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Trends in populations of elephant and other large herbivores in Gonarezhou National Park, Zimbabwe, as revealed by sample aerial surveys

Kevin M. Dunham*

PO Box CH385, Chisipite, Harare, Zimbabwe

Abstract

For 30 years, regular aerial surveys in Zimbabwean protected areas were funded, designed and executed primarily to estimate elephant numbers. Other large herbivores were recorded, even though some species were not easily seen from the air in savannah woodlands. Population estimates for species other than elephant provided indices of abundance that could be used to determine temporal trends in population size. This study tests for significant trends in the abundance of large herbivores in Gonarezhou National Park, assuming that data from aerial sample surveys designed for elephant also provide accurate estimates of real trends in the populations of other herbivores. For each species, the exponential rate of population change was calculated using weighted regression, with the variance of this rate based on the sampling variances of the population estimates. Significant population trends were detected for eight species. Before the 1992 drought, elephant number was held approximately constant by frequent culls, but afterwards, it increased at a mean annual rate of 6.2% (confidence limits 4.0% and 8.6%). Elephants in cow herds increased at 7.3%, significantly faster than elephants in bull herds (−0.5%). Buffalo, eland, kudu, nyala, waterbuck, wildebeest and zebra all increased in number, after population declines during the drought.

Key words: aerial surveys, African elephant, drought, large herbivores, population growth rates, population trends

Résumé

Pendant 30 ans, les études aériennes faites au Zimbabwe ont été financées, conçues et réalisées avant tout pour estimer le nombre d'éléphants. D'autres grands herbivores ont aussi été notés, même si certaines espèces n'étaient pas faciles à détecter d'en haut dans les forêts de savane. Les estimations de populations pour des espèces autres que l'éléphant ont donné des indices d'abondance qui pourraient servir à déterminer les tendances de la taille des populations dans le temps. Cette étude recherche des tendances significatives de l'abondance des grands herbivores du Parc National de Gonarezhou, en posant l'hypothèse que les études d'échantillonnage aériens conçues pour des éléphants donnent aussi des estimations correctes des tendances réelles des populations d'autres herbivores. Pour chaque espèce, le taux exponentiel de changement de population fut calculé en utilisant une régression pondérée, la variance de ce taux étant basée sur les variances d'échantillonnage des estimations de population. Des tendances de population significatives furent détectées pour huit espèces. Avant la sécheresse de 1992, le nombre d'éléphants était gardé à peu près constant grâce à de fréquents abattages, mais ensuite il a augmenté à un taux annuel moyen de 6,2% (limites de confiance : 4,0% et 8,6%). Le nombre d'éléphants des groupes de femelles a augmenté de 7,3%, significativement plus vite que dans les groupes de mâles (- 0,5%). Les nombres de buffles, élands, kudus, nyalas, waterbucks, gnous et zèbres ont tous augmenté après les déclins de population observés pendant la sécheresse.

Introduction

While the importance of monitoring wildlife populations in protected areas is acknowledged, the necessary resources are often lacking. Since the 1970s, elephant (scientific names in Table 1) management has been a priority in

**Correspondence:* Email: faykevin@zol.co.zw

Zimbabwe (Cumming, 1981; Martin, Craig & Booth, 1989), because of the effects of high densities of elephants on vegetation and smaller animals (Thomson, 1975; Cumming *et al.*, 1997). During the 1980s, these surveys were funded by Zimbabwean taxpayers, but since 1991 surveys have depended on outside support. Aerial surveys of Zimbabwe's elephant subpopulations still occurred regularly, because it was relatively easy to raise funds for elephant surveys, and survey designs and techniques were unchanged. The elephant is important economically (for the safari hunting industry and by providing the bulk of income in areas where natural resources are managed communally (Frost & Bond, 2008; Taylor, 2009)) and from a conservation viewpoint (because of the ivory trade ban by the Convention on International Trade in Endangered Species of Wild Fauna and Flora). While these surveys were designed to produce reasonably accurate and precise estimates of elephant numbers, using methods that were appropriate, repeatable and technically robust (Norton-Griffiths, 1978), other large herbivore species

Table 1 Trends in the estimated numbers of large herbivores in Gonarezhou NP, Zimbabwe, before and after the 1992 drought

