

Decline of sable antelope in one of its key conservation areas: the greater Hwange ecosystem, Zimbabwe

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Abstract

Land use has major effects on wildlife conservation. We studied variations of sable antelope *Hippotragus niger* densities between 1990 and 2001 in comparison with various land uses in and around Hwange National Park, Zimbabwe. Trends of other ungulates, including elephant *Loxodonta africana*, were examined simultaneously, because sable may be sensitive to forage and apparent competition and to high elephant densities. Sable densities declined in the whole region, very likely because of adverse rainfall conditions. Densities were constantly higher in the hunting areas and forestry lands than in the national park. Interestingly, elephant densities showed the opposite, with higher densities in the national park than in the adjacent areas. Whether these results reflect a negative effect of high elephant numbers on sable must still be tested directly. Likewise, while habitat characteristics and lion predation did not appear responsible for the higher sable densities outside the national park, they could not be discounted as an influence on the differing sable densities in different land-use areas. It is clear, however, that high protection status is not always sufficient to ensure adequate conservation of flagship species. We therefore call for further investigations of ecological interactions within protected areas.

Key words: African savannahs, elephant, human disturbance, land use, sable antelope, Zimbabwe

Résumé

L'aménagement du territoire a des effets majeurs sur la conservation de la nature. Nous avons étudié les variations

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de la densité des antilopes sable *Hippotragus niger* entre 1990 et 2001 en comparant différentes utilisations des terres dans et en dehors du Parc National de Hwange, au Zimbabwe. Les tendances d'autres ongulés, notamment les éléphants *Loxodonta africana*, ont été étudiées en même temps parce que les sable pourraient être sensibles à l'alimentation et à l'apparente compétition, et à une forte densité d'éléphants. La densité des sable a décliné dans toute la région, très probablement à cause de conditions pluviométriques difficiles. La densité était toujours plus élevée dans les zones de chasse et les zones boisées que dans le parc national. Il est intéressant de noter que la densité des éléphants était opposée, plus élevée dans le parc national que dans les zones voisines. Il faut encore tester directement pour savoir si ces résultats indiquent un effet négatif du grand nombre d'éléphants sur les sable. Si les caractéristiques de l'habitat et la prédation par les lions ne semblaient pas responsables de la plus forte densité des sable en dehors du parc national, leur influence sur les densités de sable différentes selon l'utilisation des aires ne peut pas être écartée. Il est clair, cependant, qu'un statut de protection élevé n'est pas toujours suffisant pour assurer la conservation adéquate d'espèces emblématiques. Nous demandons dès lors qu'il soit procédé à de nouvelles recherches sur les interactions écologiques au sein des aires protégées.

Introduction

The persistence of wildlife depends largely on the careful protection of natural habitats and varies with land uses. The species richness and/or population abundance of wildlife usually decline along a gradient of human disturbance

(e.g. Kiffner *et al.*, 2014). Strictly protected areas such as national parks (IUCN categories I–III *sensu* WRI/UNEP/UNDP/WB, 1996) are not sufficient to guarantee wildlife conservation (reviewed in Newmark, 2008). Conservation also relies on partially protected areas (IUCN categories IV and V *sensu* WRI/UNEP/UNDP/WB, 1996), often located at the periphery of national parks. These partially protected areas allow consumptive activities ranging from exclusive hunting tourism on state or private lands to a combination of hunting tourism, local hunting, timber harvesting, livestock and subsistence cropping in forestry areas. Whether wildlife populations – particularly rare species – persist across this mosaic of land uses is of key interest for conservation.

Sable antelope *Hippotragus niger* (hereafter sable) is a rare and emblematic large African herbivore, highly valued in the ecotourism and hunting industries (Lindsey, Roulet & Romañach, 2007). Its overall population is relatively stable, mainly because its abundance is increasing in private lands (IUCN SSC Antelope Specialist Group, 2008). Conversely, in some national parks, sable numbers have declined drastically over the past few decades (Ogutu & Owen-Smith, 2005; Dunham, 2012). This decline raises serious concerns about the efficacy of protected areas in ensuring long-term conservation of the species. Here, we contribute to understanding the causes of these general trends by documenting the abundance of sable across a variety of land uses in the greater Hwange ecosystem, located in north-western Zimbabwe. This region hosts one of the highest densities of sable (East, 1999) and is therefore a major conservation area for the species (IUCN SSC Antelope Specialist Group, 2008).

