Management and Conservation

Sustainability of Elephant Hunting Across International Borders in Southern Africa: A Case Study of the Greater Mapungubwe Transfrontier Conservation Area

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ABSTRACT Trophy hunting of African elephant is often implemented as an income generator for communities surrounding protected areas. However, the sustainability of hunting on elephant populations, especially with regards to international cross-border populations has not previously been evaluated. We assessed the effects of trophy hunting on the population dynamics and movements of elephant in the Greater Mapungubwe Transfrontier Conservation Area, which is spread across the junction of Botswana, South Africa, and Zimbabwe. Currently, no common policy exits in quota setting for cross-border species, and each country determines their own quota based on limited data. Using VORTEX, we determined the sustainability of current quotas of elephant off-take under different ecological and hunting scenarios. We used distribution data from 6 aerial surveys and hunting data per region to determine the disturbance effect of hunting on bulls and breeding herds separately. Hunting of bulls had a direct effect in reducing bull numbers but also an indirect effect due to disturbance that resulted in movement of elephants out of the areas in which hunting occurred. The return interval was short for bulls but longer for females. Only a small number of bulls (<10/year) could be hunted sustainably. At current rates of hunting, under average ecological conditions, trophy bulls will disappear from the population in less than 10 years. We recommend a revision of the current quotas within each country for the Greater Mapungubwe elephant population, and the establishment of a single multi-jurisdictional (cross-border) management authority regulating the hunting of elephant and other cross-border species. © 2013 The Wildlife Society.

KEY WORDS Botswana, disturbance, hunting quotas, *Loxodonta africana*, population dynamics, population viability analysis, transboundary conservation, trophy hunting.

For the conservation of species whose habitat lies mainly outside protected areas, maintaining landscape diversity, connectivity, and compatibility of wildlife habitats with human land uses is important (Karanth et al. 2010). For this reason, the development and expansion of international cross-border or transboundary conservation areas are essential (Scovronick and Turpie 2009). The objective of transboundary conservation areas is, however, not only the conservation of biodiversity but also economic development of communities within these border regions (Hanks 2003, Scovronick and Turpie 2009). This is especially important

for regions with large bodied, valuable mammals, such as African elephant (*Loxodonta africana*), which could negatively affect both ecosystems (Skarpe et al. 2004, Kerley and Landman 2006, Makhabu et al. 2006, Guldemond and van Aarde 2008, Helm and Witkowski 2012) and local communities surrounding protected areas (Naughton et al. 1999, Hoare 2000, Von Gerhardt-Weber 2011). However several challenges impede the effective management of such species across international borders (Plumptre et al. 2007).

Where wildlife has no or limited value outside protected areas, it dwindles and disappears either through active persecution, loss of habitat, competition with livestock, or overutilization (Prins and Grootenhuis 2000). In many instances where rural communities receive revenue from a species, they are more likely to conserve it, and will be more tolerant of negative impacts from such species (Barnes 1996,

Hurt and Ravn 2000, Lindsey et al. 2007, Blignaut et al. 2008). In such instances, sustainable consumptive use through trophy hunting may benefit conservation (World Tourism Organisation 1997).

In Africa, wildlife use, involving both consumptive and non-consumptive use, is commonly associated with community-based natural resource management (CBNRM) programs (Hurt and Ravn 2000, Du Toit 2002, Blignaut et al. 2008), which could include formal wildlife ranching (Earnshaw and Emerton 2000, Hurt and Ravn 2000, Kreuter et al. 2010). Such CBNRM programs are run in Botswana, Namibia, and Zimbabwe. At present, approximately 80% of the current African elephant range in southern Africa is outside formally protected areas (Blanc et al. 2007, Abensperg-Traun 2009), leading to increased conflict with local communities (Hoare 2000, Jackson et al. 2008, Riddle et al. 2010). In both Botswana and Namibia, the CBNRM involve both non-consumptive and consumptive tourism, whereas over 80% of income derived through the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) in Zimbabwe is from trophy hunting (Lindsey et al. 2007, Blignaut et al. 2008). Within the Greater Mapungubwe Transfrontier Conservation Area (GMTFCA), during the period 1999–2010 between 2 and 43 elephant were hunted from the population annually. Current quotas are set at 33 for Botswana and 14 for Zimbabwe. Although a zero hunting quota was set for elephants in South Africa, a total of 18 elephants were shot as problem elephants during 2006 to 2010. South Africa has been party to the Convention of the Conservation of Migratory Species of Wild Animals (CMS) since 1991 (CMS 2012a). Zimbabwe joined only in 2012 and Botswana is not party to this convention (CMS 2010b). This leads to little or no consultation among the 3 countries in setting quotas for hunting elephant, and each country determines their own quota based on restricted subsets of population data.

