

Trophy hunting in Africa: long-term trends in antelope horn size

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Abstract

Trophy hunting in ungulates may favour individuals with smaller horns. A decrease in horn/antler size may jeopardize the conservation potential of hunting areas, which would be a major concern in Africa where hunting zones represent over half of the total area of protected lands. We investigated horn length trends of harvested male impalas *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros* and sable antelopes *Hippotragus niger*, from 1974 to 2008 in Matetsi Safari Area, Zimbabwe. Horn length declined by 4% in impalas, partly because male harvest age decreased. In greater kudu, surprisingly, horn length increased by 14%, while mean age of harvested male greater kudu increased during the study period. Reduced hunting pressure on this species during the study may have allowed males to live longer and to grow longer horns before being harvested. Horn length declined by 6% in sable antelopes, independent of age, suggesting that trophy hunting selected male sable antelopes with smaller horns through time, provided that horn length is heritable. Hunting pressure and trophy value were higher for sable antelopes than for impalas and greater kudu. Accordingly, the decline of horn length in this species was more pronounced. More valuable trophy species, such as sable antelopes, require special attention because they may be exposed to higher hunting pressure, and are therefore more likely to experience a decrease in horn size.

Introduction

In polygynous species such as most ungulates, sexual selection favours males with rapid early growth and investment in structural size at the expense of early investment in reproduction (Trivers, 1972; Clutton-Brock, 1988). Male ungulates have thus evolved horns or antlers that are large with complex shapes through sexual selection (Geist, 1966; Packer, 1983; Caro *et al.*, 2003). By selecting males with the largest trophy traits, hunters may induce morphological change within the population by artificially favouring individuals with smaller sexually selected traits, for example shorter or thinner horns (Coltman *et al.*, 2003; Garel *et al.*, 2007). Ultimately, smaller horns may reduce individual fitness (Hartl, Zachos & Nadlinger, 2003), or be associated with lower genetic variability (Scribner, Smith & Johns, 1989; Fitzsimmons, Buskirk & Smith, 1995).

Trophy hunting as a conservation tool is widespread worldwide (Lindsey, Roulet & Romañach, 2007; Frisina & Tareen, 2009; Sharp & Wollscheid, 2009), but depends on

the presence of animals with large trophies to satisfy the expectations of hunters (Festa-Bianchet, 2007). Consequently, a decrease in trophy size may not only be detrimental to the viability of harvested populations (Hartl *et al.*, 2003; Coltman *et al.*, 2005), but also to the sustainability of trophy hunting as a conservation tool.

Development of horns and antlers may also be influenced by factors affecting resource quality and availability. Males grow shorter horns or antlers at high density because of increasing intraspecific competition (Jorgenson, Festa-Bianchet & Wishart, 1998; Festa-Bianchet *et al.*, 2004; Schmidt, Ver Hoef & Bowyer, 2007). Likewise, shorter horns and antlers have been observed in harvested populations suffering loss of suitable habitat (Garel *et al.*, 2007) or intense droughts (Torres-Porras, Carranza & Pérez-González, 2009). Finally, the proximity of a hunting-free source area from which males disperse could theoretically counteract the selective process induced by trophy hunting, and mitigate artificial selection in hunted areas (Tenhumberg *et al.*, 2004).

Although trophy hunting is a particularly well-developed industry in African savannas (Lindsey *et al.*, 2007), trends in horn size have been little studied in African ungulates. Only von Brandis & Reilly (2007, 2008) previously reported on horn size trends of African ungulates, in South Africa. However, hunting in South Africa mainly occurs on small and fenced private ranches (*c.* 2.05 ha on average, von Brandis & Reilly, 2008) where trophy quality is managed and manipulated, and is therefore not representative of trophy hunting over much of Africa. The richness of the African ungulate guild offers a unique opportunity to compare the effects of size-selective harvest on different species within the same ecosystem. Species may respond differently to trophy hunting, depending on hunting pressure and trophy value (*i.e.* prestige and/or cost of a hunt).

Here, we investigated the temporal and spatial trends in horn size for three African ungulates over three decades in the Matetsi Safari Area, a complex of hunting areas adjacent to Hwange, Kazuma Pan and Zambezi National Parks (*i.e.* hunting-free protected areas), Zimbabwe. The country is one of the most popular destinations for hunting tourism in Sub-Saharan Africa (Lindsey *et al.*, 2006). The Zimbabwean hunting industry has generated up to about 16 million US dollars of revenue per year for the past few decades, and encompasses *c.* 70 000 km², or 17% of Zimbabwe's land surface (Cumming, 1999; Booth, 2002). Under the hypothesis of a selective pressure exerted by trophy hunting against large-horned phenotypes, (1) we expected horn size to decline over time for all species, and more particularly; (2) we expected the decline of horn size to be more pronounced for species with higher hunting pressure and trophy value. If the national parks acted as a source of large-horned males, (3) we expected horn size to be on average smaller, and to decline more rapidly over the years as the distance from national parks increased. With regard to potential long-term changes in the abundance of the community of large herbivores, (4) we expected that horn size would decline with increasing abundance of competitors through reductions in forage availability.

Methods

Study area

Matetsi Safari Area (MSA), *c.* 3000 km², is one of the largest unfenced hunting complexes in Zimbabwe. It stretches along the unfenced northern boundary of Hwange National Park (HNP, hunting-free area), *c.* 15 000 km², up to the Zambian border (Fig. 1). MSA is leased to safari operators by Zimbabwe Parks and Wildlife Management Authority (ZPWMA). MSA is divided into seven hunting units, units one to five in the southern part, units six and seven in the northern part. We removed units six and seven from our study because hunting ceased in unit seven in 1995, and because vegetation types and environmental conditions (rainfall, temperature, soil characteristics) in these two units differ from the five units of the southern part (Ganzin, Crosmarj & Fritz, 2008; Peace Parks Foundation, 2009).

We thus concentrated our study on units one to five (404, 292, 356, 470 and 370 km², respectively). These units are located on well-drained shallow rocky soils, where vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands, dominated by *Colophospermum mopane* and *Combretum spp.* (Rogers, 1993; Ganzin *et al.*, 2008).