Our main objective was to use the available aerial censuses, carried out from 1990 to 2001, to explore the spatiotemporal trends of sable numbers across the variety of land uses in the greater Hwange ecosystem, that is national park, state-owned hunting areas, forestry and private lands. Wildlife densities are generally lower in these areas compared to national parks because of higher human disturbance (e.g. Caro, 1999; Stoner *et al.*, 2007). Thus, we expected to observe higher densities of sable in the national park compared to the partially protected areas. We also aimed to identify the factors that could influence the spatial and temporal trends of sable densities in the region. First, because sables preferentially graze in wooded savannah landscapes (Skinner & Chimimba, 2005) and depend on

surface water (Cain, Owen-Smith & Macandza, 2012), we accounted for variations in availability of surface water and vegetation types across the study area. We also considered a proxy of vegetation productivity, the normalized difference vegetation index (NDVI), because African ungulate densities may respond to NDVI variations (e.g. Ryan, Knechtel & Getz, 2007; Duffy & Pettorelli, 2012). In addition, we accounted for trends in abundance of other ungulate species for three reasons. First, other grazer species, such as African buffalo *Syncerus caffer* and plains zebra *Equus burchelli* (hereafter zebra) can restrict distribution and densities of sable by contributing to depletion of common resources (Macandza, Owen-Smith & Cain, 2012a). Second, the abundance of other ungulates may influence lion *Panthera leo* abundance, thereby limiting sable distribution via increased predation, that is apparent competition (Chirima *et al.*, 2012; Owen-Smith *et al.*, 2012). Finally, sable may be sensitive to high elephant *Loxodonta africana* densities. Elephants can jeopardize sable resources through alteration of wooded habitat or grass layer (Cumming *et al.*, 1997; Young, Palmer & Gadd, 2005; O'Connor, Goodman & Clegg, 2007), and in extreme situations restrict access to surface water (Valeix, Chamaillé-Jammes & Fritz, 2007a; Castelda *et al.*, 2011). Hwange National Park (HNP) hosts some of the highest elephant densities on the continent (Blanc *et al.*, 2005), and this may affect the abundance of other ungulates (Valeix *et al.*, 2008).

Materials and methods

Study site

The study was conducted in HNP and two surrounding areas – Matetsi Safari Area (MSA) and Forestry Area/Gwaii Intensive Conservation Area (FA/Gwaii) – between 17°45'S–20°30'S and 25°15'E–28°00'E, ca. 37,000 km², in north-west Zimbabwe (Fig. 1). The area experiences a range of land uses and thus, varying human disturbance levels (Table 1, Fig. 1, further information on land uses and human disturbance is provided in Supporting Information). The vegetation is typical of southern African dystrophic wooded and bushed savannahs with patches of grasslands (Table S1). Surface water during the dry season is available mainly in artificial waterholes. We restricted our study area to the northern region of HNP, and its immediate adjacent areas, that is the southern

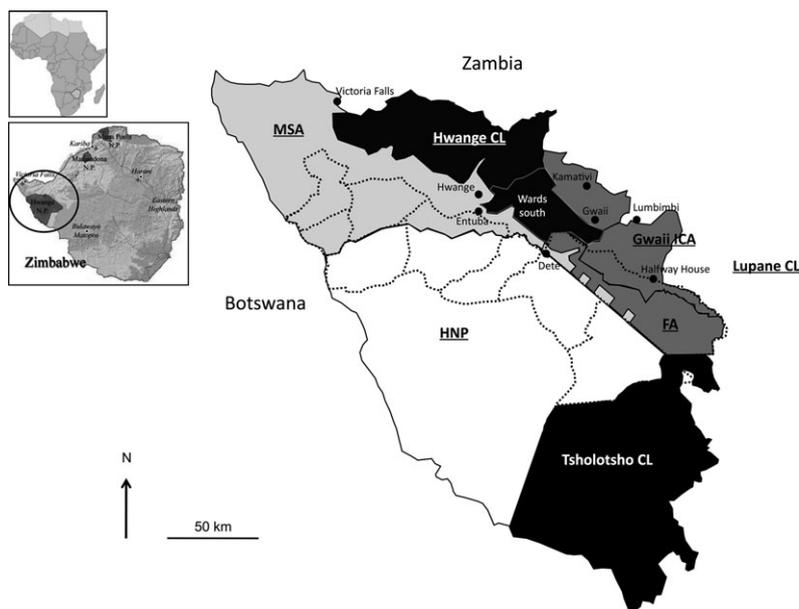


Fig 1 Hwange National Park (HNP, in white) and immediate surrounding areas; Matetsi Safari Area (MSA, in light grey), Forestry Areas/ Gwaii Intensive Conservation Area (FA/Gwaii, in dark grey) and communal lands (CL, in black) in Zimbabwe. The dashed black line delineates the study area. Dots represent locations of the principal towns and villages