Species	Period relative to 1992 drought	Years	Number of surveys	*r*	% change per annum	LCL *r*	UCL *r*	Trend[a]
Buffalo *Syncerus caffer*	Pre	1984–1991	5	0.081	8.4	−0.067	0.229	ns
Buffalo	Post	1993–2009	7	0.250	28.4	0.180	0.320	+
Eland *Taurotragus oryx*	Post	1993–2009	7	0.125	13.3	0.051	0.199	+
Elephant *Loxodonta africana*	Pre	1980–1991	8	0.002	0.2	−0.028	0.032	ns
Elephant	Post	1995–2009	6	0.060	6.2	0.039	0.082	+
Elephants in bull groups	Post	1995–2009	6	−0.005	−0.5	−0.028	0.019	ns
Elephants in cow herds	Post	1995–2009	6	0.070	7.3	0.046	0.095	+
Giraffe *Giraffa camelopardalis*	Pre	1984–1991	5	0.116	12.4	−0.068	0.301	ns
Giraffe	Post	1993–2009	7	0.036	3.6	−0.008	0.079	ns
Impala *Aepyceros melampus*	Post	1995–2009	6	0.009	0.86	−0.019	0.036	ns
Kudu *Tragelaphus strepsiceros*	Post	1993–2009	7	0.092	9.7	0.066	0.119	+
Nyala *Tragelaphus angasii*	Post	1993–2009	5	0.144	15.5	0.084	0.204	+
Ostrich *Struthio camelus*	Post	1993–2009	7	0.064	6.7	−0.012	0.141	ns[b]
Sable antelope *Hippotragus niger*	Pre	1984–1991	5	−0.144	−13.4	−0.422	0.134	ns
Warthog *Phacochoerus africanus*	Post	1996–2009	4	0.093	9.8	−0.015	0.202	ns[b]
Waterbuck *Kobus ellipsiprymnus*	Post	1993–2009	7	0.183	20.0	0.116	0.249	+
Wildebeest *Connochaetes taurinus*	Pre	1986–1991	4	−0.221	−19.8	−0.557	0.115	ns
Wildebeest	Post	1995–2009	4	0.224	25.1	0.129	0.319	+
Zebra *Equus quagga burchelii*	Pre	1984–1991	5	0.126	13.5	0.004	0.248	+
Zebra	Post	1993–2009	7	0.076	7.9	0.047	0.105	+

Predrought trends were examined using data from 1980 to 1991, and postdrought trends using data from 1993 to 2009. For elephants, the postdrought trends are those since the elephant captures during 1993. *r*, exponential rate of population change per annum; LCL *r*, lower 95% confidence limit of *r*; UCL *r*, upper 95% confidence limit of *r*.

[a]ns = no statistically significant trend; + = significant increase in estimated population number.

[b]There is a significant increase if using 90% confidence limits of *r*, instead of 95% confidence limits.

were also recorded during these surveys. Some species in woodland are not easily seen from the air, and their numbers are undoubtedly underestimated. Nonetheless, it is believed that population estimates for these species provide indices of abundance, with measures of precision, which can be used to determine temporal trends in population number. The purpose of this paper was to test for significant trends in the abundance of large herbivores, assuming that data from elephant surveys provide accurate estimates of real trends in the populations of other herbivores. The analysis uses population estimates from aerial surveys conducted during the past three decades to determine the population trends of 13 large herbivores in Zimbabwe's Gonarezhou National Park. This is the only sizeable protected area in south-eastern Zimbabwe. Since 1975, the park and its wildlife have been affected by wars (Zimbabwe's pre-independence civil war before 1980, and fighting between Zimbabwean military and Mozambican resistance forces during the late 1980s), by poaching (see Duffy, 1999), and the worst drought in living memory during 1991/92. But Gonarezhou is still the core range of one of Zimbabwe's four major subpopulations of elephant. Gonarezhou NP is within the Great Limpopo Transfrontier Park and the Great Limpopo Transfrontier Conservation Area (Fig. 1).

Methods

Study area

Gonarezhou NP lies <600 m above sea level and covers approximately 5000 km^2 in south-east Zimbabwe (Fig. 1). The Save, Runde and Mwenezi Rivers dominate the area, and other rivers flow only seasonally. The major vegetation types are as follows: (i) *Colophospermum mopane* shrubland or woodland; (ii) wooded and bushed grassland; (iii) dry deciduous woodland; and (iv) riverine woodland (Farrell, 1968; Sherry (1970) cited by Magadza *et al.*, 1993). The vegetation has been significantly impacted by drought, elephants and fires (Tafangenyasha, 1997).

Fig 1 Gonarezhou National Park lies north-eastwards of South Africa's Kruger National Park (KNP) and Mozambique's Limpopo National Park (LNP). The insert shows its location in southeast Zimbabwe. Gonarezhou NP, Kruger NP and Limpopo NP form the Great Limpopo Transfrontier Park and, together with Mozambique's Banhine and Zinave NPs and intervening communal lands, constitute the Great Limpopo Transfrontier Conservation Area

The region experiences a hot wet season during November–March, a cool dry season during April–July and a hot dry season during August–October. Mean maximum temperatures exceed 30°C during all months except June and July. The area is noted for low, but very variable, annual rainfall (Fig. 2). In the north of the park, annual rainfall averaged 516 mm (coefficient of variation 40%), ranging from 93 mm during the 1991/92 drought, to 1118 mm during 1999/2000, when cyclone Eline caused extensive flooding.

The Zimbabwe–Mozambique international border forms the eastern park boundary, part of which is sown with landmines, a legacy of Zimbabwe's pre-independence war. Elsewhere, the park borders Malapati Safari Area, Malilangwe private wildlife reserve and communal land. Coincident with the occupation of Zimbabwean commercial farms during 2000, people from the Chitsa community illegally occupied 50 km^2 in the north of Gonarezhou NP, built huts and introduced approximately 3000 cattle and 350–400 sheep/goats (Dunham *et al.*, 2007, 2010; Mombeshora & Le Bel, 2009).