Species

We studied impalas *Aepyceros melampus*, sable antelopes *Hippotragus niger* and greater kudus *Tragelaphus strepsiceros*. Impalas and greater kudus are fairly common in Southern Africa (East, 1999). The Hwange ecosystem hosts one of the highest densities of sable antelopes in Southern Africa (East, 1999), but sable antelopes are rarer than impalas and greater kudus (Chamaillé-Jammes *et al.*, 2009).

Sable antelopes and greater kudus are more popular trophy species than impalas (Lindsey *et al.*, 2006). Sable antelope hunts are more expensive than those for greater kudus or impalas, with safari and trophy fees reaching *c.* US\$23 000, US\$6500 and US\$5500, respectively (Booth, 2009; Zindele Safaris, 2012). Moreover, sable antelopes are generally sold as the flagship species of a safari, whereas greater kudu and impala usually come as add-on components of big game safaris that primarily seek species such as lions *Panthera leo*, leopards *Panthera pardus*, elephants *Loxodonta africana* or buffalos *Syncerus caffer*. Hunters are therefore expected to be more selective when hunting sable antelopes compared with impalas, and to greater kudus to a lesser extent. Hunts of the three species are essentially for trophy animals, which are mainly adult males.

Hunting organization and trophy data

The hunting season essentially runs from March to December. Professional hunting guides accompany hunters to assist selection of trophy animals and monitor hunts. Trophy fees do not increase with trophy size, so hunters preferentially target the largest-horned males. Compulsory measurement and aging of harvested animals by ZPWMA staff takes place at the MSA headquarters. ZPWMA financially penalizes safari operators for harvesting animals younger than two years. Therefore, whereas there is no lower limit on trophy size, harvested males are almost exclusively adults.

Horn length was measured on harvested males with a soft tape to the nearest 0.5 cm (Fig. 2). For consistency, we systematically used the values for the left horn of each trophy. Harvest locations were recorded to the nearest km on maps of the hunting units. We georeferenced these locations with ArcView 3.2 (ESRI, Redlands, CA, USA). Age was determined by the tooth attrition method (Spinage, 1971). Tooth wear of harvested animals was compared against a series of mounted specimens of known age.

Population data

Road counts were carried out each year late in the dry season (September/October) using most available roads as

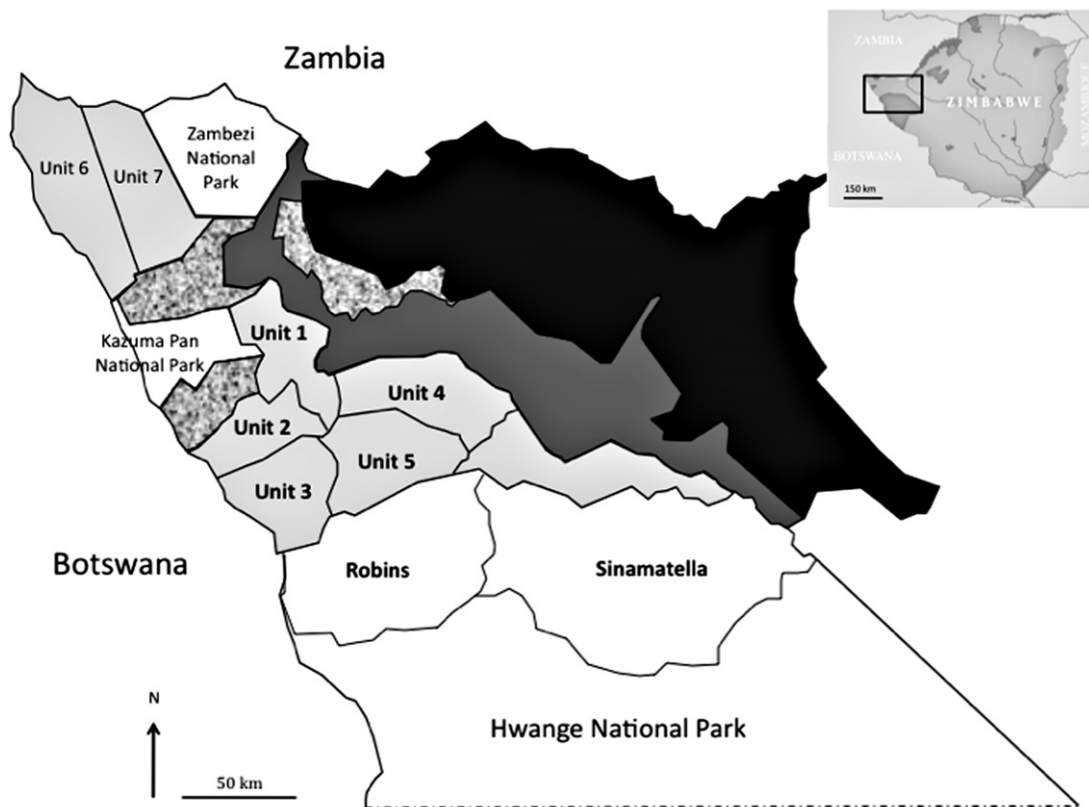


Figure 1 Northern part of Hwange ecosystem, Zimbabwe. The study area is delineated by the thick black rectangle. National parks (i.e. hunting-free areas) are coloured in white, hunting areas (units one to seven) of the Matetsi Safari Area in light grey, hunting areas of the Forestry Commission in granite.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

transects following the distance sampling procedure (Buckland *et al.*, 2001; Chamaillé-Jammes *et al.*, 2009 for a similar procedure in the neighbouring HNP). We analysed data using Distance Sampling software (Thomas *et al.*, 2006), and obtained estimates of population size/densities for most ungulate species, per year. For each group encountered, group size, sex and age class (adult, yearling, juvenile) of individuals were recorded. We could therefore estimate the number of adult males of each species. We then estimated trophy hunting pressure as adult males harvested/adult males estimated for each year.