Table 1 Categories of land use and associated land tenure across the Hwange Ecosystem, Zimbabwe, arranged along an increasing gradient of human disturbance

Site	Land use	Land tenure	Human activities	Human disturbance gradient	Studied area (km ²)	Aerial blocks (number)
Hwange National Park	National park	State-Zimbabwe Parks and Wildlife Management Authority	Viewing tourism Poaching ^a		5800	5
Matetsi Safari Area	Parastatal hunting areas	State-Zimbabwe Parks and Wildlife Management Authority	Viewing tourism Hunting tourism Poaching ^a		2200	3
Forestry Area/Gwaii Intensive Conservation Area	Forest concessions/private hunting areas	State-Forestry Commission/Private lands	Viewing tourism Hunting tourism Limited human settlements Logging Livestock Poaching ^a		3100	2

Studied areas within each land use type are indicated, as are the number of sampled aerial blocks.

^aPoaching occurs everywhere, but certainly more often in FA/Gwaii because of more human settlements and fewer antipoaching patrols than in HNP and MSA.

regions of MSA and of FA/Gwaii, because these areas are geographically close and share similar soil characteristics, vegetation structures, woody species and availability of surface water (Tables S1 and S2).

Vegetation productivity

We used 10-day NDVI images (resolution 1.2×1.2 km) derived from 1990 to 2001 to generate a proxy of vegetation productivity in the region. NDVI usually represents spatial variation in the production and retention of green vegetation adequately (Pettoirelli *et al.*, 2005), sometimes more directly than would rainfall alone (Rasmussen, Wittenmyer & Douglas-Hamilton, 2006). We summed the 10-day NDVI images corresponding to the vegetation growing season (INDVI, Pettoirelli *et al.*, 2005), from October to May (inclusive), for each year and then averaged INDVI value over the years for each block (see Supporting Information for trends in INDVI).

Long-term (i.e. 1976–2005) rainfall averaged 545 ± 174 and 10 ± 15 mm, respectively, for annual and dry seasons (Fig. 2a,b). Between 1990 and 2001, rainfall averaged 520 ± 155 and 7 ± 11 mm in annual and dry seasons, respectively (Fig. 2a,b). There was no statistical difference in annual and dry season rainfall averages between 1990–2001 and 1976–2005 (Mann–Whitney test: for annual rainfall, $W = 121$, $P = 0.6$; for dry season rainfall, $W = 143$, $P = 0.1$). However, the period 1990–2001 tended to be drier, with proportionally more years below long-term rainfall averages (annual rainfall: 39% in 1976–2005 versus 58% in 1990–2001, dry season rainfall: 61% versus 75%, Fig. 2a,b). Moreover, the decade 1984–1994 was marked by recurrent severe droughts, with dry season rainfall constantly below the long-term average and four consecutive years with no dry season rainfall (years 1989–1992, Fig. 2b).

Aerial census data

We used data from annual aerial strip transect censuses conducted during the dry season by the Zimbabwe Parks and Wildlife Management Authority between 1990 and 2001. We did not consider years after 2001 because the two aerial surveys carried out, in 2006 and 2007 (WWF Regional Office, unpublished data), were incomplete and therefore not comparable to surveys from the 1990s. Censuses followed the procedure recommended