If the profits realized from harvesting a few individuals are sufficient incentive for people to tolerate the larger population, the goals of trophy hunting and conservation are compatible (Treves and Karanth 2003, Balme et al. 2010a). However, where large mammal species, such as ungulates and carnivores, are targeted, excessive sustained harvesting can lead to extirpation (Treves and Karanth 2003, Lindsey et al. 2007, Fa and Brown 2009), or selective harvesting may have negative evolutionary consequences (Harris et al. 2002, Coltman et al. 2003, Balme et al. 2010a). In addition, studies on carnivore and antelope populations have shown that the selective removal of a few large trophy or the oldest males can potentially lead to the destabilization of social structures and the dominance hierarchy and a loss of social knowledge (Milner et al. 2007). Other possible consequences of the selective removal of large trophy males are infanticide, reproductive females using sub-optimal habitats, and changes in offspring sex ratio (Milner et al. 2007). Little is known about the disruptive effects of hunting on the dominance hierarchy through changes in stress levels, movements, and other behavior (but see Burke

et al. 2008). In situations with high hunting pressure, these effects may be significant and negative (Archie et al. 2008).

Although a few studies have investigated the potential social and demographic effects of hunting adult bulls (Archie et al. 2008, Burke et al. 2008), the results are not directly applicable when attempting to evaluate the merits of hunting cross-border populations. In these studies only the fine-scale genetic implications and stress levels as a result of poaching and hunting, respectively, were studied. We assessed the effects of hunting on the population dynamics and movements of elephants using data from the Greater Mapungubwe Transfrontier Conservation Area (GMTFCA). Specifically, we describe the current hunting quotas, examine the effects of hunting under different ecological and hunting scenarios on population sustainability using population models, and assess the effects of the spatial patterning of elephant removal by hunting on the population. We conclude by providing some suggestions towards the management of elephant and other cross-border species.

STUDY AREA

The GMTFCA is situated at the confluence of the Shashe and Limpopo Rivers and includes areas from Botswana, South Africa, and Zimbabwe (Fig. 1). It is a semi-arid area with low, unpredictable rainfall. The long-term average annual rainfall was 369 mm (1966–2001) with peak rainfall years receiving 917 mm (Jul 1999 to Jun 2000) and low rainfall years receiving as little as 136 mm (Jul 1997 to Jun 1998). Most rain fell between November and February, usually in the form of thunderstorms (Mckenzie 1990). Summer maximum temperatures exceeded 42° C and winter minimum temperatures were as low as −5° C. An elephant population of approximately $1,224 \pm 72.4$ estimated from 6 aerial counts over a 10-year period roamed freely across the 3 countries (Selier 2010).

