

Does trophy hunting matter to long-term population trends in African herbivores of different dietary guilds?

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Abstract

The persistence of large African herbivores in trophy hunting areas is still unclear because of a lack of data from long-term wildlife monitoring outside national parks. We compared population trends over the last 30 years in Hwange National Park, Zimbabwe, and the neighbouring Matetsi Safari Area where large herbivores were harvested at an average yearly rate of 2%. We investigated whether trophy hunting altered densities and the proportion of adult males in several large herbivore species. Large herbivores generally thrived as well, or even better, in the hunting areas than in the national park. The proportion of adult males did not differ between the two zones, except for species with higher harvest rates and proportionally more males harvested. Densities were not lower in the hunting areas than in the national park, except for elephant and impala. Large herbivores generally declined throughout the 30-year period in both zones, particularly selective grazers. This is probably because of their greater sensitivity to variation in rainfall compared with other herbivores. Rainfall indeed declined during the study period with droughts being particularly frequent during the 1990s. Browsers, mixed feeders and non-selective grazers generally declined less in the hunting areas than in the national park, possibly because of lower densities of natural predators and elephants outside the park. Our study highlighted that large herbivores may persist in trophy hunting areas as well as in national parks. When rigorously managed, trophy hunting areas may be relevant conservation areas for large herbivores, particularly under the current global decline of wildlife abundance across Africa.

Introduction

Hunting increases mortality in harvested populations, and may therefore alter their dynamics (Caughley, 1977). With inappropriate control, hunting may jeopardize the viability of harvested populations, and may eventually drive them to extinction (e.g. poaching: Milner-Gulland, Bennett & the SCB 2002 Annual Meeting Wild Meat Group, 2003a; high-hunting quotas: Besnard, Novoa & Gimenez, 2010). Overhunting threatens more than 30% of endangered mammal species (Baillie, Hilton-Taylor & Stuart, 2004), particularly ungulates (Price & Gittleman, 2007). Ungulates often drive the structure, composition and functioning of ecosystems (Collins *et al.*, 1998; Côté *et al.*, 2004). They moreover provide goods and income to human communities (Milner-Gulland *et al.*, 2003a). Understanding and managing the effects of hunting on ungulate population dynamics is therefore crucial to conserving the integrity of terrestrial ecosystems while considering economic interests (Gordon, Hester & Festa-Bianchet, 2004).

Trophy hunting, contrary to unregulated hunting such as poaching, is a legalized hunting mode often used as a conservation option (Dickson, Hutton & Adams, 2009). Trophy hunters are willing to pay large amounts of money to harvest individuals with large secondary sexual characters (i.e. horns or antlers; Festa-Bianchet, 2003). This creates incentives for the conservation of natural habitats and animal populations (Leader-Williams, Smith & Walpole, 2001). Horns and antlers are particularly developed in males (Johnstone, 1974; Cumming, 1989) and increase as males grow older (Côté, Festa-Bianchet & Smith, 1998; Coltman *et al.*, 2003). Consequently, trophy hunting harvests are skewed towards adult males, and their proportion may therefore decrease in hunted populations (Laurian *et al.*, 2000). Despite productivity usually being considered higher in populations with female-biased sex ratios (Caughley, 1977), it is increasingly acknowledged that the lack of adult males may alter reproduction, recruitment rates and eventually population dynamics (reviewed in Milner, Nilsen & Andreassen, 2007).

Trophy hunting has been shown to reduce horn size with time (Coltman *et al.*, 2003; Crosmar *et al.*, 2013). However, offtakes from trophy hunting supposedly represent only a small fraction of the male segment in hunted populations (Cumming, 1989; Caro *et al.*, 1998), so that the impact on population dynamics appears rather limited in polygynous ungulates (Mysterud, 2012). In Africa, long-term monitoring is rare (Caro, 2011), particularly outside national parks (but see Stoner *et al.*, 2007; Western, Russell & Cuthill, 2009). Consequently, hunting quotas are frequently set on inappropriate estimates based on historical or anecdotal observations, and are therefore often unsustainable (e.g. Elkan, 1994; Grobbelaar & Masulani, 2003). Furthermore, law enforcement, which should ensure quota compliance and limit overhunting, is financially challenging and thus often neglected in developing countries (Price & Gittleman, 2007).

These potential effects of trophy hunting on large herbivore populations have fuelled the long-standing debate whether trophy hunting may be an effective conservation option in Africa (e.g. Taylor & Dunstone, 1996). In this context, we compared population densities and proportions of adult males of several large African herbivores, between Matetsi Safari Area (MSA; trophy hunting area) and the neighbouring Hwange National Park (HNP; hunting-free area), Zimbabwe, over the past 30 years. We hypothesized that trophy hunting altered population dynamics of large herbivores. We tested in particular whether populations of hunting areas had (1) lower densities; (2) lower proportions of adult males compared with populations in the national park. We also tested whether (3) densities and proportions of adult males decreased in hunting areas throughout the past three decades in comparison with those in the national park. In addition, we discuss alternative factors that possibly explain the spatiotemporal trends of large herbivore

densities in our study area (i.e. rainfall and the densities of natural predators and elephants).

Material and methods

Study area

The study covered parts of MSA and HNP. MSA is a major hunting complex in Zimbabwe (c. 3000 km²; Cumming, 1989) at the north-western border of HNP (c. 15 000 km²) (Fig. 1). MSA and HNP are unfenced state-owned lands administrated by Zimbabwe Parks and Wildlife Management Authority (ZPWMA). MSA, however, has been leased to safari operators for hunting tourism since 1973. Seven hunting units constitute MSA, with units 1–5 in the southern part and units 6 and 7 in the northern part. Hunting ceased in unit 7 in 1995. Moreover, vegetation types and environmental conditions (i.e. rainfall, temperature and soil characteristics) in units 6 and 7 differ from the five other units (Ganzin, Crosmar & Fritz, 2008; Peace Parks Foundation, 2009). We thus focused on units 1–5 (404, 292, 356, 470 and 370 km², respectively; Fig. 1). In HNP, we covered the blocks that were adjacent to these five hunting units (i.e. Robins, c. 1000 km²; Sinamatella, c. 1000 km²; Fig. 1), because their vegetation types and environmental conditions are similar to MSA (Tables 1 and 2; Ganzin *et al.*, 2008; Peace Parks Foundation, 2009). We used 10-day Normalised Difference Vegetation Index (NDVI) images (resolution 1.2 × 1.2 km) available from 1986 to 2010 (Crosmar *et al.*, 2013) as a proxy of vegetation productivity in the region. NDVI was similar in HNP and MSA between 1986 and 2010 [HNP, NDVI average ± standard deviation (SD) = 0.48 ± 0.09; MSA: 0.45 ± 0.07; $F_{1,157} = 3.2$, $P = 0.08$]. It generally increased during this period [year, estimate ± standard error = 0.002 ± 0.002, $F_{1,157} = 14.8$,