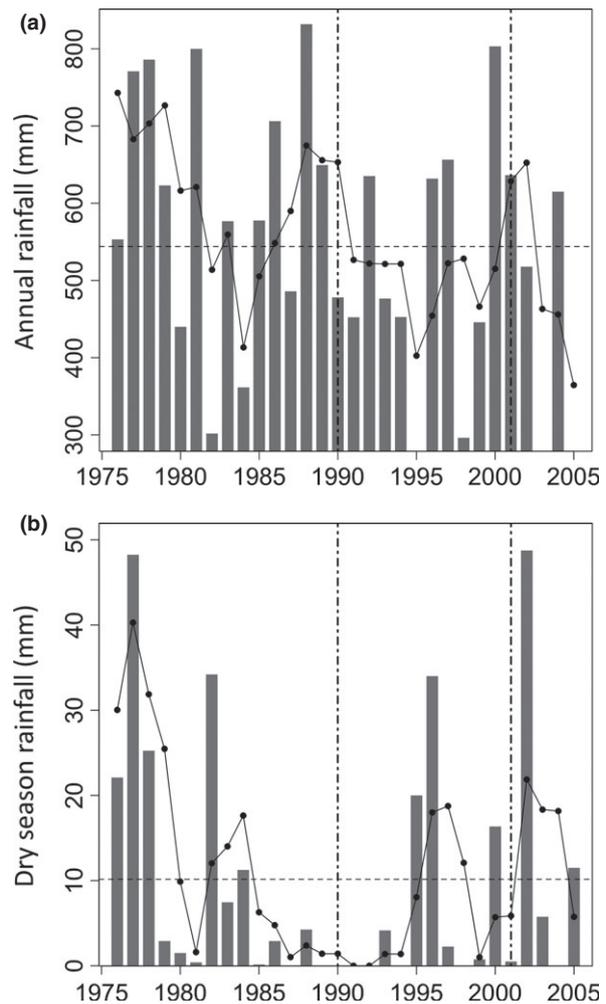


Fig 2 Trends in (a) annual rainfall and (b) dry season rainfall over 30 years in the study area. Bars indicate annual records and solid lines the 3-year running means. The horizontal dotted line represents the long-term average. The vertical dotted lines delimitate the study period, 1990–2001

by Norton-Griffiths (1978) and were analysed using Jolly's method (1969). For each aerial block sampled (Fig. 1, Table 1), population densities were estimated annually. No census was carried out in 2000, and we excluded the years 1992 and 1998 because the block design was different from the other years. Estimates from such censuses should be considered as indices of spatiotemporal variation rather than true levels of large herbivore densities because they are prone to inaccuracy and imprecision (e.g. Redfern *et al.*, 2002).

We focused on population trends of sable, buffalo, zebra, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*,

greater kudu *Tragelaphus strepsiceros* (hereafter kudu), blue wildebeest *Connochaetes taurinus* (hereafter wildebeest), and elephant. Buffalo, wildebeest and zebra are grazers, and therefore potential forage competitors for sable. This is particularly so for buffalo and zebra, which also prefer relatively tall grass (Macandza, Owen-Smith & Cain, 2012b). As a proxy of forage competition exerted on sable by these species, we aggregated the metabolic biomass of buffalo, wildebeest and zebra (hereafter biomass of forage competitors), using reference body mass (Cumming & Cumming, 2003) and population estimates from the aerial censuses. Calculations were made for each year within each block.

We could not directly investigate the role of lion predation on variations of sable densities because data on the lion populations were not available. We therefore assessed lion prey availability (van Orsdol, Hanby & Bygott, 1985; Hopcraft, Sinclair & Packer, 2005) by aggregating prey species biomass weighted by their relative contribution to lion's diet (Owen-Smith & Mills, 2008). We summed the biomass of buffalo, giraffe, impala, kudu, wildebeest and zebra, respectively, weighted by their relative contribution to lion's diet in the region (from Davidson *et al.*, 2013) and used their population estimates from the aerial censuses (hereafter biomass of lion prey). Although lions frequently consume elephants in the region (Davidson *et al.*, 2013), we did not include this species in the biomass of lion prey. We thus avoided biasing the index towards elephants, because this species greatly outweighs other prey species (Cumming & Cumming, 2003) and is present in relatively large numbers in the region. Calculations were also made for each year within each block.

Habitat variables

Sables forage within ca. 5 km from water sources during the dry season (Cain, Owen-Smith & Macandza, 2012). We therefore calculated the availability of surface water as the proportion of each block located within 5 km from a surface water supply, that is all waterholes and main rivers. During the dry season, we included only pumped waterholes, as there is no natural water available (Table S2). Vegetation structure and woody species were also expressed as the proportion of area within each block (Table S2). We assumed these proportions were relatively constant across years within blocks (Valeix *et al.*, 2007b).

Statistical analyses

We first used ANOVAs to investigate whether densities of potential competitors, the biomass of forage competitors and the biomass of lion prey varied with land use (densities and biomass were square-root transformed to meet normality assumptions). We then used multiple linear regressions to determine which combination of explanatory variables, that is year, land use, INDVI, densities of competitive species, biomass of forage competitors and biomass of lion prey, best explained the variations in sable densities. We used the Akaike's information criterion (AIC) to select the best model with the small sample adjustment AICc (Burnham & Anderson, 2002). The model with the lowest AICc value was retained. When the difference in AICc (Δ AICc) between two models was less than two, we selected the simplest model according to parsimony rules (Burnham & Anderson, 2002). We defined a set of *a priori* models for each species (Table S3). Statistical analyses were performed with R software (R Core Team, 2012).