Botswana is divided into administrative blocks called Controlled Hunting Areas (CHAs; Abensperg-Traun 2009) that each have a wildlife off-take quota designated by the Department of Wildlife and National Parks. Some CHAs, such as protected areas, have a hunting quota of zero, whereas other CHAs are designated for community use (Abensperg-Traun 2009). A community with a legally recognized trust and a land use plan can apply for a lease over the CHA from the Tribal Land Board. This will allow the Trust to sub-lease use of their land and their quota to a tourism company for photographic or hunting safaris (Abensperg-Traun 2009). Within the Central Bobonong District in Botswana (Fig. 1), 3 community trusts, Mmadinari, Mapanda, and Molema Trusts, have been developed since 2000. Each trust is allocated an annual elephant-hunting quota, and the trusts are responsible for marketing and managing hunting safaris within their community. The allocation of hunting quotas in terms of problem animal control laws have been used to deter elephants from entering communal areas, to compensate local communities for wildlife-related losses, and to improve the tolerance of communities towards elephant (M. Mamani,
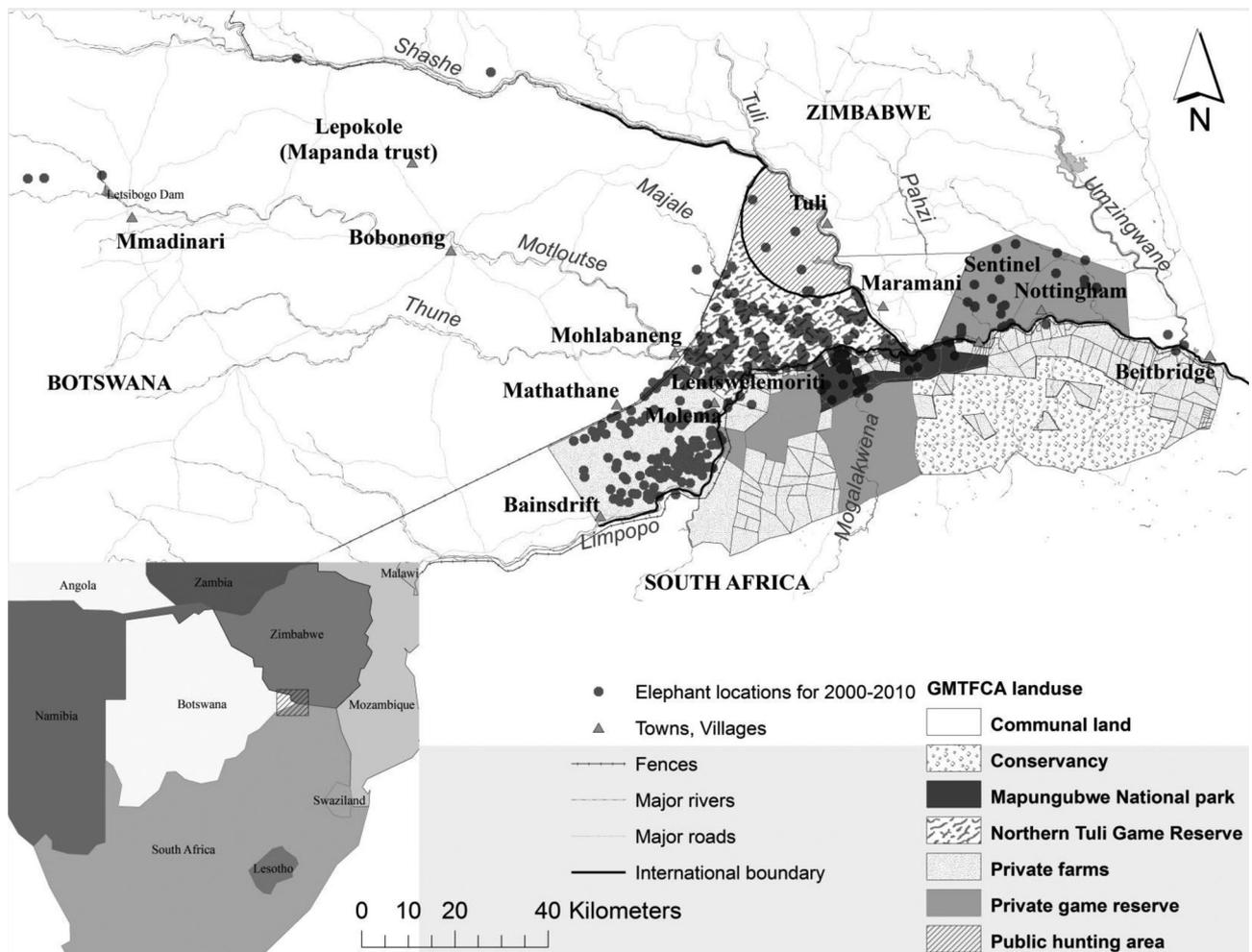
Figure 1. The Central Limpopo River study area with different land use practices and the elephant locations for 2000–2010.