Management has included the shooting of herds (culls) to reduce elephant numbers during 1971–1975, 1983, 1986 and 1987 (Booth *et al.*, 1997), and the capture and translocation of elephants in response to the 1992 drought. During that drought, 423 buffalo, 51 eland, 48 zebra, 27 waterbuck, fourteen sable and two nyala were captured and removed from the park (Tayler, 1992). It was intended that surviving animals would be returned after the drought, but few were. During some years, water was pumped to what would otherwise be seasonal pans. At various times, the park boundary was fenced during programmes to control disease (initially trypanosomiasis, later foot-and-mouth). Nonetheless, wildlife does move across the park boundary, and each year in the communal lands around the park, some animals are shot by safari hunters and during problem animal control operations. Illegal hunting of wildlife occurs in the park, but only for elephant and black rhinoceros *Diceros bicornis* have data on poaching trends been published (Martin, Craig & Booth, 1997). Poaching was common during the late 1980s, which included a period when the park was closed to the public, elements of the Zimbabwean army were in the park and conducting operations into Mozambique, and significant military engagements occurred inside the park (Saunders, 2006). There are no published data on trends in legal or illegal offtakes since 1995.

Aerial surveys

The first rigorous census of the Gonarezhou elephants was during 1980 (Coulson, 1980). Since then, similar sample aerial surveys have been undertaken regularly during the dry season by the Parks and Wildlife Management Authority [formerly Department of National Parks & Wild life Management, (DNPWLM)], often in partnership with

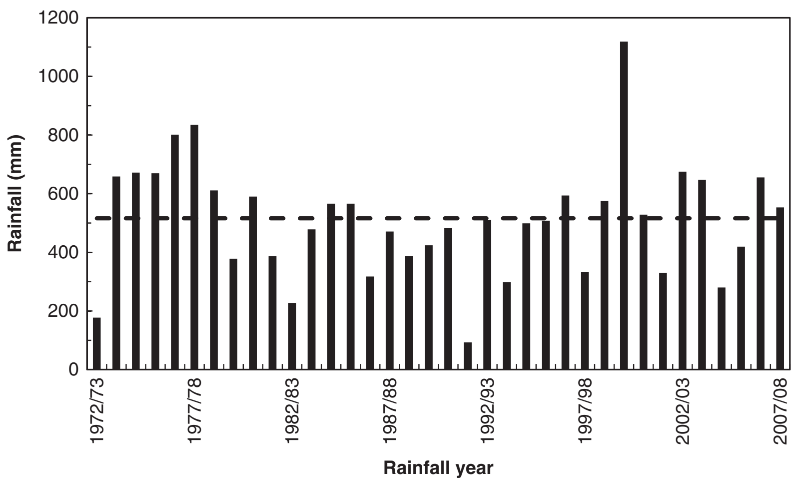

Fig 2 Trend in annual rainfall (July-June) at Chipinda Pools in the north of Gonarezhou NP since 1972. Dashed line indicates mean annual rainfall. No data are available for July 1988 to January 1992 and so data for Malilangwe reserve, just northwards of the park, were substituted

WWF, or Frankfurt Zoological Society (Coulson, 1981; Sharp, 1982, 1983, 1984, 1986, 1987; Gibson, 1989; Jones, 1991; Bowler, 1995; Davies, 1996; Davies *et al.*, 1996; Mackie, 1999; Dunham, 2002a; Dunham *et al.*, 2007, 2010). The methods were those recommended for surveys of large African herbivores (Jolly, 1969; Norton-Griffiths, 1978). Observers searched for elephants, but other large herbivores were also counted. Observer bias was minimized and held approximately constant between years by employing keen, experienced volunteers of proven ability and immune to airsickness, and ensuring that search intensity and the widths of search strips were approximately constant between years.

Data sources and data evaluation

Surveys were conducted during 16 years within the period 1980–2009. During 1982, a block count design was used, and sampling intensity was 31%. But during the other surveys, systematically arranged transects were used, and sampling intensity averaged 12.8% (n = 15 years, SD = 2.8, range 9–19%). Data on elephants and other large herbivores were extracted from the survey reports. Surveys before 1984 reported only elephants. From 1984, various large mammals (but not all) and ostrich were included in the reports, but sometimes it is not clear if animals were not seen, or seen but not reported. Species coverage was more consistent after 1993. No corrections were applied to compensate for undercounting or missed animals.

Impalas were not recorded during surveys before 1995. For eland, kudu, nyala and waterbuck, not all surveys before the 1992 drought provided population estimates: either no animals were seen (population estimate is zero), or some were seen but not reported (population estimate unknown). Hence, no attempt was made to examine predrought population trends for these species. There were eight predrought population estimates for elephant, five for buffalo, giraffe, sable and zebra and four for wildebeest.