Results

The densities of most potential competitors of sable antelope varied with land use, though not in similar ways (Table 2, Fig. 3). Elephant densities were ca. three and ten times higher in HNP than in MSA and in FA/Gwail, respectively (Fig. 3a). Likewise, giraffe densities were higher in HNP compared to MSA and FA/Gwail (Fig. 3b). Conversely, for impala, kudu and zebra, densities were higher in MSA compared to FA/Gwail and HNP to a lesser extent (Fig. 3c–e). Wildebeest densities were similar between HNP and FA/Gwail (Fig. 3f), whereas no wildebeest were observed in MSA. No significant difference in densities among the three land uses was observed for buffalo, nor for the biomasses of competitors (forage and lion prey, Table 2, Fig. 3g–i). Among the potentially competitive species, only elephant and zebra densities showed temporal trends (Table 2). Elephant densities increased between 1990 and 2001 in HNP and in FA/Gwail, but declined in MSA (Fig. 3a). Conversely, zebra densities declined in HNP and in FA/Gwail, but increased in MSA (Fig. 3e).

In multiple regressions, two equivalent models were selected (Tables 2 and S3). Both of these models included the variables 'year' and 'land use' (with no interaction), along with either 'buffalo densities' or 'biomass of lion prey' (Table S3). Sable densities generally declined in the

Table 2 Estimated parameters and their 95% confidence intervals for the most parsimonious models of population densities (square-root transformed) of sable, elephant and potential competitive species of sable in the northern blocks of Hwange National Park (HNP), and its adjacent areas – Matetsi Safari Area (MSA) and Forestry Areas/Gwaii Intensive Conservation Area (FA/Gwaii). The effect of year, land use and their interaction was tested for the potential competitive species and for the biomasses of competitors. For sable, integrated NDVI value (INDVI), densities of potential competitive species and their aggregated biomass were tested in addition to year and human disturbance type

Species and biomasses of competitors (80 observations; from 1990 to 2001)	Selected model	k^a	β	df	Estimate	CI 95%
<i>Buffalo</i>	Null	1	Intercept	1	0.54	[0.41, 0.67]
<i>Elephant</i>	Year × land use	6	Intercept	1	110.98	[24.30, 197.66]
			Year	1	-0.05	[-0.10, -0.01]
			HNP ^b	1	-139.77	[-249.41, -30.13]
			FA/Gwaii ^b	1	-171.78	[-308.82, -34.72]
			Year × HNP	1	0.07	[0.02, 0.12]
			Year × FA/Gwaii	1	0.09	[0.02, 0.16]
<i>Giraffe</i>	Land use	3	Intercept	1	0.24	[0.18, 0.30]
			HNP	1	0.17	[0.10, 0.25]
			FA/Gwaii	1	-0.14	[-0.23, -0.04]
<i>Impala</i>	Land use	3	Intercept	1	0.90	[0.76, 1.04]
			HNP	1	-0.30	[-0.48, -0.12]
			FA/Gwaii	1	-0.63	[-0.85, -0.40]
<i>Kudu</i>	Land use	3	Intercept	1	0.64	[0.57, 0.70]
			HNP	1	-0.30	[-0.38, -0.22]
			FA/Gwaii	1	-0.41	[-0.51, -0.31]
<i>Wildebeest</i>	Land use	3	Intercept	1	2.23×10^{-16}	[-0.08, 0.08]
			HNP	1	0.15	[0.05, 0.26]
			FA/Gwaii	1	0.14	[0.01, 0.27]
<i>Zebra</i>	Year × land use	6	Intercept	1	-105.66	[-167.10, -44.22]
			Year	1	0.05	[0.02, 0.08]
			HNP	1	147.26	[69.54, 224.98]
			FA/Gwaii	1	135.14	[39.99, 232.29]
			Year × HNP	1	-0.07	[-0.11, -0.03]
			Year × FA/Gwaii	1	-0.07	[-0.12, -0.02]
<i>Biomass of forage competitors</i>	Null	1	Intercept	1	7.80	[6.61, 8.99]
<i>Biomass of lion prey</i>	Null	1	Intercept	1	9.74	[8.09, 11.38]
<i>Sable</i>	Year + land use + buffalo ^c	5	Intercept	1	37.28	[6.03, 68.54]
			Year	1	-0.02	[-0.03, -0.003]
			HNP	1	-0.41	[-0.54, -0.28]
			FA/Gwaii	1	0.19	[0.03, 0.34]
			Buffalo densities	1	0.17	[0.07, 0.27]
	Year + land use + lion prey ^c	5	Intercept	1	36.06	[4.55, 67.58]
			Year	1	-0.02	[-0.03, -0.002]
			HNP	1	-0.44	[-0.57, -0.31]
			FA/Gwaii	1	0.18	[0.02, 0.34]
			Lion prey	1	0.01	[0.004, 0.02]

^aNumber of parameters.

^bResults are presented as the difference estimate between 'HNP' and 'FA/Gwaii' and the reference land use, 'MSA'.

^cThe two selected models for sable were equivalent ($\Delta AIC \leq 2$; see Table S3).