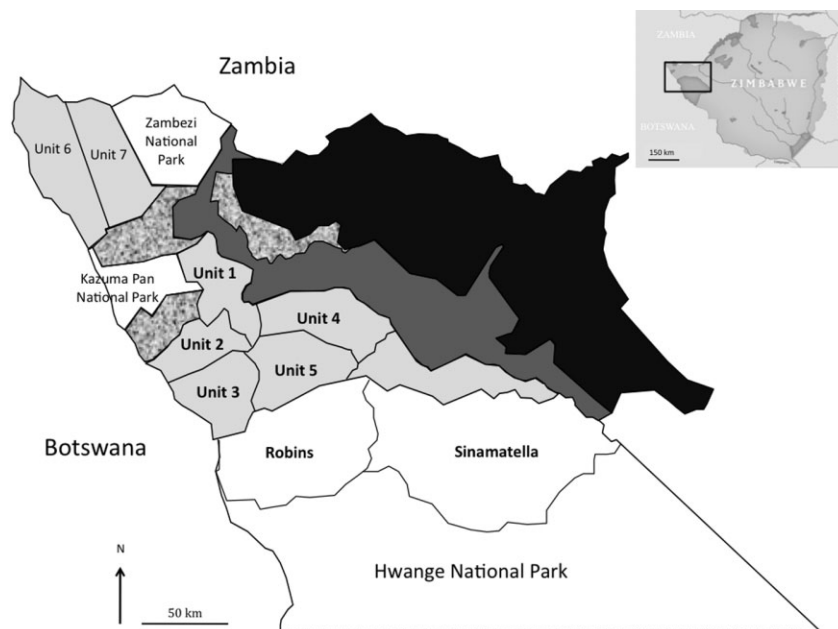


Figure 1 Northern part of Hwange ecosystem, Zimbabwe. The study area is delineated by the thick black rectangle. National parks (i.e. hunting-free areas) are in white, hunting areas (units 1–7) of the Matetsi Safari Area in light grey and hunting areas of the Forestry Commission in granite. Private lands and communal lands are, respectively, coloured in dark grey and in black. The studied hunting units of Matetsi Safari Area and blocks of Hwange National Park are indicated in bold font.

Table 1 Eco-regions, geology and soil characteristics in the north-western blocks of Hwange National Park (HNP) and the adjacent blocks of Matetsi Safari Area (MSA), Zimbabwe (adapted from Peace Parks Foundation, 2009)

Site	Eco-region	Geology	Soil types	Soil texture	Soil drainage
MSA	Zambezi and Mopane woodlands	Basalt	Leptosols (shallow, rocky)	Sandy	Well drained
HNP (western blocks)	Zambezi and Mopane woodlands	Basalt Siltstone/granite	Leptosols (shallow, rocky) Solonetz (dense, high in sodium)	Sandy Clayey	Well drained Poorly drained

Table 2 Proportion (mean % ± standard deviation) of the main vegetation structures, woody species and the availability of surface water in the north-western blocks of Hwange National Park (HNP) and the adjacent blocks of Matetsi Safari Area (MSA), Zimbabwe (from Ganzin *et al.*, 2008)

	HNP	MSA	Mann-Whitney-Wilcoxon test
Vegetation structure			
Open woodland (trees > 30 and < 50%, shrubs < 10%)	32.9 ± 26	22.8 ± 7.1	$W = 3, P = 1$
Dense woodland (trees > 50%, shrubs < 10%)	13.4 ± 8.9	5.5 ± 1.5	$W = 6, P = 0.2$
Open shrubland (shrubs > 30 and < 50%, trees < 10%)	32.1 ± 14.5	44.6 ± 7.4	$W = 1, P = 0.4$
Grassland (shrubs and trees < 10%)	14.2 ± 20.1	7.4 ± 5.5	$W = 3, P = 1$
Shrubland (shrubs > 50%, trees < 10%)	1.1 ± 1.0	1.5 ± 2.4	$W = 4, P = 0.8$
Tree to shrub (mixed woodland/shrubland)	3.2 ± 0.9	17.8 ± 6.5	$W = 0, P = 0.2$
Woody species			
<i>Colophospermum mopane</i>	68.4 ± 27.8	61.1 ± 7.0	$W = 3, P = 1$
<i>Combretum</i> spp.	6.1 ± 1.6	21.1 ± 2.1	$W = 0, P = 0.2$
<i>Baikiaea plurijuga</i>	5.4 ± 7.6	3.8 ± 3.9	$W = 3, P = 1$
<i>Terminalia sericea</i>	1.7 ± 0.1	4.4 ± 0.5	$W = 0, P = 0.2$
<i>Brachystegia</i> spp.	0.2 ± 0.2	0.9 ± 0.6	$W = 1, P = 0.4$
<i>Burkea africana</i>	0.9 ± 1.2	0.9 ± 1.2	$W = 2, P = 0.8$
Water availability ^a			
All waterholes and main rivers	76.5 ± 15.8	78.4 ± 17.6	$W = 3, P = 1$
Pumped waterholes	53.2 ± 28.	47.9 ± 25.8	$W = 3, P = 1$

^aExpressed as the proportion of area in each block located within 5 km from potential surface water supply during the dry season.

$P = 0.0002$), with no difference between HNP and MSA ($F_{1,157} = 1.3, P = 0.2$). Finally, as state-owned lands, MSA and HNP are similarly managed regarding anti-poaching, surface water provision and controlled fires (ZPWMA, unpubl. data).

Species

We studied African buffalo *Syncerus caffer*, Burchell's zebra *Equus burchelli*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, greater kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus*, reedbuck *Redunca arundinum*, sable antelope *Hippotragus niger*, warthog *Phacochoerus aethiopicus* and waterbuck *Kobus ellipsiprymnus*. These species are fairly common large herbivores encountered in southern Africa (Skinner & Chimimba, 2005) and are hunted for trophies (Lindsey, Roulet & Romañach, 2007). They have distinct diets and body weight, but most are water dependent (except for warthog and giraffe; Table 3). This allows comparisons that may provide insights on alter-

Table 3 Main large herbivores of Matetsi Safari Area (MSA, hunting areas) and Hwange National Park (HNP, hunting-free area), classified by diet and dependency on surface water, and ranked according to increasing body weight

Species	Diet	Surface water dependency	Mean body weight (kg)
Warthog	Selective grazer ^a	No	30
Impala	Mixed feeder	Yes	41
Reedbuck	Selective grazer	Yes	55
Greater kudu	Browser	Yes	136
Waterbuck	Selective grazer	Yes	205
Sable antelope	Selective grazer	Yes	210
Zebra	Non-selective grazer	Yes	216
Buffalo	Non-selective grazer	Yes	495
Giraffe	Browser	No	700
Elephant	Mixed feeder	Yes	1725

^aWarthogs are less selective than other selective grazers, and may occasionally browse (Bothma *et al.*, 2004). Adapted from Bothma, van Rooyen & du Toit (2002).

native factors that could have influenced population density trends in our study area. For instance, selective grazers are particularly sensitive to a low rainfall regime (Owen-Smith, 2008), so their densities may be more affected than other species during dry years. In addition, herbivores with a smaller body size are more vulnerable to natural predators than larger prey (Sinclair, Mduma & Brashares, 2003). Their densities may therefore be more influenced by variation in natural predator abundances than larger herbivores.