Department of Wildlife and National Parks, Botswana, personal communication).

In the Beitbridge Rural District in Zimbabwe (Fig. 1), the CBNRM program is run as a CAMPFIRE Project (CESVI 2001). Three hunting concessions occur within this area, of which 2 (Sentinel Limpopo Safaris and Nengasha Safaris) operate west of Beitbridge. Elephant trophy hunting is also offered within the Tuli Circle Safari Area, Zimbabwe. In South Africa, all elephant crossing out of reserves are considered problem animals, and with the acquisition of a hunting permit from the provincial conservation agency, can be hunted by the farmer or a paying client (Hopkinson et al. 2008).

Several tourism operations operate within the current boundaries of the GMTFCA. Even though photographic tourism is the main economic driver within the area at present (Evans 2010), several operations rely on a combination of trophy hunting and photographic tourism. The Northern Tuli Game Reserve (NTGR) is a private game reserve within Botswana (Fig. 1), focusing purely on photographic tourism. Within the Zimbabwean section, 2 private commercial tourism operations focus on a combination of trophy hunting and photographic tourism (Notting-

ham Estate and Sentinel Ranch), whereas the Mapungubwe National Park (MNP) in South Africa (Fig. 1) is solely a photographic tourism destination. All of the tourism destinations use, either for viewing or trophy hunting, a single cross-border elephant population that moves freely between the 3 countries.

METHODS

Current Hunting Quotas

We obtained data on quotas for trophy hunting and kill rate of elephants for all 3 countries from the respective wildlife departments, private landowners, and reserve and farm managers within the 3 countries. We obtained data on population numbers and the distribution of elephant within the GMTFCA from 6 aerial surveys conducted within the study area over the period 2000–2010 (Selier 2010). We divided numbers and distribution of elephant into the following regions: 1) Botswana, which included 2 separate sections, the Northern Tuli Game Reserve (NTGR) and the Tuli Block from the Motloutse River to Baines Drift (TLBL); 2) the Zimbabwean section along the Limpopo River, including Maramani, Sentinel Ranch, and Notting-

ham Estate up to the Umzingwane River (ZIM); and 3) the South African section, including Mapungubwe National Park and private properties bordering the Limpopo River where elephants had access (MNP; Fig. 1). Major rivers (Limpopo, Shashe, and Motloutse rivers) form natural boundaries between the above-mentioned regions (Fig. 1). Hunting occurred in all of the regions other than the Northern Tuli Game Reserve, and all but 2 of the Tuli Block properties in Botswana.

Population Projections

We used VORTEX 9.50 (Lacy et al. 2005) population simulation software to determine the impact of different harvest rates of mature elephant bulls on the viability of the elephant population in the GMTFCA. The VORTEX model has been used extensively and the internal logic and the assumptions inherent in it have been evaluated in terms of its ability to emulate the known behavior of the populations (Armbruster et al. 1999, Brook et al. 2000, Lindenmayer et al. 2000, Nilsson 2004, Rija 2009).

Van Aarde et al. (2008) summarized the annual survival rate of elephant in different age classes, the length of calving intervals, and the age at first calving for different African populations from published data. We used these values to determine the above average, average, and below average demographic parameters (age at first calving and mortality; Table 1). We used the maximum values obtained by populations outside South Africa as the parameters for above average conditions. Likewise, we obtained the average demographic parameters by selecting the median values for all population data (populations outside South Africa only), and obtained the below average parameters by selecting the population outside South Africa with the lowest values. We did not use data from Luangwa National Park, Bugongo, or Murchison North and South, which we considered outliers because their values were significantly lower or higher than the other areas presented in their table (van Aarde et al. 2008). Luangwa suffered extreme poaching and this could possibly be the reason for the lower survival rates