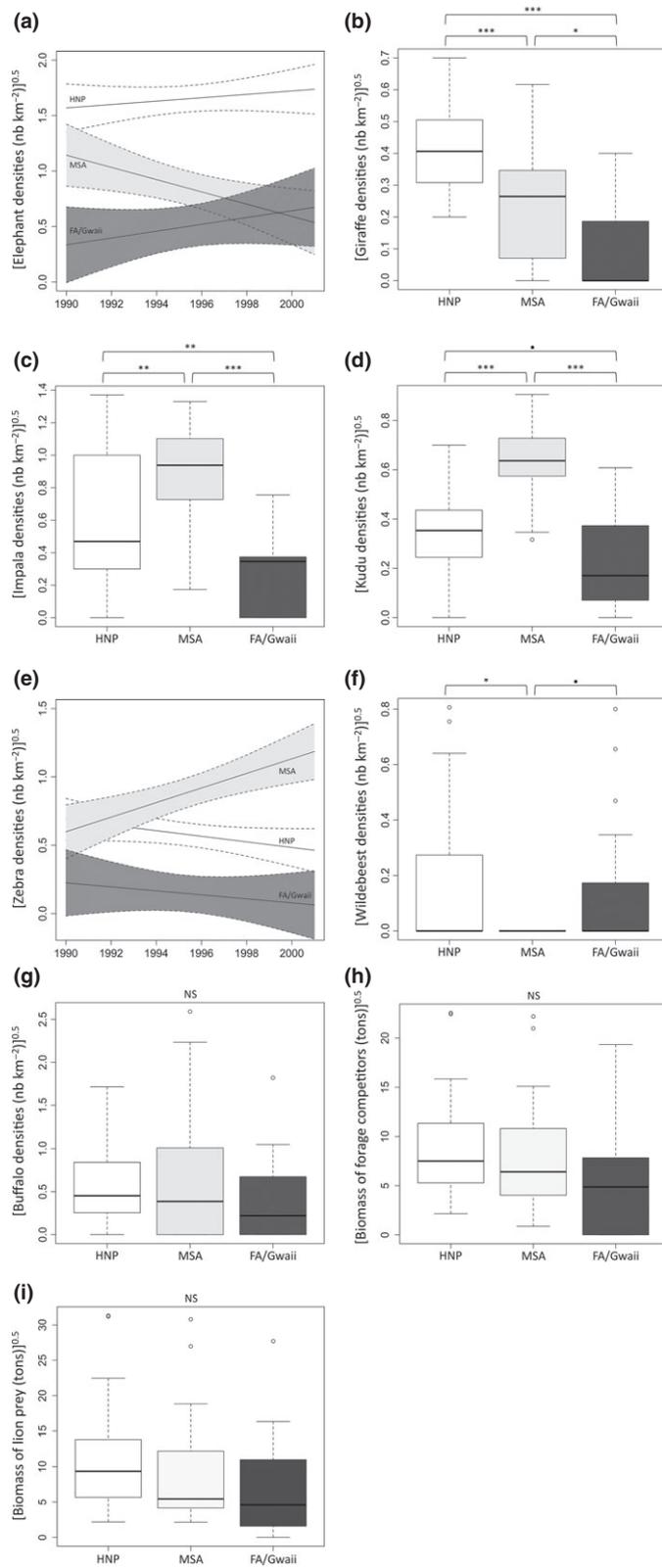


Fig 3 Population densities (square-root transformed) of (a) elephant, (b) giraffe, (c) impala, (d) kudu, (e) zebra, (f) wildebeest, (g) buffalo and biomass (square-root transformed) of (h) forage competitors and (i) lion prey in HNP, MSA and FA/Gwaii between 1990 and 2001. The horizontal line within 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 dots are observations <10th or >90th percentile. $P < 0.1$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; Tukey's studentized range was used to test for significant differences between land-use types. Temporal trends with their 95% confidence intervals are illustrated when significant

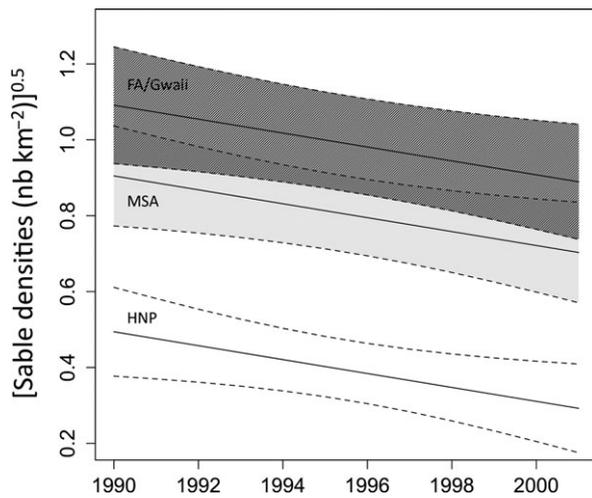


Fig 4 Sable densities (square-root transformed) along the years in HNP, MSA and FA/Gwaii between 1990 and 2001. Solid lines are used for significant trends and dotted lines for 95% confidence intervals