Population trends

Yearly road counts were carried out in late dry season (September/October) from 1977 to 2010 in the MSA hunting units and HNP management blocks. Data, however, were missing between 1987 and 1994 in HNP. We therefore divided the dataset into two periods (i.e. 1977–1986 and 1995–2010 in both zones). Most available roads were used as transects following the distance sampling procedure with two observers, whose effect was accounted for in the analyses (Buckland *et al.*, 2001; Chamaillé-Jammes *et al.*, 2009 for similar procedure in HNP). Penetration of roads was 0.7 and 3.2 km km⁻² in HNP and MSA, respectively. The distance travelled was 12 536 km in HNP, and 24 920 km in MSA. These were very high compared with other studies in African savannas (e.g. Fischer & Linsenmair, 2001; Brashares & Sam, 2005; Gaidet-Drapier *et al.*, 2006; Caro, 2011). The two areas were thus well covered by road counts, so the data collected were representative of the two areas and comparable between them. For each group of herbivores encountered, species, group size and number of adult males were recorded.

We analysed data using distance sampling software (Thomas *et al.*, 2006) and obtained estimates of population densities per species and per year in each unit/block. Coefficients of variation associated with population estimates averaged 17% in warthog, 14% in impala, 34% in reedbuck, 16% in greater kudu, 35% in waterbuck, 25% in sable antelope, 20% in zebra, 44% in buffalo, 26% in giraffe and 36% in elephant. We then computed the proportion of adult males as the ratio of the total number of adult males counted over the total number of individuals counted per species and per year in each unit/block. Because seasonal migrations in southern Africa are less common than in eastern Africa (Walker, 1979), and because most large herbivores in HNP and MSA are sedentary and do not migrate (V. Booth, pers. comm.), the risk of dependency of population data between the two areas was limited.

Rainfall regime

Fluctuations in the abundance of herbivore populations in African semi-arid savannas are largely driven by rainfall, particularly during the dry season (Mduma, Sinclair & Hilborn, 1999; Ogotu & Owen-Smith, 2003). Although most rain falls in the wet season, from November to April, some falls during the dry season. Data on annual and dry season rainfalls in the study area were available for 1976–2005.

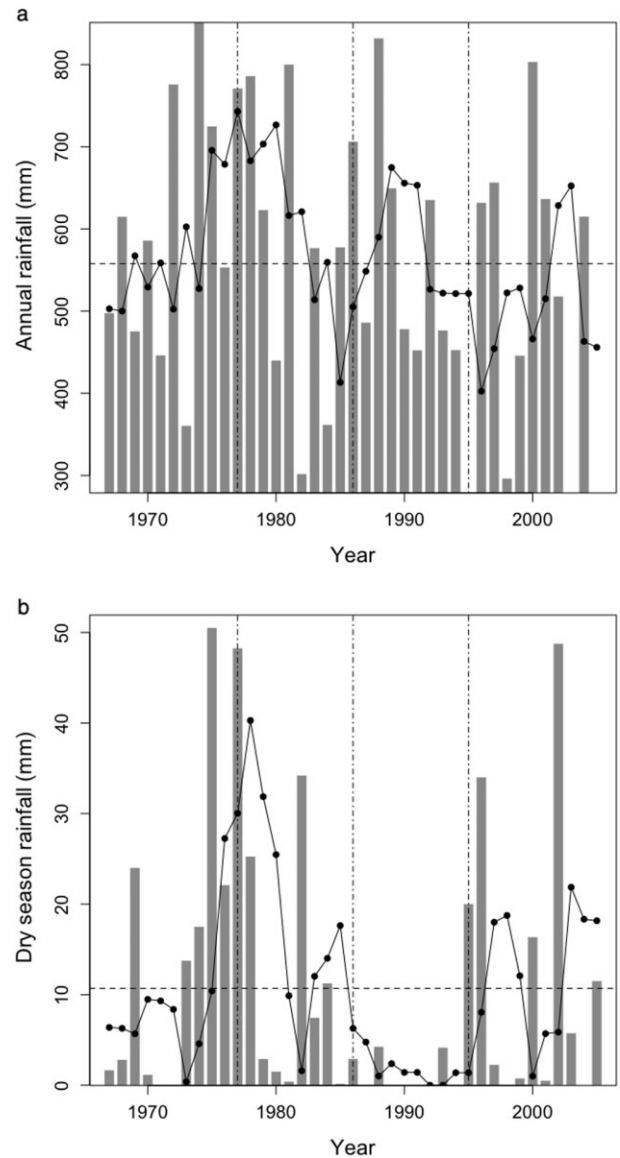


Figure 2 Trends in (a) annual rainfall and (b) dry season rainfall over 30 years in units 1–5 of Matetsi Safari Area (hunting areas), and the Robins and Sinamatella blocks in Hwange National Park (hunting-free area), Zimbabwe. Bars indicate annual records and solid lines indicate the 3-year running means. The horizontal dotted line represents the long-term average. The vertical dotted lines separate the study periods (see text for details).

Annual and dry season averages were 544 (Fig. 2a) and 10.2 mm (Fig. 2b), respectively. There was, however, a high variability associated with average annual and dry season rainfalls (coefficient of variation, 32 and 142%, respectively). Although the period from 1995 to 2010 experienced more years below the long-term average than 1977–1986 (i.e. six vs. three), annual rainfall did not significantly differ between the two periods (average annual rainfall \pm sd: 591 ± 170 vs. 487 ± 198 ; Mann–Whitney test: $W = 77$, $P = 0.3$) (Fig. 2a). However, the 3-year running means of

annual rainfall linearly decreased from 1977 to 2010 (Fig. 2a; mean year effect \pm SE: -6.7 ± 1.7 , $F_{1,28} = 15$, $P < 0.001$). Dry season rainfall did not significantly differ between the two periods (14 ± 16 vs. 13 ± 16 ; Mann–Whitney test: $W = 68$, $P = 0.6$) (Fig. 2b). However, the period from 1995 to 2010 followed a dry spell decade (i.e. 1986–1994), with dry season rainfall constantly below the long-term average (Fig. 2b). Therefore, if annual or dry season rainfall were of primary influence on herbivore population dynamics, population densities should generally be lower in 1995–2010 than from 1977 to 1986 for most herbivore species, both in MSA and HNP.