Approximately, 600 elephants were captured during 1993, and the 1993 survey occurred while the captures were underway. Therefore, the postdrought time series for elephant was for 1995–2009. Separate estimates of the numbers of elephants in cow herds and in bull groups were available. Elephants in cow herds included adult cows, immature elephants of both sexes and probably some adult bulls. For buffalo, eland, giraffe, kudu, ostrich, waterbuck and zebra, postdrought trends in numbers were examined for the 16-year period 1993–2009. The postdrought trend for impala was for 1995–2009. For nyala, sable, warthog and wildebeest, only four or five of seven postdrought surveys produced population estimates greater than zero.

Data analysis

In this analysis, the exponential model is used to determine population growth rates, with natural logarithms of the population estimates regressed against time. An advantage of the weighted regression method used here to calculate population growth rates and their confidence intervals is its simplicity (Gasaway *et al.*, 1986).

The population estimates and variances extracted from the survey reports were calculated using Jolly's (1969) method 2 (transect surveys), or method 3 (block count surveys). For consistency, I recalculated 95% confidence limits for all mean estimates of population number as: Population estimate ± (t_v .√Total Variance); where t = Student's t, and v = degrees of freedom estimated by Satterthwaite's rule (Snedecor & Cochran, 1980).

All time series of population estimates were graphed and examined visually to see whether there appeared to be trends in the estimates. If, for any species and survey, the calculated lower confidence limit was less than the number of individuals seen in the search strips, this latter number was substituted for the lower confidence limit. Separate predrought and postdrought time series were examined.

Trends in animal numbers were determined assuming that an exponential model was appropriate for estimating the rate of population change for each species. The exponential rate of population change per annum (r) was calculated using Gasaway *et al.*'s (1986) method based on weighted regression of natural logarithms of the population estimates against time, with the variance of r based on the sampling variances of the population estimates. The percentage rate of population change per annum was $100\ (e^r - 1)$. A population was considered to have increased significantly if lower and upper confidence limits of r were positive, or to have declined significantly if both limits were negative.

This method of trend analysis cannot handle population estimates of zero. Examination of the postdrought population estimates for nyala, warthog and wildebeest suggested that they were rare during the decade following the drought, but not uncommon during 2007 and 2010 (population estimate 150 or greater). Hence, a population estimate of zero during any earlier postdrought survey probably resulted from sampling error, with the species so rare that none were seen along the transects. In other words (for these species during this period), population estimates of zero are erroneous. Hence, for nyala, warthog and wildebeest, postdrought trends were determined using only the population estimates greater than zero. Sable was rare after the drought, and no attempt was made to calculate a rate of population change.

Results

Predrought trends

The estimated number of elephants in Gonarezhou declined noticeably after the 1983 cull of more than 2000 animals (Fig. 3a), but overall during the 1980s, the number of elephants did not decline or increase: r was close to zero (Table 1). Only for zebra was there a significant trend (an increase) in the predrought population (Fig. 4a), but for most species, there were few or no predrought population estimates.

Postdrought trends

After the 1992 drought, the numbers of all elephants, elephants in cow herds, buffalo, eland, kudu, nyala, waterbuck, wildebeest and zebra in Gonarezhou all increased significantly (Table 1, Figs 3 and 4). Increases in the numbers of ostrich and warthog were nearly significant, but an apparent increase in giraffe number was not significant (Fig. 5). Only for impala and sable was there no suggestion of a consistent trend in population number after the drought (Fig. 5). But while impalas were numerous; the number of sable was small.

The number of elephant bulls did not change significantly after 1995 (Fig. 3c), and elephant bulls were the only 'species' to have a mean estimate of r that was negative during the postdrought period. The absence of any overlap in the confidence intervals of r for elephant cows and elephant bulls (Table 1) indicates that the rate of change in the number of elephants in bull groups was significantly less than the rate of increase in the number of elephants in cow herds. The number of zebra in