study area between 1990 and 2001, and the decline was similar over the three land uses (Fig. 4, Tables 2 and S3). Sable densities were on average ca. five times higher in FA/Gwaii compared to HNP, and slightly higher in FA/Gwaii compared to MSA (Table 2, Fig. 4). Sable densities increased with buffalo densities, or with the biomass of lion prey (Table 2). The estimated parameters of the selected models were all significantly different from zero (see the CI95% in Table 2).

Discussion

General decline of sable population

Between 1990 and 2001, the sable population declined by ca. 25% in the northern region of HNP and the neighbouring partially protected areas. Concomitant declines were observed in Gonarezhou National Park, Zimbabwe (Dunham, 2012), and in Kruger National Park, South Africa (Ogutu & Owen-Smith, 2003). Between 1983 and 1995, el Niño conditions caused recurrent droughts in southern Africa (Trenberth & Hoar, 1996; Ogutu & Owen-Smith, 2003); in particular, a severe drought in 1992/1993 was simultaneously observed in Hwange, Gonarezhou and Kruger National Parks. Very low rainfalls could therefore explain the general decline of sable populations in the region during the 1990s. This scenario is consistent with the

concomitant declines of other grazers in the Gonarezhou and Kruger National Parks (Dunham, 2012; Owen-Smith *et al.*, 2012). However, this is less consistent with the absence of temporal trends for buffalo and wildebeest densities across the Hwange region and for zebra densities in MSA. Thus, rainfall alone is probably not sufficient to explain the broad decline of sable in the Hwange region.

In Kruger National Park, roan antelope *Hippotragus equinus* declined both because of recurrence of droughts and an increase in lion numbers following a rise in zebra numbers (Harrington *et al.*, 1999). In the Hwange region, however, neither the lion prey species nor the biomass of lion prey increased. Only zebra in MSA and elephant in HNP and FA/Gwaii increased during the 1990s. Additionally, no major concomitant increase in lion abundance was observed in the region in the 1990s (Loveridge, 2002), which makes the idea of an increase of lion predation on sable during this period unlikely.

Unexpected spatial pattern of sable densities

Densities of sable were, surprisingly, ca. five times higher outside HNP than in the national park itself, despite the park providing the highest level of protection legally and in practice. Outside HNP, densities tended to be higher in FA/Gwaii area compared to MSA. This contrasts with previous studies in other African savannahs where ungulate densities are generally higher in national parks (e.g. Caro, 1999; Stoner *et al.*, 2007).

Habitat conditions. Availability of surface water and woodlands (i.e. open woodlands and dense woodlands) were not lower in HNP than in MSA and FA/Gwaii. Likewise, the studied part of HNP has similar soil characteristics to adjacent areas. Moreover, because INDVI was rather similar among the three study sites, we believe that forage availability and/or quality was not higher outside HNP. This seems to be consistent with the absence of any difference in the densities of buffalo among the three land uses and with the lower densities of zebra observed in FA/Gwaii compared to HNP. This, however, remains to be investigated because we lacked data on the species composition of the grasses and on nutrient content. Likewise, we cannot exclude an influence of habitat conditions at a finer scale. For instance, rather than the overall availability of surface water and woodlands, the relative distribution of water sources could affect

movements for sable, thereby inflicting substantial costs in terms of time and energy (Cain, Owen-Smith & Macandza, 2012).

Forage competition. The biomass of forage competitors was similar among the three study sites. Sable densities were, moreover, positively correlated with buffalo densities, probably because of similar habitat preferences; sable densities were less consistently related to zebra densities (as in Kruger National Park, Chirima *et al.*, 2012). Thus, we doubt that lower levels of competitive displacement outside HNP could be the underlying mechanism causing the higher densities of sable in FA/Gwaii and MSA compared to HNP. We acknowledge, however, that the scale of our study might be too broad to detect competitive displacement between sable and other grazers, which may occur at a more local scale (Macandza, Owen-Smith & Cain, 2012a).

Lion predation. In Kruger National Park, sable herds avoid high concentrations of wildebeest and impala (apparent competition, Chirima *et al.*, 2012). In the Hwange region, contrary to Kruger National Park, the wildebeest is not a major prey for lions (Davidson *et al.*, 2013), and sable densities remained high despite high abundance of impalas (e.g. in MSA). Finally, the biomass of lion prey was similar among the three study sites, and sable densities were positively correlated to this biomass. Thus apparent competition via lion predation does not appear to be a good explanation of the higher densities of sable observed outside HNP.