Forage competition may be exerted by conspecifics, and by buffalos, elephants, greater kudus, warthogs *Phacoch-oerus africanus* and plains zebras *Equus quagga chapmanii* for impala; by common duiker *Sylvicapra grimmia*, elephant, and impala for greater kudu; by buffalo, elephant, reedbuck *Redunca arundinum*, waterbuck *Kobus ellipsiprymus*, and plains zebra for sable antelope (Bothma, van Rooyen & Toit, 2002). We calculated the total metabolic biomass of competitors for each species, per year and unit, using referenced metabolic body mass (Cumming & Cumming, 2003) and population estimates from road counts. For harvested males of known age, we computed the average densities of conspecifics, referred as 'density' effect,

and the average metabolic biomass of potential competitors, referred as 'competitors' effect during the years when most horn growth was achieved: the first two years of life for impala, and four years for greater kudu and sable antelope as determined later.

Environmental variables

For harvested males with a location recorded, we calculated the distance to the closest national park ('distance NP' effect) with the nearest features extension in ArcView 3.2 (Jenness, 2007). Around each harvest location, we drew a circle with a radius of 4 km for sable antelopes and 3 km for impalas and greater kudus with the Xtools extension (DeLaune, 2003). We chose slightly larger circles than the average home ranges of species in this region (*c.* 25, 8.5–13 and 4–10 km², for sables, greater kudus and impala, respectively; Estes, 1991) to account for the maximum uncertainty of 1 km in reported locations. These species are sedentary and constrained in their movements by the location of water sources (Estes, 1991; Redfern *et al.*, 2003). We used the satellite-derived normalized difference vegetation index (NDVI) as a proxy of vegetation productivity in the drawn circles ('productivity' effect) (Ganzin *et al.*, 2005). We used

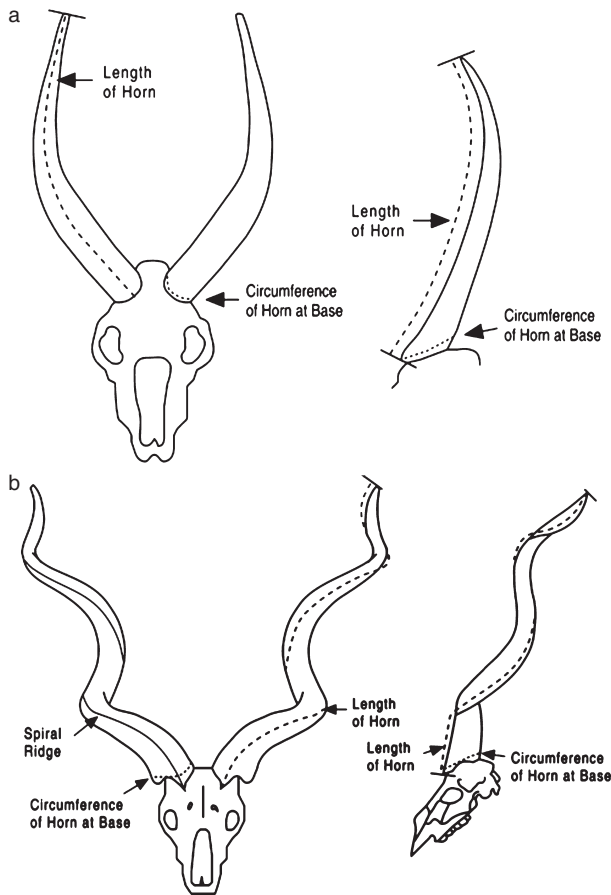


Figure 2 Measurement of horn size according to the Safari Club International system (<http://www.scirecordbook.org/docs/methods>) for (a) simple horned species (i.e. impalas and sable antelopes), and (b) spiral-horned species (i.e. greater kudus).

10-day NDVI images (resolution 1.2×1.2 km) derived from 1986 to 2008 from Advanced Very High Resolution Radiometer/National Oceanographic and Atmospheric Agency satellites. The Institute for Soil, Climate, and Water, from the South African National Agricultural Research Council, provided NDVI images. We summed the 10-day NDVI images corresponding to the vegetation growing season (INDVI, Pettoelli *et al.*, 2005), from October to May for each year (see Supporting Information Fig. S2 for trends of mean INDVI in the study area). INDVI values observed in the home range of harvested males during the years when most horn growth was achieved were then averaged, so that we obtained one INDVI value per home range.

Most data were collated by ZPWMA officers on printed datasheets, and filed in folders at MSA Headquarters since 1974. While the database is largely complete, some datasheets were lost and some variables were not consistently recorded over the 30-year period. Consequently there are a few gaps in the data available for analysis (Table 1).

Statistical analyses

Because horn length is usually positively related to age (e.g. Côté, Festa-Bianchet & Smith, 1998; Festa-Bianchet *et al.*, 2004), we first investigated patterns of horn growth using regressions of horn length against age of harvested males. We tested second and third orders for the age variable using smoothing splines. The second-order term was the best relationship. Under the hypothesis of a selective effect of trophy hunting on horn size, horns should grow more slowly over time in hunted populations. We therefore expected the slope of horn length over age to be steeper in the early decade than in the late decade of our study period. Consequently, we tested for an interaction between age and decade on horn length for impala (comparing 1986–1995 and 1996–2006), and for sable antelopes (1982–1990, 1991–1999 and 2000–2008). For greater kudus, however, we could not test for an interaction with decade, because harvested male kudus were only aged in 1991–1994 and in 2007–2008. We then used regressions between age of harvested males and year to test whether trophy hunting reduced the average age of males in the population.

For the analyses of temporal trends in horn length, it was essential to control for age of harvested males, to determine whether possible trends in horn length originated from the alteration of male age structure or another factor. Because this was only feasible for a restricted period (Table 1), we performed the analyses in two steps: (1) we first carried out regressions of horn length on years over the entire study period to document the general temporal trend of trophy size from the mid-1970s to 2008 for each of the three species; and (2) we then accounted for age for the years with age data available (Table 1) by including the age of harvested males as a covariate in linear models with year as the main variable, and density of conspecifics, biomass of competitors, habitat productivity, and distance to the nearest national park as other co-variables. We also tested the interaction between year and distance to national parks because we expected that the possible decline of horn length would be more pronounced further away from hunting-free areas. For greater kudus, because trophy animals were only aged in 1991–1994 and in 2007–2008, we could not correct for age in the analyses. We thus cannot not exclude that any trend observed in horn size could be due to changes in age of harvested males.