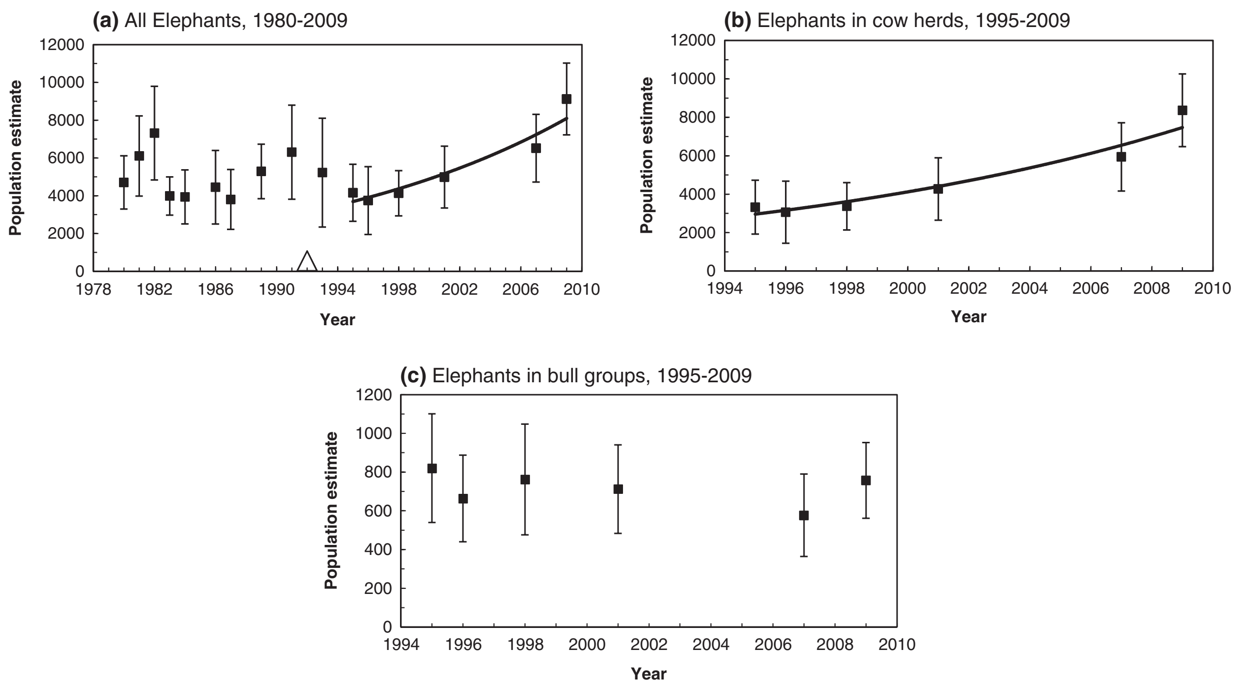

Fig 3 Trend in the number of elephant in Gonarezhou NP: (a) trend in the number of all elephants, 1980–2009 (triangle indicates 1992 drought); (b) postdrought trend in the number of elephants in cow herds, 1995–2009; and (c) estimated number of elephants in bull groups after the 1992 drought, 1995–2009. Mean population estimates and 95% confidence intervals shown. Elephants were culled (killed or captured) in Gonarezhou NP during 1983, 1986, 1987, 1992 and 1993. Bold solid lines indicate significant trends in estimated population number