Harvest rates

Cumming (1989) reported that annual harvest rates for large herbivores in MSA were *c.* 2%. Data on offtakes for the study period were only available for buffalo, elephant, impala, greater kudu and sable antelope. Thus, we were only able to compute harvest rates (i.e. number of harvested animals over the estimated population size) for these species, and found an average of $1.7 \pm 1.2\%$ throughout the study period, similar to Cumming (1989). This varied among species [analysis of variance (ANOVA), $F_{4,104} = 10.5$, $P < 0.0001$], with sable antelope and elephant experiencing higher average harvest rates than impala, buffalo and greater kudu (Fig. 3a). Trophy hunters essentially harvest large-horned animals (i.e. adult males). Females can nonetheless be on quotas for food rations and bait for hunting carnivores. On average, $80 \pm 17\%$ of the animals on quotas were males; this varied among species (ANOVA, $F_{4,150} = 15.7$, $P < 0.0001$), being higher for sable antelope and elephant and lower for impala (Fig. 3b). If trophy hunting alters population dynamics and structure, then density and proportion of adult males should be especially low in hunting areas compared with the national park for species like sable antelope and elephant.

Analyses

To test whether population densities and the proportion of adult males differed between hunting areas and the national park, we performed ANOVAs with zone (i.e. MSA vs. HNP) and period (i.e. 1977–1986 vs. 1995–2010) as factors. We also tested the interaction between zone and period because we expected differences between hunting areas and the national park to increase through time. Because temporal serial autocorrelation may affect time series counts, we controlled for temporal autocorrelation using a first-order autoregressive covariance structure (Pinheiro & Bates, 2000). Densities were square root transformed and proportions of adult males were log transformed to meet normality assumptions. We used units/blocks as random effects in the ANOVAs using the R nlme package (<http://www.r-project.org/>).

We then built a tree-based model to test whether there were groups of species whose densities had been similarly affected by zone and period (Breiman *et al.*, 1984). For trends in densities to be compared among species, we first normal-

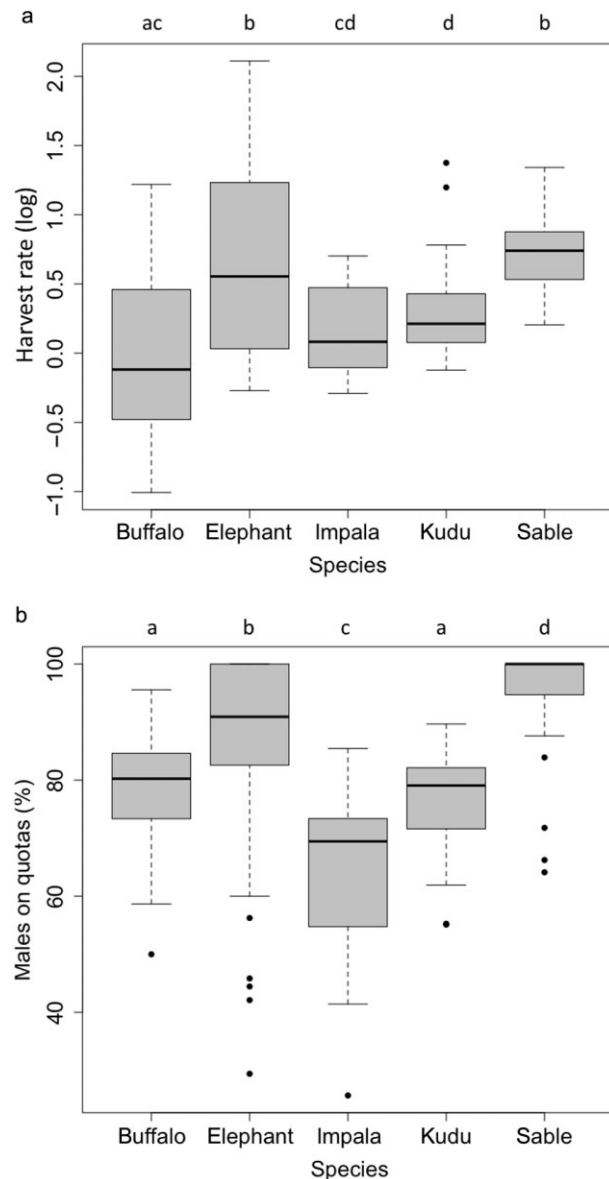


Figure 3 Observed values of (a) harvest rate (number of harvested animals over the estimated population size) and (b) proportion of males in hunting quotas between 1978 and 2008 in hunting units 1–5 of Matetsi Safari Area, Zimbabwe, for buffalo, elephant, impala, greater kudu and sable antelope. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are the observation $< 10\%$ or $> 90\%$ percentiles. Different letters indicate significant differences at $P < 0.05$.

ized densities for each species before pooling them in a single dataset, with zone, period and species as factors. We then used the R rpart and partykit packages (<http://www.r-project.org/>) to build a classification tree of the normalized densities according to these three factors, and then simplified it using the pruning method (Breiman *et al.*, 1984).

Results

Population densities

Throughout the study period, population densities did not differ between MSA and HNP for buffalo, giraffe, greater kudu, reedbuck, warthog and zebra, whereas they were significantly higher in MSA than in HNP for sable antelope and waterbuck (Table 4; Fig. 4). Densities were significantly lower in MSA than in HNP for elephant and impala (Table 4; Fig. 4).

Densities generally declined between 1977–1986 and 1995–2010 in both zones for selective grazers (Table 4; Fig. 5). In HNP, this decline was *c.* 94, 73, 50 and 90% for reedbuck, sable antelope, warthog and waterbuck, respectively. The decline was milder in MSA (*i.e.* *c.* 80, 62, 31 and 56%, respectively, for the same species; Fig. 5), although the differences were not statistically significant (Table 4). Sable

antelope densities remained higher in MSA compared with HNP throughout the study period (Table 4; Fig. 4). Densities of giraffe, impala and greater kudu were higher in HNP than in MSA from 1977 to 1986 (Table 4; Fig. 4). However, they declined between 1977–1986 and 1995–2010 in HNP (about 60, 48 and 52%), whereas they increased in MSA (about 49, 32 and 61%) (Table 4; Fig. 5); densities did not differ between zones from 1995 to 2010. Buffalo tended to experience similar trends as giraffe, impala and greater kudu (Fig. 4), although not significantly (Table 4). For zebra, we observed no significant temporal trend in densities and no significant difference between MSA and HNP (Table 4; Figs 4 and 5). In elephant, densities were generally *c.* 98% higher from 1995 to 2010 compared with 1977–1986. Densities were higher and seemed to increase more in HNP compared with MSA, but not significantly (Table 4; Figs 4 and 5).