For model selection, we used the Akaike's information criterion (AIC; Burnham & Anderson, 2002). The model with the lowest AIC value was retained. When Δ AIC between two models was less than two, we selected the simplest model according to the parsimony rule (Burnham & Anderson, 2002). We defined a set of *a priori* models for each species and each dependent variable (Supporting Information Table S1). Observations with values for 'competitors' and 'productivity' were only available for a restricted part of our dataset. Therefore, on the restricted dataset, we first tested whether the variables 'competitors' and 'productivity' remained in the selected models. If they did not, we tested models without 'competitors' and 'productivity' with

Table 1 Sample size (*n*) and period for which data were available for each trophy variable (i.e. horn length, age, distance NP, density, competitors, and productivity) for impalas, greater kudus, and sable antelopes, in hunting units one to five of Matetsi Safari Area, Zimbabwe

Dataset		Impala	Sable antelope	Greater kudu
Horn length	<i>n</i>	1435	1560	1163
	Period	1974–2008	1974–2008	1976–2008
Horn length,	<i>n</i>	609	614	158 ^a
Age	Period	1986–2007	1982–2008	1991–1994, 2007–2008
Mean age	<i>n</i>			31 ^b
	Period			1974–2008
Horn length,	<i>n</i>	443	600	
Age	Period	1986–2002	1982–2005	
Distance NP				
Density				
Horn length,	<i>n</i>	335	108	
Age	Period	1988–2002	1983–2005	
Distance NP,				
Density				
Competitors,				
Productivity				
Horn length	<i>n</i>			955
Distance NP	Period			1979–2003
Density				
Horn length	<i>n</i>			83
Distance NP	Period			1991–1994
Density				
Competitors				
Productivity				

^a158 animals for which we had both horn measurements and age estimate.

^bFrom a summary table provided by Zimbabwe Parks and Wildlife Management Authority, where mean ages (and standard deviations) from 1057 trophy animals were computed for each year over the period 1974–2008. We used this table to explore temporal trends in mean age of greater kudus.

the complete dataset (Supporting Information Table S1). Statistical analyses were performed with R software (<http://cran.r-project.org>).

Results

Hunting pressure

Mean trophy hunting pressure throughout the study period was 0.10 ± 0.09 . However, it differed among the three studied species ($F_{2,294} = 16.3$, $P < 0.0001$), with higher averaged trophy hunting pressure for sable antelope [estimate \pm standard error (SE) = 0.13 ± 0.01] than for impala (estimate \pm SE = 0.06 ± 0.01), and greater kudu (estimate \pm SE = 0.08 ± 0.01 ; see Supporting Information Fig. S1a, b for trends of trophy hunting pressure and densities).

Horn growth patterns

Harvested male impalas and sable antelopes required more years to develop long horns during the latest decade (Table 2, Fig. 3a,b). For impalas in 1986–1995, males between 2 and 9 years old wore horns of equal average length, or 52.1 ± 1.7 cm (Table 2, Fig. 3a). In 1996–2007, horn length increased quadratically with age (Table 2,

Fig. 3a) and did not reach 52 cm until males were between 3 and 4 years old (Fig. 3a). During this decade, males that reached the age of 9 years had shorter horns than younger males, except for 2-year-olds (Fig. 3a). For sable antelopes, in the 1980s, males aged between 4 and 10 years wore horns of equal length in average, that is 106.5 ± 6 cm (Table 2, Fig. 3b). For the two following decades, horns grew linearly with age, but at a slower rate in the 2000s than in the 1990s (Table 2, Fig. 3b). Overall, in greater kudus, horns grew quadratically (diminishing increase) with age (years merged together; Table 2, Fig. 3c). In impalas, horns averaged over 45 cm long at 2 years old, and oscillated around 50 cm for subsequent age classes (Fig. 3a). Most horn growth therefore occurred during the first 2 years of life. In sable antelopes and greater kudus, age of harvested males ranged from 4 to 10 years, limiting our understanding of how horns grew over the first years of life. At 4 years old, horns averaged 102 ± 7 cm in sable antelopes (Fig. 3b), and 122 ± 5 cm in greater kudus (Fig. 3c). Horns did not grow over *c.* 110 cm in sable antelopes, and stabilized between *c.* 120 and 130 cm in greater kudus. Most horn growth therefore occurred before 4 years of age in these two species. We thus predicted that the potential effects of density of conspecifics, biomass of competitors, and vegetation productivity on horn length should occur during the first 2 years for impala, and the first 4 years for sable antelope and greater kudu.

Table 2 Estimated parameters and their 95% CIs for the most parsimonious models of horn growth with age for impalas, sable antelopes, and greater kudu from males harvested in units one to five of Matetsi Safari Area, Zimbabwe

Horn length	Selected model	k ^a	Parameter	d.f.	Estimate	[CI 95%]
Impalas	Age × decade + age ² × decade	6	Intercept	1	52.1	[48.8, 55.4]
			Age	1	−0.6	[−1.9, 0.7]
			1996s ^b	1	−9.2	[−14.4, −3.9]
			Age ²	1	0.05	[−0.08, 0.2]
			Age × 1996s	1	3.7	[1.5, 5.9]
			Age ² × 1996s	1	−0.3	[−0.5, −0.1]
Sable antelopes	Age × decade	6	Intercept	1	105.5	[102.4, 108.6]
			Age	1	0.15	[−0.3, 0.6]
			1990s ^c	1	−9.9	[−14.8, −5.0]
			2000s ^c	1	−17.6	[−26.7, −8.5]
			Age × 1990s	1	1.2	[0.5, 1.9]
			Age × 2000s	1	1.9	[0.6, 3.2]
Greater kudu	Age + age ²	3	Intercept	1	95.4	[71.4, 119.4]
			Age	1	8.6	[1.6, 15.7]
			Age ²	1	−0.6	[−1.1, −0.1]

^aNumber of parameters.