within the population (Owens and Owens 2009). Calving intervals for elephant populations outside South Africa vary between 2.1 and 9.1 years, with the majority of the populations falling between a 3- and 5-year calving interval (van Aarde et al. 2008). We thus used a 3-year calving interval or 0.33 breeding rate for above average conditions, a 4-year calving interval or 0.25 breeding rate for average conditions, and a 5-year calving interval or 0.20 breeding rate for below average conditions. We designated 15 years as the age at maturity for bulls in the model (Poole 1994). According to age structure data from Amboseli National Park, Kenya, the percent of males >15 years within the population is approximately 48% of the total male population (Moss 2001). We used this value as the percent of males within the breeding pool of the initial population. To determine mortality rate, the model required the percent of females and males dying for each year from birth to age of first offspring. To model natural mortalities, we used the age-specific survival rates given in van Aarde et al. (2008) and divided them by the number of years within each of the categories to get an age-specific mortality (up to 60 years of age). We used the average mortality rate for the age groups 20–29, 30–44, and 45–60 as the adult mortality (van Aarde et al. 2008). The maximum age of reproduction for both males and females was 45 years. Moss (2001) showed that female fecundity declines after 40 years with a rapid drop after 50 years of age.

We set the upper and lower limits for the elephant population based on rainfall variation in the area. We calculated average annual rainfall from 4 rainfall stations: Mashatu Main Camp, Mashatu Tented Camp, Pont Drift border post, and Platjan border post. Over the period, mean rainfall was 324 mm with a 20% variation, which is 8% below the long-term mean of 351 mm with a variance of 11% for the period July 1989 to June 2010. To use these limits for average, below average, and above average conditions we used the following logic. The Northern Tuli Game Reserve was an open system with very few barriers to movement. The South African border was fenced in places but open in others, and the backline of the Tuli Block farms was fenced with a non-elephant proof fence. No barriers prevented movement to the north, east, or southwest. No hunting occurred within the reserve (Selier 2007). We therefore calculated the density of elephants within the Northern Tuli Game Reserve for each year between 1988 and 2010. We then used the maximum, average, and minimum densities of elephants for these years as estimates of the limits during above average, average, and below average conditions, respectively. The maximum density observed in the Northern Tuli Game Reserve since 1988 was 1.22 elephant/km^2 (2001, above average rainfall conditions; Selier 2010). Extrapolating this density across the total area available to elephant within the proposed GMTFCA (3,065 km^2) resulted in a maximum population of 3,740 elephants. We determined average density (0.74) and low density (0.37, Sep 1996, below average rainfall conditions) in the same manner and, when extrapolated to the GMTFCA, gave an average population of 2,299, and a low population of 1,134 elephants.

Table 1. Parameters used within the VORTEX analysis for above average, average, and below average environmental conditions with 7 different harvesting rates of elephant bulls in the Greater Mapungubwe Transfrontier Conservation Area. Data are the low, median, and high values of mean annual survival rates of elephant in different age classes and populations from published data. Actual is the average observed over the past 10 years in our population.

Conditions	Above average	Average	Below average	Actual data
Age females at first calving	10	13	15	15
Age bulls sexual maturity	15	15	15	15
Max. age reproduction	45	45	45	45
% Females breeding/year	33	25	18	25
Mortality rate				
<1 yr	2%	8%	18%	5%
1–9 yr	1%	5%	13%	4%
10–15 yr	2%	5%	10%	4%
>15 yr (adult)	2%	5%	10%	5%
% Males in breeding pool	48%	48%	48%	48%
Initial population size	1,224	1,224	1,124	1,224
Upper population limit	3,740	2,299	1,134	2,299

Current evidence indicates that the GMTFCA population is stable (Selier 2007), and, until 2009, the population was not controlled and levels of hunting and poaching were relatively low. For the 10 years between 2000 and 2010, the elephant population ranged in an area of 2,016 km^2 at an average density of 0.61 elephant/km^2, with biennial aerial censuses varying between 1,080 and 1,294 elephants with a mean count of 1,224 ($\pm$72.4 SD) elephants (Selier 2010). If the population is currently at biological carrying capacity and the birth death rate that we observed reflected the population density, we can validate these numbers by running the model at average conditions. We thus assumed that the observed birth and death rates were those that determined the population densities at biological carrying capacity.