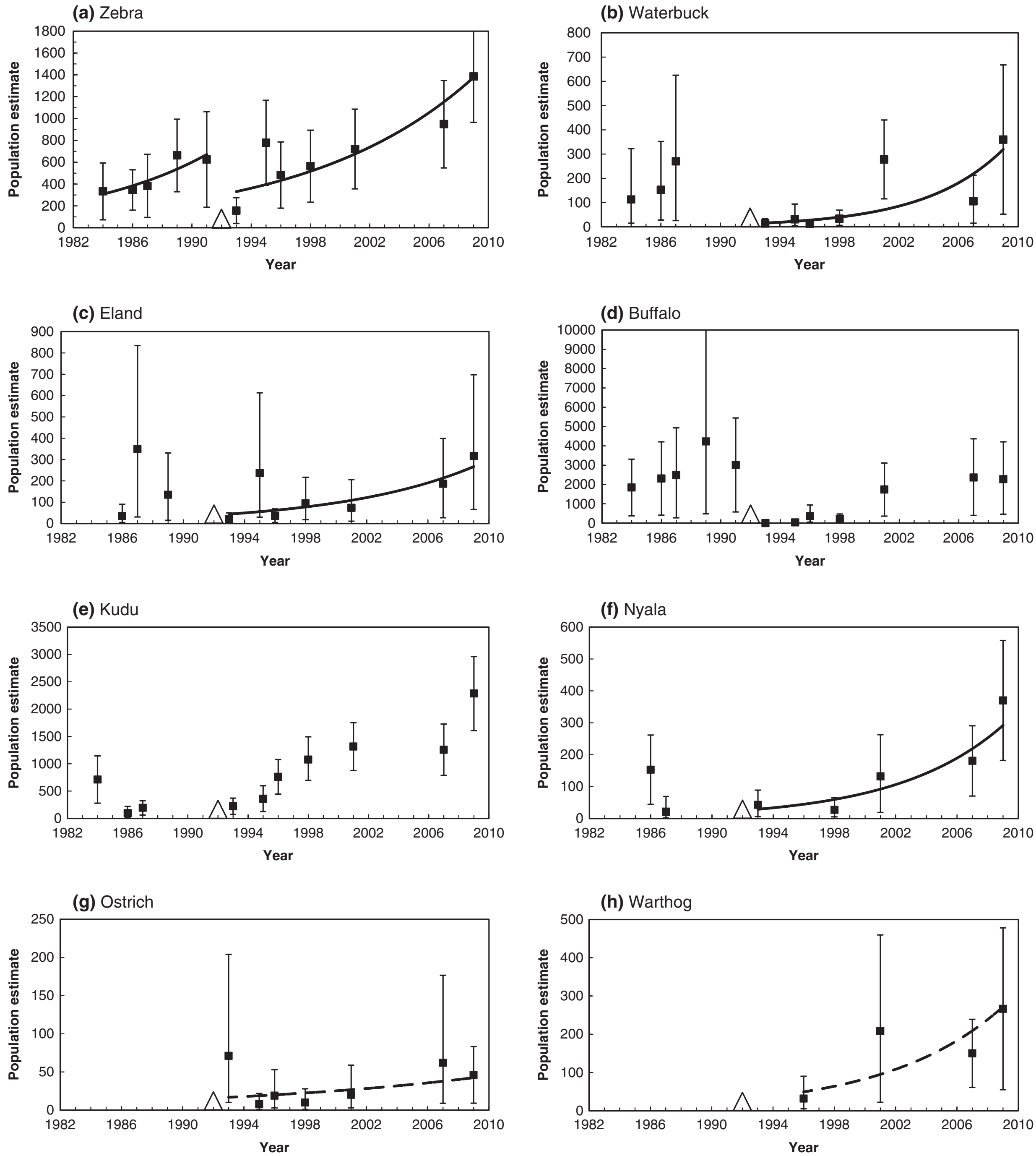

Fig 4 Trends in the number of: (a) zebra; (b) waterbuck; (c) eland; (d) buffalo; (e) kudu; (f) nyala; (g) ostrich; and (h) warthog in Gonarezhou NP. Mean population estimates and 95% confidence intervals shown. Bold solid lines indicate significant trends in estimated population number. Bold dashed lines indicate trends in estimated population number that approach significance (see Table 1). For zebra, the bold lines indicate the trends in the number of zebra before (left line) and after (right line) the 1992 drought: these trend lines suggest that the number of zebra declined by approximately 50% during that drought. The numbers of both buffalo and kudu increased significantly after the 1992 drought, but no trend lines are shown because an exponential model is probably not the most appropriate model for these species. Triangle indicates 1992 drought

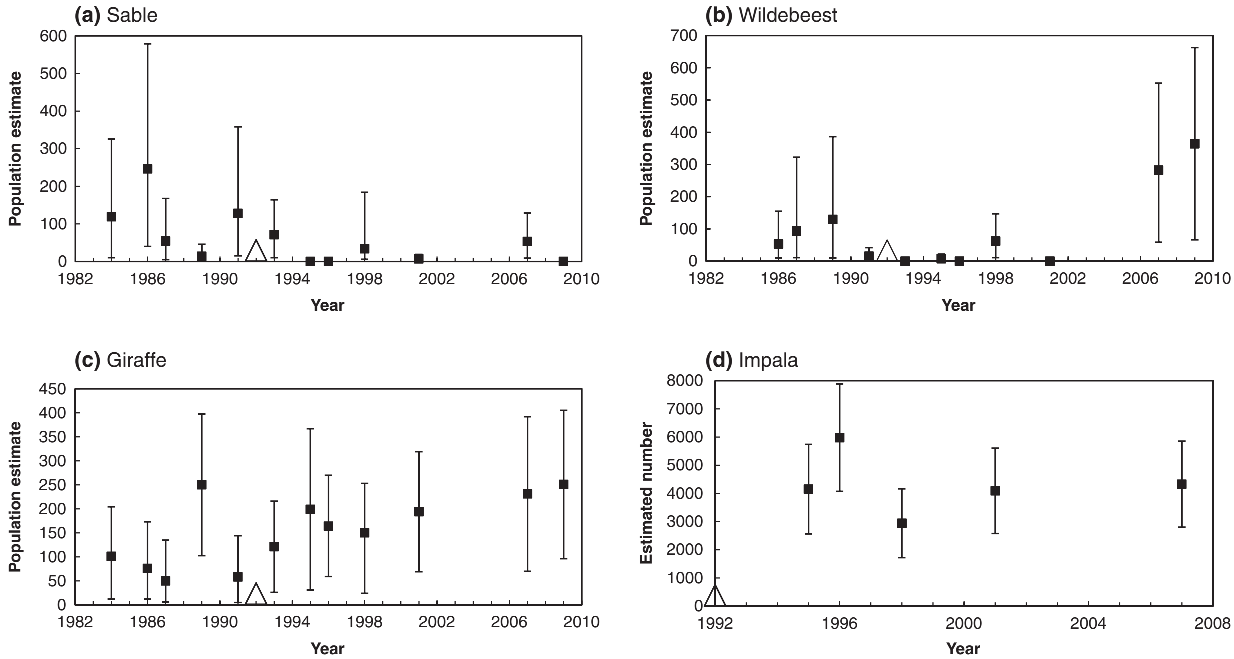

Fig 5 The estimated number of (a) sable antelope; (b) wildebeest; (c) giraffe; and (d) impala in Gonarezhou NP. Mean population estimates and 95% confidence intervals shown. Triangle indicates 1992 drought

Gonarezhou was increasing before the 1992 drought, declined by some 50% during (and presumably as a consequence of) that drought, and increased again afterwards.

Discussion

Observed population trends and drought effects

Gonarezhou populations of buffalo, eland, elephant, kudu, nyala, waterbuck, wildebeest and zebra, and probably ostrich and warthog, all increased in number after the 1992 drought. Although there were few predrought estimates for most species (except elephant), the available data for three grazers – zebra, buffalo and waterbuck – suggest that these had experienced population declines during the drought.