^bResults are presented as the difference estimate between the decade '1996s' (i.e. from 1996 to 2007) and the reference decade '1986s' (i.e. from 1986 to 1995).

^cResults are presented as the difference estimate between the decade '1990s' (i.e. from 1991 to 1999), the decade '2000s' (i.e. from 2000 to 2008), and the reference decade '1980s' (i.e. from 1982 to 1990).

CI, confidence interval; d.f., degrees of freedom.

The effect of decade, and its interaction with age, could be tested for impalas and sable antelopes, but not for greater kudu.

Temporal trend in age of harvested males

Because age is a major determinant of horn length, we first explored the possibility of a change in age of hunted males during the study period. Harvest age decreased with year in impala ($F_{1,607} = 20.1$, $P < 0.0001$; Fig. 4a), increased quadratically in greater kudu (year, $F_{1,28} = 6.7$, $P = 0.02$; year², $F_{1,28} = 9.6$, $P = 0.004$; Fig. 4c), whereas we observed no change for sable antelopes ($F_{1,612} = 1.1$, $P = 0.3$; Fig. 4b).

Covariates of horn length trends

From 1974 to 2008, in general, horn length decreased in impala ($F_{1,1433} = 46.1$, $P < 0.0001$; Fig. 5a) with a loss of *c.* 2 cm (i.e. 4%), and in sable antelopes ($F_{1,1558} = 135.3$, $P < 0.0001$; Fig. 5b) with a loss of *c.* 6 cm (i.e. 6%). In greater kudu, however, horn length increased quadratically (year, $F_{1,1160} = 109.4$, $P < 0.0001$; year², $F_{1,1160} = 60.9$, $P < 0.0001$), with a sharp increase of *c.* 15 cm (i.e. 14%) from 1976 to the mid-1980s, and stable horn length thereafter (Fig. 5c). Using a grouping variable for year, and thus reducing the denominator degrees of freedom from individuals to year did not affect our results.

In impala, horn length declined quadratically between 1986 and 2002, independently of age (Table 3, Supporting Information Table S1). In sable antelopes, we also observed a decrease in horn length after accounting for age between 1983 and 2005 (Table 3). In greater kudu, once we included the co-variables, we still observed a sharp increase of horn length between 1979 and the mid-1980s, and stable horn length thereafter (Table 3). Two distinctly contrasted periods were apparent for greater kudu: pre-1985 [mean

horn length ± standard deviation (SD) = 114.9 ± 8.3 cm] and post-1985 (mean horn length ± SD = 125.4 ± 8.6 cm) (Welch two-sample *t*-test: $t_{321,617} = -15.4$, $P < 0.0001$). During each period, we observed no change in horn length over time (pre-1985, $F_{1,199} = 0.8$, $P = 0.4$; post-1985, $F_{1,693} = 0.2$, $P = 0.7$).

Horn length decreased with distance from national parks in impala, whereas it increased in greater kudu, and showed no significant spatial trend in sable antelope (Table 3, Supporting Information Table S1). There was no interaction between distance to national parks and year for any species (Table 3, Supporting Information Table S1). In sable antelopes and greater kudu, horn length increased quadratically (diminishing increase) with density (Table 3), whereas density had no effect on horn length in impalas (Supporting Information Table S1). Average metabolic biomass of competitors and vegetation productivity during years of horn growth did not significantly affect horn length for the three species (Supporting Information Table S1).

Discussion

Horn growth, trophy size, and access to females

Most horn growth appeared completed before 2 years of age in impala, and 4 years in sable antelopes and greater kudu. Because our samples only included harvested trophy males, we cannot conclude that our results are representative of the entire male populations. They are nonetheless similar to those observed in non-hunted populations (impalas,