The selected classification tree indicated that period was the factor explaining most variation in normalized densities among studied species, with densities being generally lower in 1995–2010 than in 1977–1986 (Fig. 6). Trends for selective grazers (*i.e.* reedbuck, sable antelope, warthog and waterbuck) differed from trends of browsers, mixed feeders and non-selective grazers (*i.e.* giraffe, greater kudu, elephant, impala, buffalo and zebra). For selective grazers, overall densities did not differ between MSA and HNP, and both zones experienced a decrease in densities of similar magnitude between 1977–1986 and 1995–2010. For browsers, mixed feeders and non-selective grazers, densities were generally lower in MSA than HNP from 1977 to 1986, particularly for buffalo, giraffe, impala and greater kudu (Fig. 6). However, this difference in densities between MSA and HNP disappeared in 1995–2010 (Fig. 6), which indicated a greater decrease of densities in HNP compared with MSA for these species (Fig. 6). Elephant and zebra were a distinct subgroup within the group of browsers, mixed feeders and non-selective grazers, because their density trends differed from those of the rest of the group (Fig. 6). This was consistent with the results from the ANOVAs because elephant were the only species whose density increased during the study period, and zebra did not show any significant spatial pattern or temporal trend of densities.

Table 4 Two-way analysis of variance of densities (square root transformed) of African ungulate species according to period (1977–1986 vs. 1995–2010), zone (hunting-free area vs. hunting areas), and their interaction in Hwange National Park and the adjacent Matetsi Safari Area, Zimbabwe

Species	Factor	d.f.	Densities		
			r.d.f.	<i>F</i>	<i>P</i>
Buffalo	Period	1	88	0.3	0.6
	Zone	1	5	2.8	0.2
	Period × zone	1	88	0.6	0.4
Elephant	Period	1	88	18.1	0.0001
	Zone	1	5	11.2	0.02
	Period × zone	1	88	2.6	0.1
Giraffe	Period	1	88	1.2	0.3
	Zone	1	5	4.1	0.1
	Period × zone	1	88	26.4	0.0001
Impala	Period	1	87	3.0	0.1
	Zone	1	5	12.5	0.02
	Period × zone	1	87	25.6	< 0.0001
Greater kudu	Period	1	88	1.2	0.3
	Zone	1	5	12.5	0.6
	Period × zone	1	88	25.6	< 0.0001
Reedbuck	Period	1	88	31.5	< 0.0001
	Zone	1	5	1.1	0.4
	Period × zone	1	88	3.6	0.06
Sable antelope	Period	1	88	73.9	< 0.0001
	Zone	1	5	21.4	0.006
	Period × zone	1	88	1.1	0.3
Warthog	Period	1	88	16.6	0.0001
	Zone	1	5	1.3	0.3
	Period × zone	1	88	2.0	0.2
Waterbuck	Period	1	88	95.2	< 0.0001
	Zone	1	5	11.7	0.001
	Period × zone	1	88	1.3	0.3
Zebra	Period	1	88	0.3	0.6
	Zone	1	5	1.6	0.3
	Period × zone	1	88	2.8	0.1

d.f., degrees of freedom; r.d.f., residual degrees of freedom.

Proportion of adult males

For sable antelope and elephant, the proportion of adult males was significantly lower in MSA than in HNP, declining in MSA but not in HNP between the two periods (Table 5; Fig. 7). For waterbuck and zebra, this proportion declined between the two periods, and tended to be lower in MSA than HNP (Table 5; Fig. 7). We found no significant effect of zone, period or their interaction on the proportion of adult males for the other species (Table 5), but this proportion seemed to be lower in MSA than in HNP for most of them, more particularly from 1995 to 2010 (Fig. 7).

