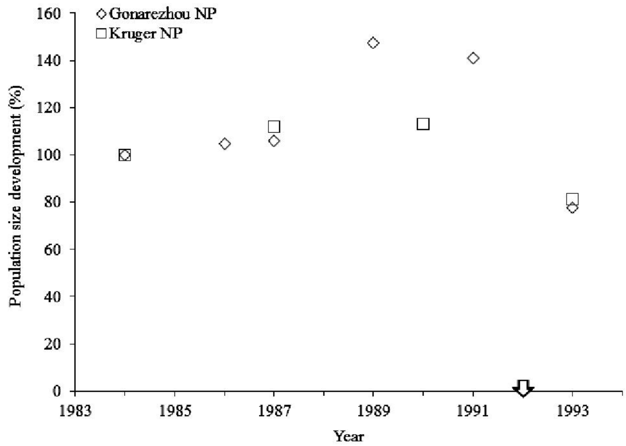

Fig. 5. Population size development for nine large herbivores in Gonarezhou and Kruger National Parks between 1984 and 1993 with reference to the 1984 total populations. Notes: Data only cover the period 1984 and 1993 to primarily show the influence of the 1992 severe drought. Down-arrow represents the 1992 severe drought which was common in both protected areas.

the Kruger, suggesting a synchrony in large herbivore population response to bottom-up processes between Gonarezhou and Kruger. Environmental variation can explain the spatial population synchrony (Hegel *et al.* 2012; Moran 1953), in our case rainfall variation. In addition, only kudu and waterbuck appeared to be slightly negatively affected by the less severe drought of 2005 in Gonarezhou. It has been reported that a total of 592 elephant carcasses were counted in 1993 and 2700 buffaloes died in the period 1992 - 93 in Gonarezhou whereas about 750 elephants, 400 buffaloes, 60 zebra, 50 elands and 64 waterbuck were translocated outside of Gonarezhou between 1984 and 1993 to rescue them from dying due to droughts (Bowler 1993; Leggett 1994; Sharp 1986). Approximately, 3800 elephants and 380 buffaloes were culled in Gonarezhou between 1984 and 1993 (Bowler 1993; Sharp 1986). Culling in Gonarezhou was stopped in 1993. Although we didn't use the index-removal analyses (Garrott *et al.* 1991) to determine the impact of animal culling and/or translocations from Gonarezhou in the present study, it is likely that the recorded population trend for some of the studied large herbivore species could also have been influenced by the animal culling and/or translocations that took place between 1984 and 1993. In southern Africa, culling was practiced in order to avoid progressive deterioration of habitat (Walker *et al.* 1987), a practice commonly associated with rangeland management using the equilibrium concept. However, the non-equilibrium concept suggests that rangeland degradation is unlikely to occur where rainfall variability is high, because herbivore populations collapse in periods of drought, enabling vegetation to recover (Von Wehrden *et al.* 2012).

Only giraffe appeared to be least affected by the four droughts (1989, 1992, 1994 and 2005) recorded in Gonarezhou between 1984 and 2009 possibly due to availability of browsing resources, for some time, during the drought periods. Similarly, in Kruger, giraffe was slightly negatively affected by the 1992 severe drought (Fig. 4) as has also been previously reported (Owen-Smith & Ogutu 2003). In contrast, sable populations in Gonarezhou and Kruger showed little recovery after the 1992 drought and even in years with average to above average rainfall. This trend of declining sable population could be a result of the high variation in annual rainfall influencing the important forage resources (Georgiadis *et al.* 2003; Owen-Smith *et al.* 2012) and/or other top-down forces such as natural predation which, however, still need to be further investigated. Surprisingly elephant populations in Kruger were less affected by the 1992 drought than elephants in Gonarezhou. Gonarezhou had a density of 1.2 elephants km^{-2} in 1991 whereas Kruger had a density of 0.3 elephants km^{-2} in 1990. Elephants in Kruger were maintained at low densities through culling between 1967 and 1994 (Van Aarde *et al.* 1999). Hence, it's likely that due to the higher elephant densities in Gonarezhou, massive die-offs occurred following the 1992 drought due to reduced forage resources availability than in Kruger. But there was culling (too). Moreover, it is not easy to understand from Fig. 3 why elephant decline continued till 1996 in Gonarezhou.

Declines in large herbivores associated with severe droughts negatively affecting forage availability have been documented in savanna ecosystems in the past. For example, the 1983 and 1992 droughts were reported to have led to declines in large herbivore populations in Botswana (Williamson & Mbano 1988) and in Kruger (this study; Harrington *et al.* 1999; Marshal *et al.* 2011; Seydack *et al.* 2012). Foley *et al.* (2008) documented the decline of elephant populations during a severe drought in Tanzania in 1993 which coincided with an upsurge in elephant poaching (Prins *et al.* 1994; Prins & Van Der Jeugd 1993). Similarly, Dunham (1994) reported a high mortality of large grazers in the Mana Pools National Park, northern Zimbabwe, following the 1992 drought. Droughts have been reported to have devastating effects on large herbivore populations directly through starvation, and indirectly by weakening animals and hence, amplifying their vulnerability to predation, diseases and parasites (Ogutu *et al.* 2008). Quantity and quality of forage in semi-arid areas is largely influenced by rainfall which is a proxy for primary productivity (Deshmukh 1984; Mduma *et al.* 1999). The occurrence of a drought in an ecosystem negatively influences wildlife populations through reduced food availability (Grange *et al.* 2012; Ogutu *et al.* 2011b), negatively affecting the nutritional status of herbivores (Owen-Smith 1990; Prins & Olff 1998). Moreover, it has been suggested that rates of decrease in drought years are typically greater than rates of increase in wet years for large-bodied herbivore populations which are limited by rainfall (Illius & O'Connor 2000). Similarly, our study also provides evidence to suggest that most of the herbivore species' populations slightly increased after average and above average rainfall (1985, 1986, 1996 and 2007) and wet year (2000), with only a few species' abundances slightly declining and/or remaining the same following average, above average rainfall and wet year. It is, therefore, likely that animal population growth in most large herbivore species is best promoted when annual rainfall is close to the long-term average for a few years.