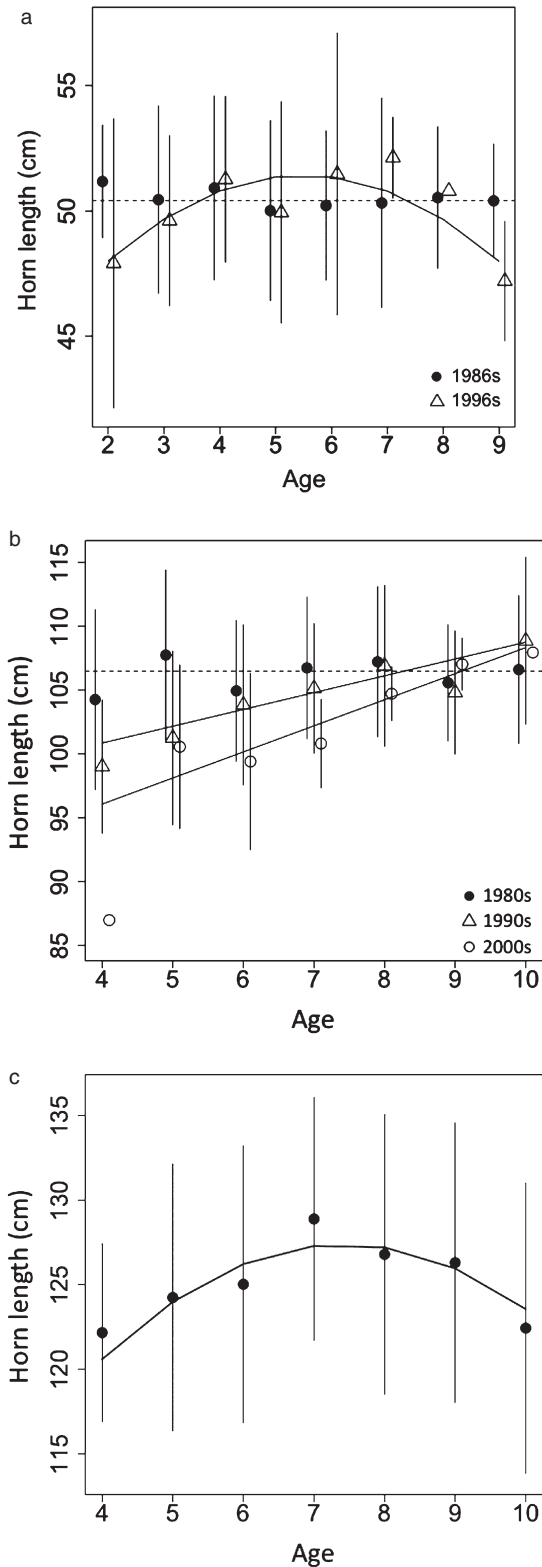


Figure 3 Horn length as a function of the age of harvested males in hunting units one to five of Matetsi Safari Area, Zimbabwe, for (a) impalas; (b) sable antelopes; and (c) greater kudus. For impalas and sable antelopes, figures represent the effect of age, the decade, and their interaction, conversely to greater kudus for which only the effect of age could be tested. Dots represent the average horn length of trophy animals per age, and bars the standard deviations. Solid lines are used for significant trends, and dotted lines to illustrate absence of trend.

Spinage, 1971; sable antelopes, Grobler, 1980). Males of these species do not mate before 5 or 6 years of age, when they can monopolize mating opportunities, although they are physiologically able to reproduce before (Wilson & Hirst, 1977; Murray, 1982; Owen-Smith, 1993). This indicates that males become potential trophies for hunters before reaching the age and social status allowing them to reproduce. Therefore, the selective effect of trophy hunting in these species is likely to be high. Interestingly, over time, trophy males in impalas and sable antelopes required more years to develop long horns. Trophy males of the same age, particularly in sable antelopes, had shorter horns in the latest decade compared with the past, suggesting possible life-history changes due to trophy hunting. Similarly, several studies previously highlighted evolutionary effects of size-selective harvesting on somatic growth (e.g. in fish, Conover & Much, 2002; in bighorn sheep *Ovis canadensis*, Coltman *et al.*, 2003). For greater kudus and impalas in the latest decade, horn length declined in older age classes. This could simply be the result of horn attrition with age (Spinage, 1971). Alternatively, it could also be explained by higher chances of survival for males with short horns in populations hunted for trophy (Coltman *et al.*, 2003; Garel *et al.*, 2007).

Changes in horn length over time

From 1974 to 2008, horn length of trophy males decreased by 4% in impalas and 6% in sable antelopes. In impalas, both age of harvested males and horn length declined over time, suggesting that horn length partly declined because trophy males were harvested at increasingly younger ages over time. Trophy hunters preferentially harvest older males because they generally have longer horns than younger males. Harvests may therefore shift the surviving male segment towards younger age classes (e.g. Solberg *et al.*, 1999; Laurian *et al.*, 2000). Conversely, in sable antelopes, age of trophy males did not change over time, whereas horn length declined. This suggests that males, following years of selective harvesting regime, require a longer time to grow horns of a given length (Pérez *et al.*, 2011). Trophy hunting may thus have promoted the reproduction of males with slow-growing or smaller horns, provided horn length is heritable (Garel *et al.*, 2007).

Differences in temporal trends between impala and sable antelope are consistent with our prediction based on

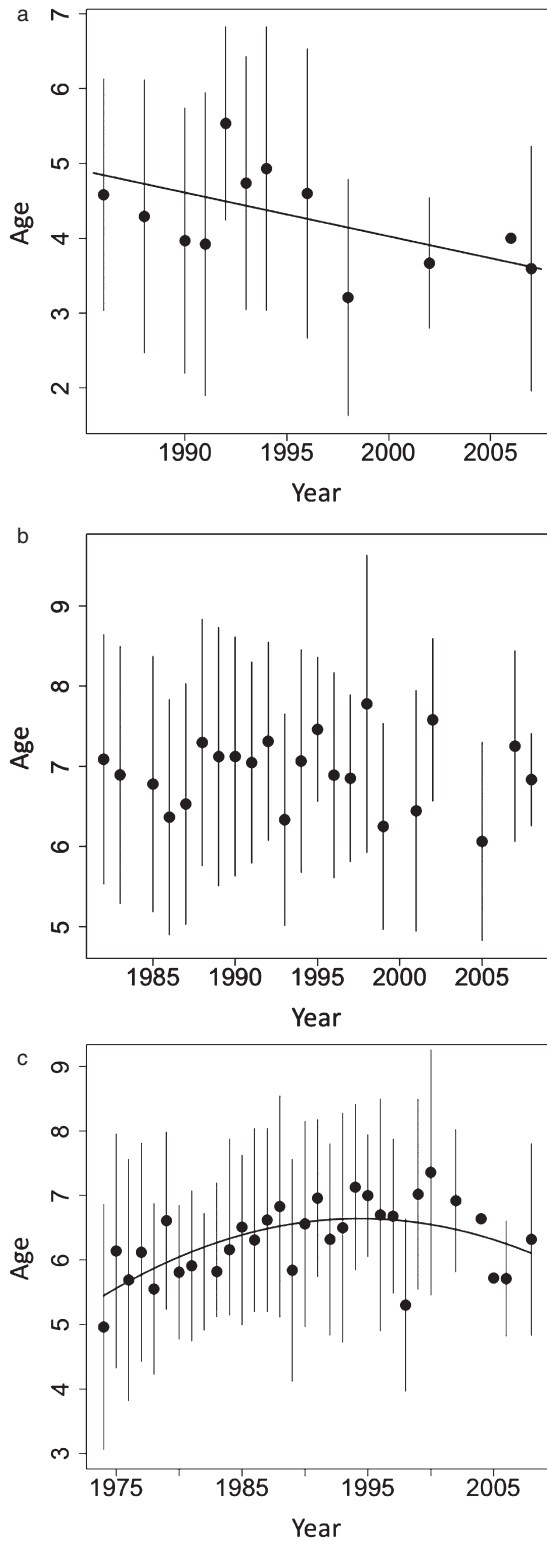


Figure 4 Temporal trend of age of harvested males in hunting units one to five of Matetsi Safari Area, Zimbabwe, for (a) impalas; (b) sable antelopes; and (c) greater kudus. Lines are used for significant trends. Dots represent the average age of trophy animals per year, and bars the standard deviations.