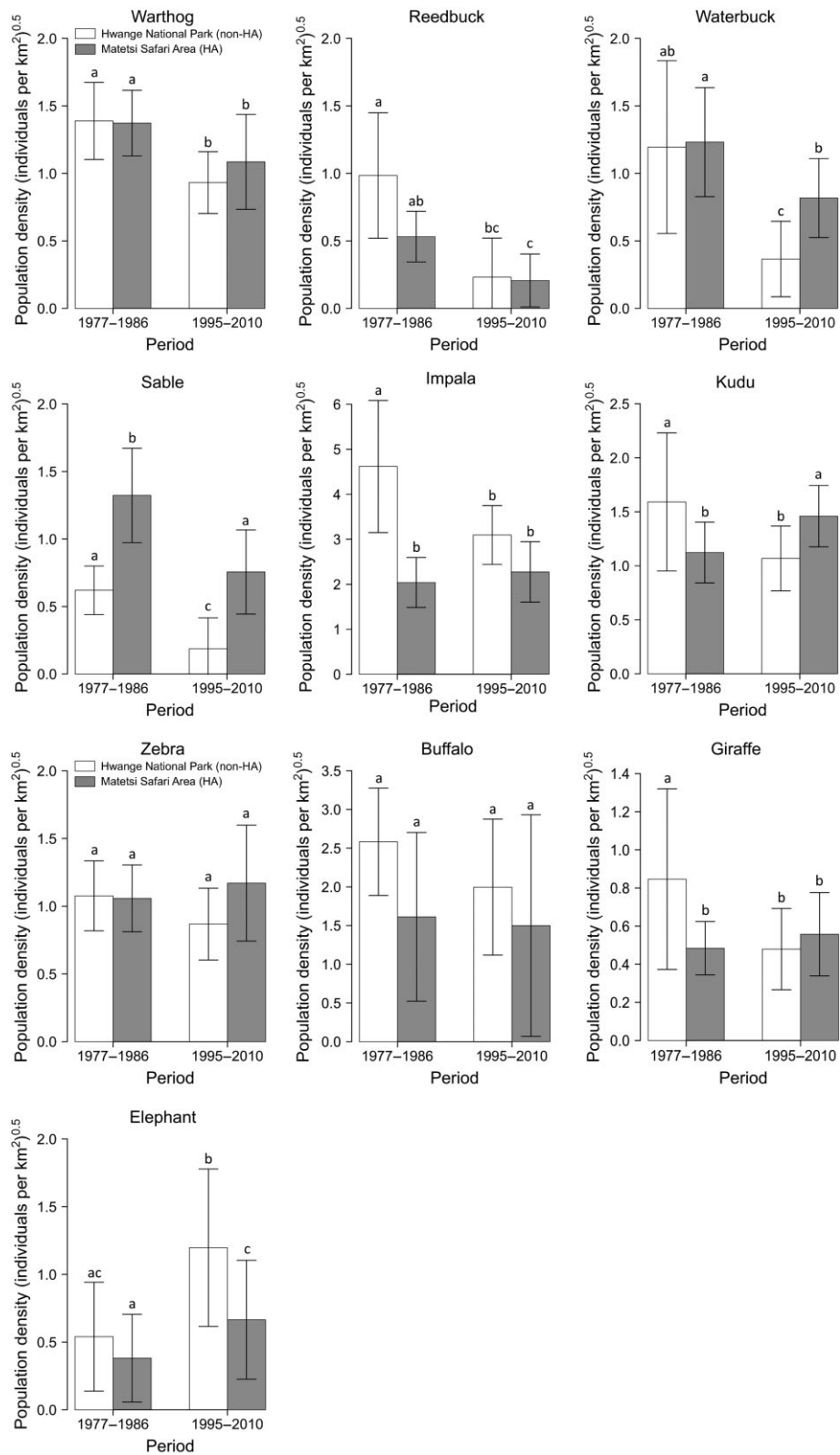


Figure 4 Population densities in Matetsi Safari Area (Hunting Areas, HA, grey) versus Hwange National Park (hunting-free area, non-HA, white), Zimbabwe, from 1977 to 1986 and 1995 to 2010. The bars indicate the average values and their associated standard deviation. Different letters indicate statistically significant difference at $P < 0.05$.

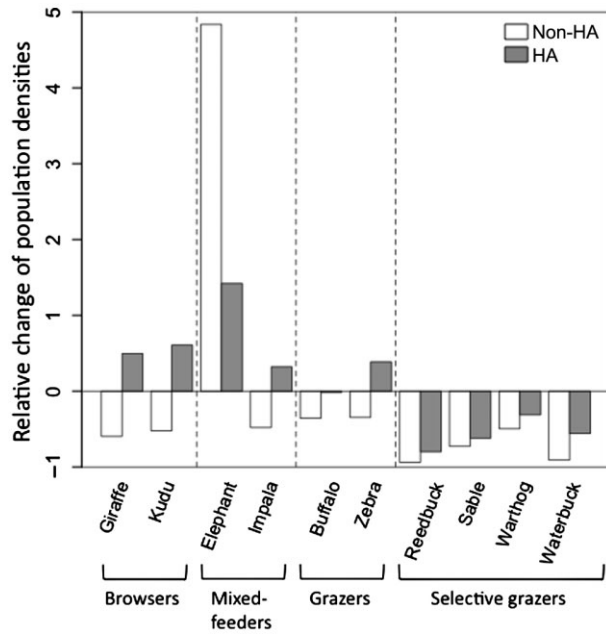


Figure 5 Relative change of mean population densities between 1977–1986 and 1995–2010 for ungulate species in Hwange National Park (hunting-free area, non-HA, white) versus Matetsi Safari Area (Hunting Areas, HA, grey), Zimbabwe. The ungulate species are grouped by dietary guild (browsers, mixed feeders, grazers and selective grazers) and separated by dashed lines.

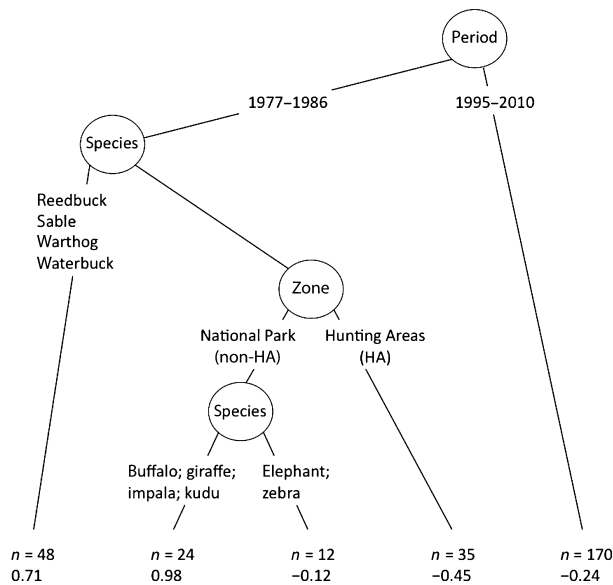


Figure 6 Classification tree of the normalized densities according to the zone (national park vs. hunting areas), period (1977–1986 vs. 1995–2010) and species (buffalo, Burchell’s zebra, elephant, giraffe, greater kudu, impala, reedbuck, sable antelope, warthog and waterbuck), Zimbabwe. Circles are the nodes of the tree. The number of observations (*n*) and the mean value of normalized densities are indicated at the end of each branch.

Table 5 Two-way analysis of variance of proportion of adult males (log transformed) of African ungulate species according to period (1977–1986 vs. 1995–2010), zone (hunting-free area vs. hunting areas) and their interaction, in Hwange National Park and the adjacent Matetsi Safari Area, Zimbabwe

Species	Factor	d.f.	Adult male %		
			r.d.f.	<i>F</i>	<i>P</i>
Elephant	Period	1	72	0.1	0.8
	Zone	1	5	7.1	0.04
	Period × zone	1	72	5.4	0.02
Giraffe	Period	1	84	2.8	0.1
	Zone	1	5	4.1	0.1
	Period × zone	1	84	0.4	0.5
Impala	Period	1	89	2.5	0.1
	Zone	1	5	2.4	0.2
	Period × zone	1	89	2.9	0.1
Greater kudu	Period	1	89	2.4	0.1
	Zone	1	5	0.6	0.5
	Period × zone	1	89	0.2	0.7
Reedbuck	Period	1	59	0.9	0.3
	Zone	1	5	0.0	1.0
	Period × zone	1	59	0.3	0.6
Sable antelope	Period	1	73	2.0	0.2
	Zone	1	5	9.1	0.03
	Period × zone	1	73	6.9	0.01
Warthog	Period	1	88	0.2	0.6
	Zone	1	5	0.8	0.4
	Period × zone	1	88	0.6	0.4
Waterbuck	Period	1	81	5.3	0.02
	Zone	1	5	5.8	0.06
	Period × zone	1	81	0.3	0.6
Zebra	Period	1	86	3.8	0.0002
	Zone	1	5	14.5	0.06
	Period × zone	1	86	2.7	0.1

Buffalo groups were too large to identify individuals. d.f., degrees of freedom; r.d.f., residual degrees of freedom.