A sensitivity analysis was run to determine the sensitivity of the model output to changes in parameter values. To evaluate whether the birth and death processes kept the population below the limit we raised the upper limit to a very high level (35,000 elephants/km^2) in the sensitivity analysis.

We ran the model for 10 years under 3 scenarios of above average, average, and below average rainfall to determine the total elephant numbers and number of bulls in different age classes at the end of the simulation. Because VORTEX is a stochastic model, we used the average of 100 iterations as the final output. We evaluated different annual harvest rates (0, 5, 10, 20, 30, 40, 50) of bulls >15 years in the analysis. In order to calculate the maximum sustainable yield (MSY), we determined harvest rates based on starting population numbers for the total GMTFCA set at 68% below (current population), 47% below (average conditions), and 8% above (below average conditions) the upper, high-resource limit (Table 1) only because at biological carrying capacity, any harvesting would result in a decline in the population numbers. Given that the existing population showed no trend in population numbers in the past 10 years, but fluctuated around a mean of 1,224 $\pm$ 72.4 SD, we assumed that the population had a stable age distribution. In the model, we ignored inbreeding depression and incorporated environmental variability under the 3 environmental scenarios described above.

We assessed the effect of hunting at different levels on the population trend. Even though bulls 15–35 years are unlikely to mate under natural conditions, bulls at this age are sexually active and, in the absence of older bulls, they are capable of reproducing (Poole 1989, Slotow et al. 2000, Moss 2001). Adult bulls >35 years are favored by trophy hunters (Archie et al. 2008). For this reason, we ran the VORTEX model with bull breeding age at 35 years for all 3 environmental scenarios (above average, average, and below average), with different harvest rates (0–50 bulls/yr) to determine the impact of harvest rates on bulls >35 years. From the VORTEX output, we determined population size, the total number of bulls, number of bulls >15 years, number of bulls >35 years, and the sex ratio between breeding age females and adult bulls >35 years for the 3 environmental scenarios. As a comparison and evaluation of the VORTEX output, we also used the formulae of Caughley (1993) and Martin et al. (1997) to determine maximum sustainable yield. Caughley (1993) determined that the MSY for elephant was approximately half the population's maximum rate of increase, multiplied by half the size of the population when not harvested. The MSY of a growing population is therefore greater than that of a stable population. On the other hand, Martin et al. (1997) recommended that, to sustain good quality trophy elephant hunting, quotas ideally should not exceed 0.7% of the total population.

Effect of Hunting on Movement

To assess whether hunting influenced movements and visibility of adult bulls, we used regression analysis (Sokal and Rohlf 1995) to relate the number of bulls observed during the aerial surveys in each region to the number of bulls hunted during the same year and in the previous year. We used population numbers from the 6 biennial aerial surveys between 2000 and 2010 (Selier 2010) The hunting season extended between May and October and most of the hunts occurred prior to the annual count survey of a given year. We also related the number of females observed during the surveys to the number of bulls hunted in the same year and in the previous year.

RESULTS

Current Hunting Quotas

For the 2010 hunting season, 40 bulls >35 years old were killed within Botswana and Zimbabwe combined (Fig. 2A). Since 2006, within Botswana between 16 and 36 trophy bulls annually were allocated to various community trusts within the Central Bobonong District (Fig. 2B). Since 2006, within Zimbabwe the quota remained steady at approximately 11 elephants per year (6 bulls and 5 tuskless cows) for the Beitbridge District, and additional 3 elephant bulls for the Tuli Circle Safari area (Fig. 2B). Despite no annual quota being allocated since 2006, 18 elephants were shot on the South African side as problem elephants. Eleven of these were mature breeding bulls hunted by paying clients (L. De Jager, Limpopo Nature Conservation, personal communication).