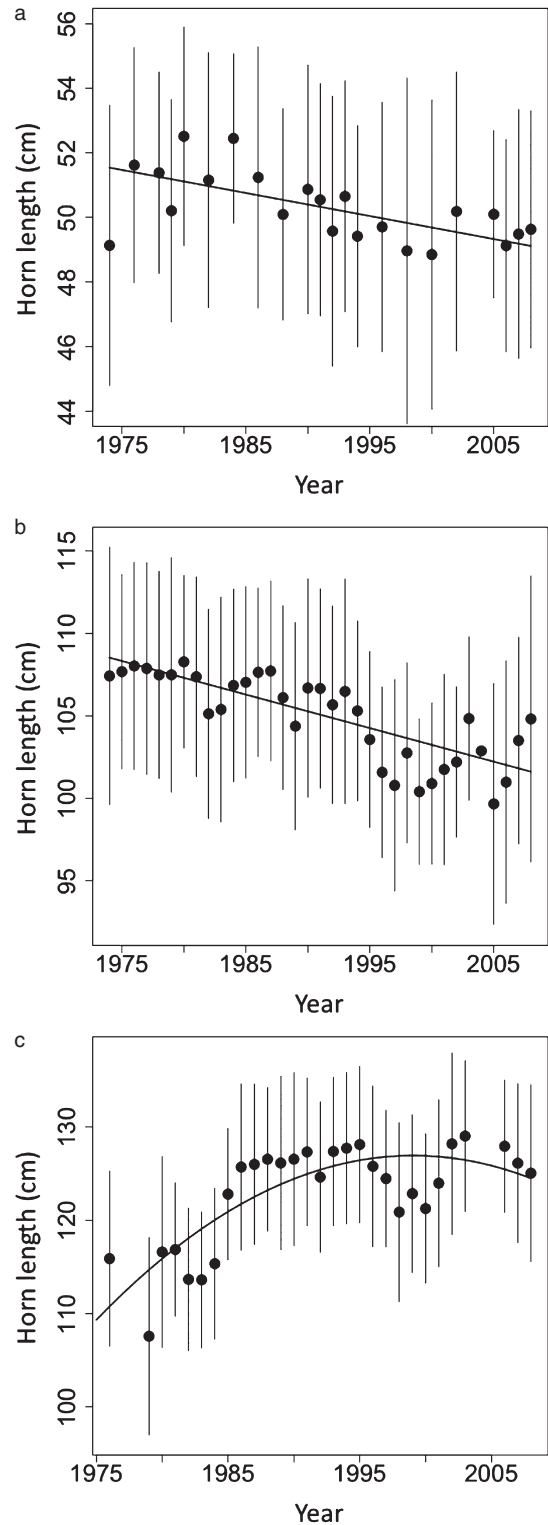


Figure 5 Overall temporal trend in horn length of harvested males in hunting units one to five of Matetsi Safari Area, Zimbabwe, for (a) impalas; (b) sable antelopes; and (c) greater kudus. Lines are used for significant trends. Dots represent the average horn length of trophy animals per year, and bars the standard deviations.

Table 3 Estimated parameters and their 95% CIs for the most parsimonious models of horn length from males harvested for impala, sable antelope, and greater kudu in units one to five of Matetsi Safari Area Zimbabwe

Horn length	Selected model (number of observations; range of years)	k ^a	Parameter	d.f.	Estimate	[CI95%]
Impalas	Year + year ² + distance NP (443; from 1986 to 2002)	4	Intercept	1	56 920	[3 760, 110 088]
			Year	1	-57.98	[-110.31, -3.65]
			Year ²	1	0.01	[0.001, 0.03]
			Distance NP	1	-0.03	[-0.06, -0.001]
Sable antelopes	Age + year + year ² + density + density ² (600; from 1982 to 2005)	6	Intercept	1	-68 000	[-120 220, -15 780]
			Age	1	0.61	[0.29, 0.93]
			Year	1	68	[16, 121]
			Year ²	1	-0.02	[-0.03, -0.004]
			Density	1	3.46	[1.76, 5.15]
			Density ²	1	-0.656	[-1, -0.15]
Greater kudu	Year + year ² + distance NP + density + density ² (955; from 1979 to 2003)	6	Intercept	1	-105 000	[-161 386, -47 920]
			Year	1	105	[48, 162]
			Year ²	1	-0.03	[-0.04, -0.01]
			Distance NP	1	0.06	[0.01, 0.11]
			Density	1	4.56	[1.98, 6.93]
			Density ²	1	-0.40	[-0.85, -0.01]

^aNumber of parameters.

CI, confidence interval; d.f., degrees of freedom.

Age of harvested males could be accounted for in impalas and sable antelopes, but not in greater kudu.

hunting pressure and trophy value. Sable antelope were subjected to higher hunting pressure and higher hunting fees than impala. Not surprisingly then, the decline of horn size was higher in sable antelope. Interspecific comparisons of responses to trophy hunting are rare because earlier studies focused on single species (Coltman *et al.*, 2003; Garel *et al.*, 2007).

For greater kudu, we expected horn length to decline at an intermediate rate compared with those observed in impalas and sable antelopes because hunting pressure and hunting fees were higher for greater kudu than for impalas, but lower than for sable antelopes. Horn length in greater kudu surprisingly increased by 14% from 1976 to 1985, and remained constant from 1985 to 2008. Because mean age of harvested males also increased in a quadratic way during the study period, the increase in horn length could be due to an increasing proportion of older males in the harvest. Interestingly, during the study period, densities of greater kudu globally increased whereas hunting quotas did not, so that hunting pressure declined (Supporting Information Fig. S1a). With a lower hunting pressure, males may survive to older ages, and therefore grow longer horns.