Discussion

Populations of large herbivores are generally declining in African-protected areas (reviewed in Caro & Scholte, 2007; Craigie *et al.*, 2010). This decline raises concerns about the efficiency of protected areas as a conservation tool (Newmark, 2008), and suggests there is potential in alternative conservation zones such as trophy hunting areas (Lindsey *et al.*, 2007). Because long-term monitoring of wildlife outside national parks is rare (Caro, 2011), we lack empirical data to investigate the long-term effects of trophy hunting on population structure and density. This lack of data seriously limits our capacity to evaluate the conservation potential of trophy hunting areas. We provide here a rare analysis of long-term impacts of trophy hunting on densities and proportions of adult males of several large herbivore populations.

Trophy hunting

Overall, trophy hunting had a marginal effect on the temporal trends of the structure and density of large herbivore

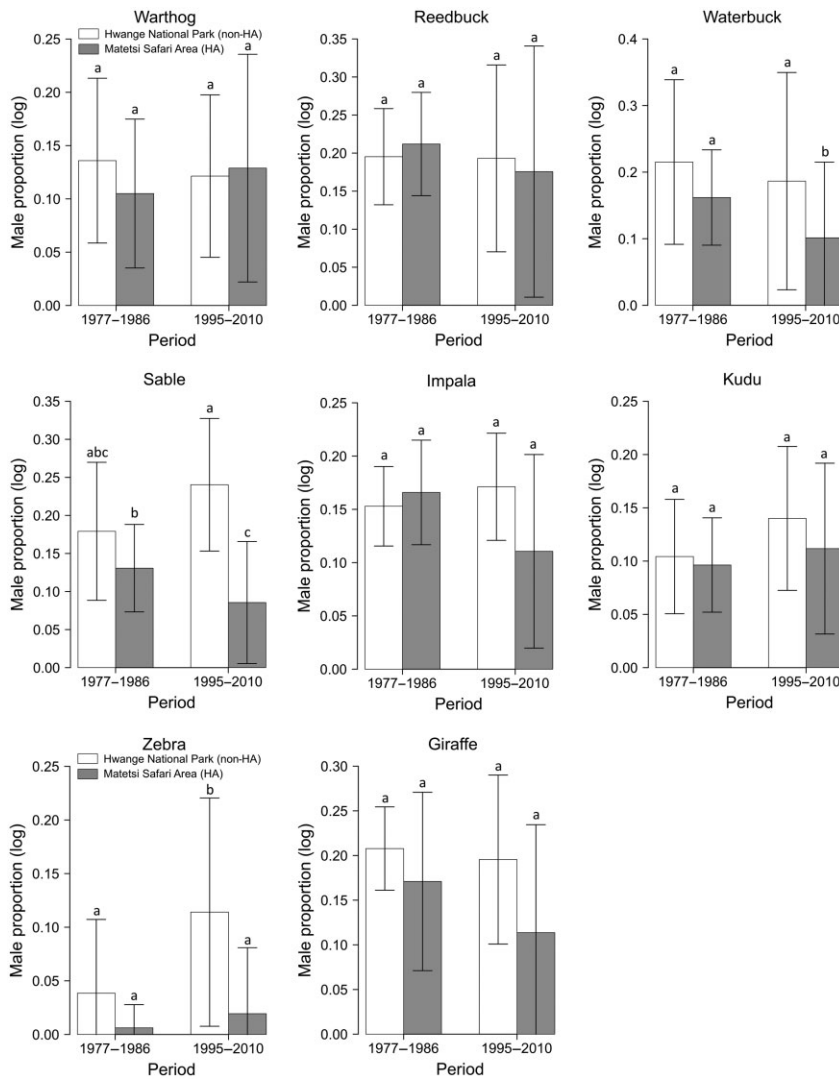


Figure 7 Proportion of adult males in Matetsi Safari Area (Hunting Areas, HA, grey) versus Hwange National park (hunting-free area, non-HA, white), Zimbabwe, between 1977–1986 and 1995–2010. Bars indicate the average values and segment their associated standard deviation. Different letters indicate statistically significant differences at $P < 0.05$.

populations in the study area. Only elephant and impala showed lower densities in MSA than HNP throughout the study period. Conversely, densities of sable antelope were higher in the hunting areas than in the national park. Under the hypothesis of a detrimental effect of trophy hunting on population densities, we would have expected opposite results because harvest rates were higher for sable antelope than for other species. Harvest rates, however, were generally low in MSA, *c.* 2% per year (this study; Cumming, 1989). It is likely that at this level of harvest, the impact of trophy hunting on population densities was minimal. For instance, Caro *et al.* (1998) found few significant differences in mammal densities between hunting areas and national parks in Tanzania, and suggested that harvest rates below 10% per year were unlikely to impact population sizes. Examples in other ecosystems revealed no impact of trophy hunting on ungulate dynamics (Milner *et al.*, 2007; Mysterud, 2012; but see Palazy *et al.*, 2012). Surprisingly, for some species (i.e. giraffe, impala, greater kudu), densities

declined from 1977 to 1986 and 1995 to 2010 in HNP, whereas they did not change or increased in MSA. For species whose densities declined in MSA (i.e. reedbuck, sable antelope, warthog and waterbuck), there was a decline of similar magnitude in HNP. This suggests a limited effect from trophy hunting and that other factors were responsible for this general decline (see below).

We expected lower proportions of adult males in hunting areas than in HNP because trophy hunting is male biased (this study; Festa-Bianchet, 2003). For sable antelope and elephant, harvest rates and proportions of males on quotas were higher than for other species. This probably explains why, for these two species in particular, the proportion of adult males was significantly lower in MSA than in HNP, and declined in MSA but not in HNP. For the other species, we observed the same trend overall, although not significantly. This trend may be due to the high variance associated with the proportion of adult males. Decreased male proportions have been documented in many other ungulates

hunted for trophies worldwide (e.g. Langvatn & Loison, 1999; Garel *et al.*, 2006; Holand *et al.*, 2006). However, only rare examples reported reproductive collapse due to extreme lack of males (e.g. Milner-Gulland *et al.*, 2003b). Alternatively, the removal of only a few experienced adult males may be sufficient to jeopardize population growth or maintenance through the alteration of reproductive phenology (Noyes *et al.*, 1996; Singer & Zeigenfuss, 2002). However, we doubt that it occurred in our study areas; despite the proportion of adult males tending to be lower and to decline in the hunting areas compared with the national park, the same pattern was not observed in population densities.

Poaching

With the economic decline and political instability that Zimbabwe has been facing since 2000, there is concern about poaching increasing inside and around protected areas (but see Gandiwa *et al.*, 2013). Around HNP, land use changed and human encroachment increased, particularly on the eastern side, which has triggered poaching there in the recent years (Animal Life Line for Anti-poaching, unpubl. data). The Robins and Sinamatella blocks are far from settlements and are therefore less exposed to poaching. Historically, there was no significant poaching for bushmeat in MSA or in Robins and Sinamatella (V. Booth, pers. comm.). Any poaching or evidence of snaring was quickly resolved either by ZPWMA patrols or by the safari operators. Therefore, it is unlikely that differences in poaching intensity could have been responsible for the lower herbivore densities and for their faster decline in the park.