The zebra population was increasing in number before the 1992 drought, and probably it was recovering from the effect of an earlier, countrywide drought (1983) during which southern Gonarezhou experienced three successive years when rainfall was 50% of the long-term mean (Department of National Parks & Wild life Management, 1998). The data for buffalo and waterbuck hint that these populations may also have increased after this earlier drought. Rainfall records reveal yet another drought (during 1973), and one can speculate that, in this region of highly-variable rainfall, the population of zebra (and maybe other species also) is in near-constant flux, declining during droughts and then increasing afterwards.

Most herbivore populations in Gonarezhou are probably geographically isolated. Major declines during droughts leave the postdrought populations small in number and susceptible to inbreeding depression (Johnson *et al.*, 2011) and extinction, for example as a consequence of the Allee effect (Bourbeau-Lemieux *et al.*, 2011). The sable population was small before the drought and declined during it. The absence of a postdrought recovery may be a consequence of the small-population effect (Caughley, 1994), or perhaps of drought-induced changes to the grass layer. In theory, formation of the Great Limpopo Transfrontier Park should promote connectivity between the populations in Gonarezhou, Kruger and Limpopo NPs and thus reduce the likelihood of inbreeding depression and extinction. But Gonarezhou is separated from the other parks by 20 km of heavily settled communal land. In the north, the boundary between Gonarezhou NP and Malilangwe reserve is fenced. Furthermore, there are health concerns about promoting the movement out of Kruger NP of animals that may be infected with bovine tuberculosis (Caron, Cross & Du Toit, 2003).

Buffalo number in Kruger also declined during the 1992 drought, as lions *Panthera leo* killed proportionally more buffalo during relatively dry years (Mills, Biggs & Whyte, 1995; Funston & Mills, 2006). Kudu and waterbuck numbers in Kruger also declined during dry years. In contrast, the abundance of wildebeest and zebra in Kruger was greater during drier years than during wetter years, possibly because these species were more vulnerable to predation when the grass cover was high. It is unclear why the wildebeest populations in Gonarezhou and Kruger reacted differently during dry years, but there are two obvious differences between these parks. First, there are many artificial sources of drinking water in Kruger, and most of Kruger is within 5 km of water (Redfern *et al.*, 2005), while much of Gonarezhou was distant from water, even during years when artificial sources of water were provided. Secondly, the wildebeest population of Gonarezhou was very small, cf. Kruger, and thus susceptible to the small-population effect.

Number of elephants and rate of population increase

There were estimated to be 9123 (confidence interval 20.6%) elephants during 2009, which was the greatest ever estimate for the number of elephants in Gonarezhou. The previous highest estimate was 7315 during 1982 (Sharp, 1982), and more than 2000 elephants were culled during the following year. Elephant number declined noticeably after that cull, but overall during the 1980s, the number of elephants did not decline despite the culls and significant poaching during the 1980s (Gibson, 1989). But neither did it increase. In Gonarezhou, the culling of numerous elephants by shooting entire herds ended during 1987 after the few people with experience of these operations left the DNPWLM. Soon afterwards, the CITES ivory trade ban made it difficult to recover the costs of culling by selling the resulting ivory. Capturing and translocating entire herds of elephants was pioneered in Gonarezhou during 1993 (Coetsee, 1996), when more than 600 elephants were moved. But such operations are expensive, and suitable release sites are scarce in southern Africa. Hence, there have been no further translocations on this scale in Zimbabwe.

Estimates from surveys since 1993 imply that the number of elephants in Gonarezhou increased at a mean annual rate of 6.2% over 16 years, which is close to the theoretical maximum rate of increase for the African elephant (Calef, 1988; Foley & Faust, 2010). The high rate of increase in Gonarezhou reflects the heavy mortality of immature elephants during the 1992 drought (Leggett, 1994) and hence the high proportion of adult cows amongst the survivors (the late Clem Coetsee, unpublished data). The number of elephants in cow herds increased at a faster rate than the number of elephants in bull groups, which may have increased slightly, remained constant or declined. The surveys provide no indication as to why cows and bulls show different population trends. The offtakes of cows and bulls do differ. While recently, there has been little legal hunting of elephant cows, some bulls are shot annually in areas bordering the park by sport hunters or during problem animal control and others are killed illegally. Bulls are more likely than cows to raid crops (Chiyo & Cochrane, 2005) and thus to be shot. But without information on the offtakes, it is not possible to determine whether the different population trends result from differing rates of exploitation.

Rate of increase of buffalo population

After the 1992 drought, buffalo displayed the greatest rate of population increase (28%), although previous work suggests that r should be negatively related to body size (Western, 1979). Some elephants and probably buffaloes move between Kruger and Gonarezhou (Ministry of Lands, 1965; De Garine-Wichatitsky *et al.*, 2010; Henley, 2011), and immigration would increase population growth rates. Also, there are no published records of the number of animals released in the park after the drought. Studies of foot-and-mouth disease topotypes suggest that buffalo from western Zimbabwe have been introduced to Gonarezhou since the 1992 drought (Bengis, 2005): such introductions may explain the high rate of population growth for buffalo.