Effects of resources availability

Contrary to previous studies on Northern ungulates (Ashley, McCullough & Robinson, 1998; Jorgenson *et al.*, 1998; Schmidt *et al.*, 2001, 2007; Festa-Bianchet *et al.*, 2004), availability of forage did not significantly determine the variations of horn length in our studied species. Indeed, neither density of conspecifics nor the metabolic biomass of guild competitors, an index of interspecific competition, negatively affected horn length in impalas, greater kudu, or

sable antelope. It could be that changes in density of forage competitors were insufficient to affect growth, or that greater density may have corresponded to periods of greater resource abundance. However, this latter point could be ruled out because we found no effect of vegetation productivity on horn length. Alternatively, density of conspecifics could rather be viewed as a factor of dilution (Hamilton, 1971; Dehn, 1990), with the risk for a given male to be encountered, and shot by hunters, possibly decreasing as densities of conspecifics increase. Therefore, the likelihood that a male would survive longer and grow longer horns increases with densities of conspecifics. Additionally, we suspect that as densities decrease, the opportunities for hunters to find large trophy males also decrease. Therefore hunter selectivity should decline along with horn length of harvested individuals.

Effects of distance from hunting-free areas

Horn length decreased with distance from national parks for impalas, but not for greater kudu and sable antelopes. Interspecific differences in the effect of distance from national parks on horn length could have been expected because home range size is positively related to body mass in African antelopes (du Toit, 1990). Therefore, males of the smallest species, that is impalas, should disperse over shorter distances from national parks compared with males of larger species, that is greater kudu and sable antelopes. For greater kudu, longer-horned males were surprisingly found further from national parks. This counter-intuitive result could be explained by hunting pressure that tends to be higher closest to the national parks (Supporting Information Fig. S1a). Higher hunting pressure in the immediate

periphery of national parks may act as a barrier to males' dispersal into hunting areas. In addition, densities of sable antelopes have declined in the region for the past decades, particularly in Hwange National Park where densities are four times lower than in the hunting areas (Crosmary *et al.*, unpubl. data). In this case national parks are unlikely to act as a source for the hunting areas.

Management implications

Overall, we reported trends of horn size of lower magnitude than in previous studies, e.g. 30% decline observed over 30 years for bighorn sheep on Ram Mountain (Coltman *et al.*, 2003), 12% decline recorded over 20 years for mouflon (*Ovis gmelini musimon* × *Ovis sp*) of the Caroux-Espinouse Massif (Garel *et al.*, 2007). This was probably due to lower harvest rates, that is 5.0, 7.5, and 12.0% in our study for impalas, grater kudus, and sable antelopes, respectively, compared with those practised in Ram Mountain and Caroux-Espinouse Massif, c. 40 and 20%, of legal adult males, respectively (Coltman *et al.*, 2003; M. Garel pers. comm.). The other major difference with these sheep populations is that the antelope populations of Matetsi Safari Area are relatively large and regionally connected with potential gene flow into the area from protected populations. Accordingly, trends of horn size for such populations are likely to be less marked, and to take place at a much slower rate than for small and isolated populations (Pérez *et al.*, 2011).

Nonetheless, data from selective harvests tend to underestimate temporal trends in horn size (Pelletier, Festa-Bianchet & Jorgenson, 2012). Thus, managers of Matetsi Safari Area should be aware that the declines of horn size we reported could be worse in reality. Reducing offtakes of trophy males is an option to lower hunting pressure on horn size (Thelen, 1991). In addition, selective hunting of young males with small trophy size could be used as a complementary option to counter the decline of horn size (Mysterud & Bischof, 2010). This could be achieved by resident local hunters if foreign hunters are reluctant to hunt males of lower trophy size (Mysterud, Tryjanowski & Panek, 2006). We strongly encourage wildlife managers to continue measuring trophy traits of harvested animals, because such data are essential to assess the effects of selective harvest.

Conclusion

Our study is a rare empirical example of long-term trends in horn size of ungulates hunted as trophies, and the only one for free-ranging African populations.

Species exposed to higher hunting pressure and higher trophy selectivity are more likely to experience a decrease in horn size. This is particularly the case for sable antelopes in our study. The situation of this species in Matetsi Safari Area is critical because there is evidence that the decline in horn size could be genetic, and the neighbouring national parks may not be a source of individuals for the hunting areas. In this case, it may be difficult to reverse the decline in

horn size naturally even if hunting quotas were reduced, threatening the genetic integrity and conservation of the species in the region. Finally, decline in trophy size could potentially affect income for the hunting industry if hunters choose to travel to areas where sizes of trophies remain attractive. If this occurs eventually the amounts that can be reallocated to conservation programmes in affected areas may be reduced.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Temporal trends of (a) trophy hunting pressure (i.e. number of adult males harvested / estimated number of adult males in the population), and (b) population densities in hunting units one to five of Matetsi Safari Area, Zimbabwe, from 1978 to 2008, for (1) impala, (2) greater kudu, and (3) sable antelope. Data points indicate annual mean values of trophy hunting pressure and densities. Box plots represent hunting pressure or population densities averaged over the study period for each species across the five hunting units. 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 <10th or >90th percentiles. Averaged

hunting pressures and population densities are compared among hunting units for each species. Different letters indicate hunting pressures or population densities different at $P < 0.05$.

Figure S2. Temporal trends of NDVI in hunting units one to five of Matetsi Safari Area, Zimbabwe, from 1986 to 2008. Data points indicate annual mean values of NDVI per year.

Table S1. Model selection procedure to investigate trends in horn length of harvested males in impala, sable antelope,

and greater kudu over the years in Matetsi Safari, Zimbabwe. The dependant environmental co-variables are distance to national parks (i.e. distance NP), average densities of conspecifics (i.e. density), average metabolic biomass of potential competitors (i.e. competitors), and vegetation productivity (i.e. productivity). The age of harvested males could be accounted for in impala and sable antelope, but not in greater kudu. Selected models for each species and each dataset, are indicated in bold letters.