Large African predators are generally less abundant outside national parks (Caro, 1999; Wallgren *et al.*, 2009), and lions were hunted for trophy outside HNP (Loveridge *et al.*, 2007). Thus, we can assume their densities were lower outside than inside HNP during the study period, which could explain why sable densities were higher outside HNP. This, however, was not the case for the other prey species. Buffalo densities were similar among the three study sites, while densities for impala, kudu and zebra were not consistently higher outside HNP. Moreover, despite lion densities that were ca. 1.5 times higher in MSA than in HNP in recent years (Elliot, 2007), indices suggest that sable abundance is still ca. five times higher in MSA than in HNP (Crosmarj *et al.*, 2012). This challenges predation by lion as a major mechanism responsible for the lower densities of sable observed in HNP compared to its peripheral areas.

Elephant. Sable densities did not directly correlate with elephant densities; this suggests there is no detrimental effect of elephants on sables. Interestingly, however, elephant densities followed the exact opposite spatial pattern of sable densities – they decreased along the gradient of human disturbance, a pattern also observed elsewhere (e.g. Hoare & Du Toit, 1999; Graham *et al.*, 2009). Because elephants can negatively affect other large herbivore species, through vegetation change (Cumming *et al.*, 1997; Young, Palmer & Gadd, 2005; O'Connor, Goodman & Clegg, 2007) or reduced access to surface water (Castelda *et al.*, 2011), sables may have thrived better outside HNP because of lower elephant densities. Previous studies reported evidence of elephant damage on trees in our study area (Campbell *et al.*, 1996; Valeix *et al.*, 2011), but we did not find lower proportions of woodlands in areas of higher elephant densities (see also Valeix *et al.*, 2007b). Possible detrimental changes of vegetation for sable induced by high elephant densities need to be investigated at a finer scale. For instance, higher vegetation use due to elephant's aggregation around waterholes in the dry season (Van Rooyen *et al.*, 1994; de Beer *et al.*, 2006; but see Chamailé-Jammes, Fritz & Madzikanda, 2009) could particularly affect sable herds through increased travel costs between waterholes and feeding sites in wooded habitats (Redfern *et al.*, 2003; Rahimi & Owen-Smith, 2007; Cain, Owen-Smith & Macandza, 2012). Sable may also suffer from competition with elephant for access to waterholes. Visits to waterholes by several medium-sized herbivores, including sable, decrease in likelihood or shift from late afternoon to late morning, when elephant numbers increase (Weir & Davison, 1965; Valeix, Chamailé-Jammes & Fritz, 2007a; Castelda *et al.*, 2011). This may jeopardize drinking opportunities for sable (but see Valeix *et al.*, 2009) and reduce time left for foraging and resting.

The conservation status of sable after 2001 in the region is unclear, because recent aerial data are lacking. Considering the economic crisis, land use change and human population increase around HNP since 2000 (Central Statistical Office, 1992, 2002; Coltart, 2008), however, we suspect that the sable population has continued to decline (Crosmarj *et al.*, 2012, 2013).

Conclusion

Rare species may perform better in human-disturbed areas than in national parks (Creel & Creel, 1996; Durant,

2000). Confounding factors such as habitat characteristics, predators and highly competitive species may obscure the respective effects of legal protection of natural habitats and human disturbance. This calls for further investigations of ecological interactions within and around protected areas.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Data S1 Additional information on study context, study sites and methods.

Table S1 Proportion (mean % \pm standard deviation) of the main vegetation structures, woody species, and the availability of surface water across the studied blocks of Hwange National Park (HNP) and the adjacent areas – Matetsi Safari Area (MSA) and Forestry Areas/Gwaii Intensive Conservation Area (FA/Gwaii) (Rogers, 1993; Ganzin *et al.*, 2008).

Table S2 Eco-regions, geology, and soil characteristics in the northern blocks of Hwange National Park (HNP), and in the adjacent areas – Matetsi Safari Area (MSA) and Forestry Areas/Gwaii Intensive Conservation Area (FA/Gwaii) (adapted from Peace Parks Foundation, 2009).

Table S3 Model selection procedure to investigate trends in population densities (square-root transformed) of sable and its potential competitive species (i.e., buffalo, elephant, impala, wildebeest, zebra) for the aggregate biomasses of forage competitors and of lion prey, between 1990 and 2001 in the northern blocks of Hwange National Park, and in the adjacent areas – Matetsi Safari Area and Forestry Areas/Gwaii Intensive Conservation Area.