Rainfall

The general decline of population densities between 1977–1986 and 1995–2010 observed in most species across the study area indicated that factors other than trophy hunting were involved. In African savannas, rainfall is a proxy of primary productivity that may determine population numbers of large herbivores (Fritz & Duncan, 1994) and annual changes of densities (Mduma *et al.*, 1999). Annual rainfall declined over the last 30 years in the study area. In particular, the period from 1995 to 2010 followed an unprecedented dry spell (i.e. 1986–1994; Fig. 2; Chamaillé-Jammes, Fritz & Murindagomo, 2006), during which dry season rainfall was constantly below the long-term average. Droughts may be particularly detrimental for large African herbivore populations (e.g. Ottichilo, de Leeuw & Prins, 2001; Dunham, Robertson & Grant, 2004). Interestingly, population decline was more pronounced for selective grazers (i.e. reedbuck, sable antelope, warthog, waterbuck) than for non-selective grazers (i.e. buffalo, zebra), mixed feeders (i.e. elephant, impala) and browsers (i.e. giraffe, greater kudu). This is in accordance with a scenario proposing rainfall as a primary factor determining temporal trends of large herbivore densities in our study area. Browse production is more constant over time than grass production (Rutherford, 1984), making browsers and

mixed feeders potentially more resistant to droughts than grazers (Hillman & Hillman, 1977; Owen-Smith, 2008), and selective grazers in particular (e.g. Murray & Brown, 1993). Indeed, most examples of large herbivore declines related to droughts in Africa involve grazers (e.g. Mduma, Hilborn & Sinclair, 1998; Harrington *et al.*, 1999). Among the selective grazers, warthog experienced a twofold milder decline than reedbuck, sable antelope and waterbuck. This is not surprising because warthog can sometimes feed on browse and forbs (Bothma, van Rooyen & van Rooyen, 2004), and because their high reproductive rate may enable their population to recover quickly from droughts. Given the actual recurrence of long and severe dry episodes in southern Africa (Hulme *et al.*, 2001; Nicholson, 2001), selective grazers may deserve particular conservation focus in hunting areas because they may be less able to cope with additional sources of mortality compared with non-selective grazers, browsers and mixed feeders.

Natural predation

During the study period, population densities of large herbivores generally declined more in HNP than in MSA. Trophy hunting and rainfall alone are not sufficient to explain this result, and we suspect that natural predation may have played a role. Indeed, predators can negatively impact large herbivore populations (Schmitz, Hambäck & Beckerman, 2000; Sinclair *et al.*, 2003; Ripple & Beschta, 2004). Between 1971 and the early 1990s, lion *Panthera leo*, leopard *P. pardus* and spotted hyaena *Crocuta crocuta* numbers doubled in HNP (Wilson, 1997), but declined afterwards (Drouet-Hoguet, 2007; Loveridge *et al.*, 2007a). Equivalent information does not exist for MSA. However, during this period, large carnivore hunting occurred in MSA at a rate of *c.* 8% per year (Cumming, 1989). The removal of adult males in lion and leopard populations is particularly detrimental for recruitment and population dynamics (Loveridge *et al.*, 2007a; Packer *et al.*, 2011). Moreover, densities of large African carnivores are generally lower outside national parks than inside (e.g. Caro, 1999; Wallgren *et al.*, 2009). Therefore, we can assume that densities of lion and leopard remained lower in MSA than in HNP, at least until the mid-1990s. This could be why large herbivore densities generally declined more in HNP than in MSA between 1977–1986 and 1995–2010. Additionally, impala and greater kudu are major prey species for most large African carnivores in the region (Drouet-Hoguet, 2007; Loveridge *et al.*, 2007b; Rasmussen, 2009), which may explain why these species' densities decreased in HNP while remaining constant or increasing in MSA. The same argument may be formulated for giraffes, which are common lion prey in Hwange (Loveridge *et al.*, 2007b). The pattern tended to be the same, although not significantly so, for buffalo and zebra, two other major lion prey species in Hwange (Loveridge *et al.*, 2007b). Conversely, for selective grazers, the difference in temporal density trends between HNP and MSA was less stark, possibly because rainfall was

the primary driver for these species (e.g. Mduma *et al.*, 1999).

Elephant

The African bush elephant was the only large herbivore species whose densities increased in both zones during the study period. Chamaillé-Jammes *et al.* (2008) previously showed that elephant numbers in HNP drastically increased from 15 000 to 35 000 since the cessation of culling in 1986. Elephant densities increased in both zones, but remained higher in HNP compared with MSA throughout the study period. This is coherent with elephant behaviour, because elephants tend to avoid human-disturbed areas (van Aarde, Whyte & Pimm, 1999; Caro, 1999). High elephant densities are suspected to be detrimental for other large herbivores, because of habitat modification and competition for food and surface water (Cumming, 1982; Fritz *et al.*, 2002; Parker, Bernard & Adendorff, 2009; Castelda *et al.*, 2011), but this is still widely debated (Skarpe *et al.*, 2004; Guldemond & van Aarde, 2008; Valeix *et al.*, 2009). Further investigation is required to conclude whether temporal trends and spatial patterns of elephant densities could be partly responsible for the greater decline of large herbivore densities in HNP compared with the neighbouring MSA during the study period.

Conclusion

Our study illustrates that when removal is rather conservative and rigorously managed, trophy hunting areas may be valuable conservation zones for large herbivores. However, natural factors may obscure the effect of trophy hunting on spatial and temporal trends of herbivore densities. For instance, hunting areas might act as refuges for some large herbivores from high densities of predators and dominant competitive species. This remains to be investigated in our study area. Finally, herbivore dietary guilds should be considered in the management of hunting areas, because diet requirements can influence herbivore responses to additional sources of mortality such as trophy hunting.

There are other examples of high densities of large herbivores in hunting areas of Zimbabwe (Lindsey, Románach & Davies-Mostert, 2009) and of Africa (Lindsey *et al.*, 2007). However, the results of these studies should not be generalized. Where hunting is poorly managed, where land tenure authorizes human settlement or where local human populations do not benefit from hunting, hunting areas are less likely to host high densities of large herbivores (e.g. Caro, 1999; Dunham, 2002; Setsaas *et al.*, 2007). Whereas ungulate populations may persist in trophy hunting areas as well as in national parks, this is usually not the case for large carnivores. In addition, trophy hunting may come with undesirable evolutionary changes that may weaken harvested populations (Coltman *et al.*, 2003). These considerations demand caution when considering the potential of wildlife conservation in trophy hunting areas.

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