Detection of trends

The techniques used in Zimbabwe to estimate elephant numbers appear to provide accurate estimates because, at least in the Sebungwe, there is good agreement between survey estimates and the numbers of elephants killed (Dunham, 2008). But for other species, the population estimates are probably minimum figures, because smaller species are difficult to see from the air and because the observers' search image is elephants, and other species are more likely to be overlooked. Determining the actual abundances of the smaller species would require use of the double-count technique (Bayliss & Yeomans, 1989; Marsh & Sinclair, 1989), or DISTANCE sampling (Thomas *et al.*, 2010). The former requires extra observers and thus a larger aircraft, while application of the latter method to an aerial survey conducted with a fixed-wing aircraft can be complicated by uneven terrain and a variable flying height (which is easily corrected for during transect surveys).

This analysis has emphasized the value of aerial sample surveys for monitoring trends in animal numbers, even when the surveys were designed to monitor one particular species (elephant), the data on other species were collected only incidentally and some of the species are difficult to see from the air. The confidence intervals of the estimates for these other species are high, but a trend in estimated population number can often be detected even if a dataset initially appears unpromising. For example, the variances of the postdrought population estimates for eland were so high that the calculated lower confidence limits were usually negative, but it was still possible to detect a significant trend in estimated population number.

Suitability of exponential model

For elephant, eland, nyala, waterbuck, wildebeest and zebra, the exponential model appeared from visual inspection to be a suitable model for the observed postdrought changes in population number. The same was true for zebra before the drought. For buffalo and kudu after the drought, the exponential model may not be the most suitable model. The postdrought population estimates for buffalo suggest that the population number may have increased immediately after the drought, but that it may have levelled off since 2001 (Fig. 4d). Such a pattern is typical of the logistic growth curve, with the rate of increase declining as population number reaches a limit set by some limiting factor, such as the population's food supply (Caughley & Sinclair, 1994). Recent estimates of the number of buffalo in the park are broadly similar to the predrought estimates. No attempt is made to fit a logistic growth curve to the buffalo data because the high rate of growth suggests that the population may have increased by both births and immigration, assisted or otherwise.

The population trend for kudu is more complex, with the postdrought population increasing in number initially, then levelling off and then again increasing (Fig. 4e). During 2004, anthrax killed many kudus in Malilangwe reserve and Save Valley Conservancy (Clegg *et al.*, 2007). However, there is no record of anthrax in Gonarezhou, although anthrax is common in Kruger (Bengis, Grant & De Vos, 2003).

Management implications

During 2010, it was proposed that eland, zebra, giraffe, wildebeest and impala be released in Gonarezhou. This study has shown that the numbers of eland, wildebeest and zebra in Gonarezhou are increasing, and that impalas are numerous and apparently stable in number. Hence the biological justification for the proposed releases is unclear – so far, they have not happened. Although there might appear to be a case for releasing sable antelope in Gonarezhou, studies at Malilangwe suggest otherwise. The Malilangwe sable population also declined during the 1992 drought, and there the surviving population was supplemented by translocations, but the population decrease continued. Lion predation seems to be the principal cause of the decline, but the role of predation may be influenced by vegetation cover and surface water distribution (Capon, 2011).

Long-term monitoring

Apart from revealing trends in the abundance and spatial distribution of wildlife, sample aerial surveys can provide similar information on environmental aspects that influence wildlife. For example, elephant carcasses and poachers' camps recorded during aerial surveys reveal trends in illegal hunting (Dunham, 2008), and huts and domestic livestock reveal trends in illegal settlement by people (Dunham *et al.*, 2007, 2010), and the adverse effects of squatters on wildlife numbers and distribution (Dunham, 2002b, 2003).

Trend analyses depend on the use of similar methods during successive surveys, so that differences in population number can be assumed to be genuine and not a consequence of changing methods. Given the difficulty of ensuring that methods are identical (for example, the same observers are often not available for successive surveys), the application of high and consistent standards during survey execution is important. The difficulties of maintaining a long-term monitoring programme of large herbivores using aerial surveys should not be underestimated. Surveys require a specialized aircraft (fitted with a radar altimeter) and dedicated staff (not many people retain their enthusiasm and breakfast after hours of flying in the hot, bumpy conditions that prevail during the season when trees are leafless and visibility is at a maximum). But sample aerial surveys can be executed relatively quickly and thus inexpensively. The Gonarezhou survey programme has extended over three decades whereas, for example, the Kruger programme of costly total-area counts of large ungulates was discontinued (Redfern *et al.*, 2002). The Gonarezhou surveys continued over 30 years that included significant annual variations in climate and poaching, and even warfare across the international border that forms the park's eastern boundary. Long-term perspectives are required to guide management that is evidence-based and to understand ecosystem dynamics (Sinclair *et al.*, 2007), and the Gonarezhou survey programme provides a long-term perspective.

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