Variations in large herbivore species responses to rainfall across ecosystems could possibly be related to landscape heterogeneity in grass production which is influenced by soil fertility and rainfall (Augustine *et al.* 2003). However, it should be noted that rainfall in southern Africa is characterised by a cyclical pattern with a quasi-periodicity of 18 - 20 years (Tyson 1986; Tyson & Preston-Whyte 2000). We, thus, deduce that the rainfall cyclic pattern in the study area could also influence animal population trends. This, therefore, points to the importance of including the analyses of rainfall cyclical patterns, for example with over 60 years of rainfall data (Mazvimavi 2010), in order to tease out the influence of cyclic behaviour of rainfall on wild animal population trends in future studies. Furthermore, it has been suggested that a CV of 33 % or greater is a threshold for which non-equilibrium dynamics become relevant in an area (Boone & Wang 2007; Ellis & Swift 1988). Therefore, for some species non-equilibrium dynamics may be very important (e.g., buffalo) and others not (e.g., giraffe).

Our findings on the basis of long-term aerial survey data show that despite the negative influence of the 1992 severe drought on most large herbivore species in Gonarezhou, the park still contains growing populations of large herbivore populations (with the exception of sable). Our results are consistent with earlier studies which have documented that protected areas in southern Africa have largely maintained their animal populations during the last decades (Craigie *et al.* 2010; Fynn & Bonyongo 2011). The recorded increases in some wild large herbivore populations in Gonarezhou could partly be attributed to the consistent and recent increases in law enforcement which helped reduce illegal hunting, particularly, during Zimbabwe's economic decline associated with the political crisis and land reforms that were widely publicized in the international media (Gandiwa 2013b; Gandiwa *et al.* 2013b; Gandiwa *et al.* 2014a; Gandiwa *et al.* 2014b). Moreover, the linkages (collaborative management of wildlife) between Gonarezhou and adjacent wildlife areas, for instance, under the Communal Areas Management Programme for Indigenous Resources, within the southeast lowveld of Zimbabwe, and the GLTFCA could also have helped in the protection of large herbivore species. Elsewhere, several authors have reported steady reductions in wild herbivore abundances in some African wildlife areas in the recent past (Caro 2008; Estes *et al.* 2006; Ogutu *et al.* 2011a; Ottichilo *et al.* 2001). These declines in large herbivore populations have been attributed to recurrent droughts, human encroachment into wildlife areas, land-use changes, poaching, diseases, and competition with domestic stock (Biru & Bekele 2012; Du Toit & Cumming 1999; Gandiwa *et al.* 2013a; Ogutu *et al.* 2011a; Okello 2012; Ottichilo *et al.* 2000; Scholte 2011).

Although the statistical model used in this study produced relatively satisfactory results in terms of understanding the role of the 1992 severe drought and the general trends of large herbivores in Gonarezhou between 1984 and 2009, it must be pointed out that the relative confidence limits of some species population estimates are broad, e.g., waterbuck and eland (see Dunham *et al.* 2010), and hence the modeled trend appeared not to fit very well at some period in time for these species. Sample aerial surveys of large herbivores in savanna ecosystems are generally associated with wide confidence limits of population estimates, especially of low abundant species due to observer bias, sampling intensity and clustering patterns of some species (Caughley 1974; Khaemba & Stein 2002). Overall, the statistical model provides a useful approach to evaluate the long-term trends of large herbivores and the bottom-up effects of severe droughts in savanna ecosystems. For instance, the statistical model was instrumental in showing the species that were most negatively affected, e.g., buffalo, elephant and zebra, by the 1992 drought and those that were not affected, e.g., giraffe in Gonarezhou. Our study, therefore, suggests that it is also important to really understand fecundity, calf survival, and age- and condition-related mortality (Ogutu *et al.* 2010; Trimble *et al.* 2009), particularly following wet and drought periods, thus, emphasizing that aerial census data are no substitute for large herbivore population studies when it comes to understanding animal population fluctuations in these communities. Hence, this calls for ground surveys, e.g., road counts, to complement aerial survey data on large herbivore population composition.

Conclusions

Our results provides some evidence that there is a synchrony in rainfall and drought occurrence patterns in Gonarezhou and the adjacent areas within the GLTFCA since we found some variations in drought occurrences across the five rainfall study areas. Furthermore, our results showed that there were some dips, some upswings associated with only one drought (i.e., 1992) in seven large herbivore species in Gonarezhou. Similarly, declines in some large herbivore species were also recorded in Kruger following the 1992 drought, suggesting a synchrony in large herbivore population response to bottom-up processes between Gonarezhou and Kruger. Moreover, annual rainfall appeared not to significantly influence large herbivore abundances in the long-term in Gonarezhou. Our results also showed that large herbivore species' populations variably respond to droughts. Overall, our results suggest that variations in rainfall (bottom-up processes), does have a strong influence on large herbivore population dynamics especially in severe drought years in African savanna ecosystems but our data show a very variable response between different herbivore species, thus precluding general conclusions.

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