Population Projections

The model evaluation showed that the average values we used were able to reproduce the numbers counted in the 6 biennial censuses over the period 2000–2010. Model output using the average current harvesting rate over the past 10 years (14 bulls/yr), a starting population of 1,102 elephants, which was 10% below current density, and a upper limit for average conditions of 2,299 elephants gave a population with a low rate of increase ($r = 1.47\%$ SD $\pm$ 0.80), which started at an average of 1,102 and ended at 1,277 (SD $\pm$ 30.83) animals over the 10-year period. The range in counts over the past 10 years was between 1,080 (2007) and 1,294 (2001). The simulation over 10 years was therefore in agreement with the aerial counts over the 2000 to 2010 period. When we ran the model with observed birth and death rates determining population density under average conditions, the population increased marginally to 1,539.

Sensitivity analysis indicated that the model was most sensitive to changes in the percent of females breeding in any
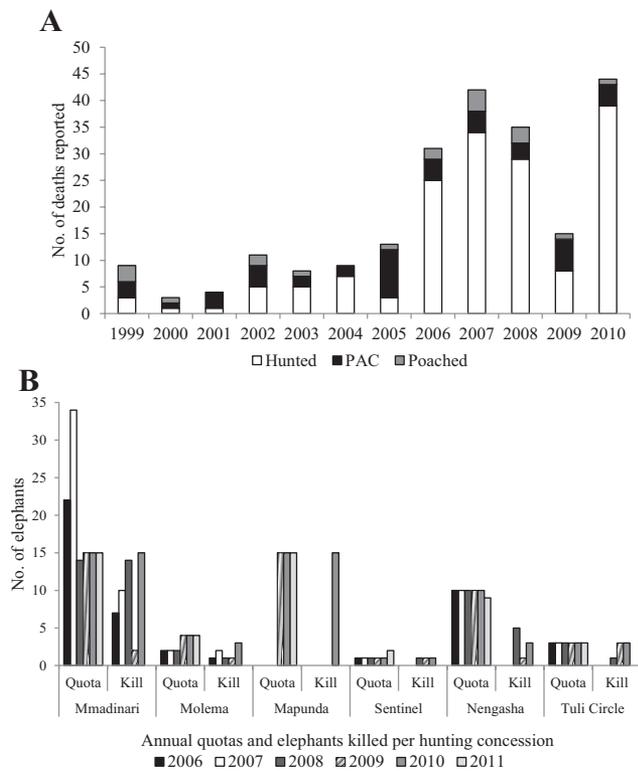
Figure 2. Number of elephant killed per annum through unnatural causes within the Greater Mapungubwe population between 1999 and 2010 (A), and a comparison of the annual hunting quota and kill rate for each of the hunting concessions from 2006 to 2011 (B). PAC, problem animal control.

1 year (which is equivalent to calving interval). A change from 10% females breeding in any 1 year to 45% breeding resulted in an increase in the population after 10 years from 1,057 to 2,013 (with all other variables kept constant at average values), and, after 50 years, from 587 to 14,503. The model was also sensitive to adult mortality rate, for which a decrease from 13% to 1% resulted in a population change after 10 years from 1,096 to 1,851 and from 699 to 9,739 after 50 years, for the respective mortality rates. To test the effect of the upper limit of the model, we raised the upper limit to 35,000 elephants/km^2. The population did not reach this limit for average conditions of 2,299 after 10 years, but after 50 years, the population exceeded the upper limit of 2,299 (3,837 $\pm$ 123.65 SD, 39.10 SE). Because our simulations were for 10 years, errors in the estimate of the upper limit did not affect the results of the simulation.

For all 3 rainfall scenarios, modeled population growth rate declined steadily as the number of bulls harvested per year increased. With 10 years of above average conditions, the population growth rate increased 6.34 $\pm$ 0.59% without harvest but only increased by 1.76 $\pm$ 3.24% when 50 adult bulls were harvested/yr (Fig. 3A). Under average conditions, the population growth rate increased 2.29 $\pm$ 0.69% without harvest and decreased by 1.51 $\pm$ 1.92% when 50 bulls were harvested per annum. With below average conditions after 10 years, the population growth rate decreased by 2.10 $\pm$ 0.92% with no harvesting and decreased by approxi-
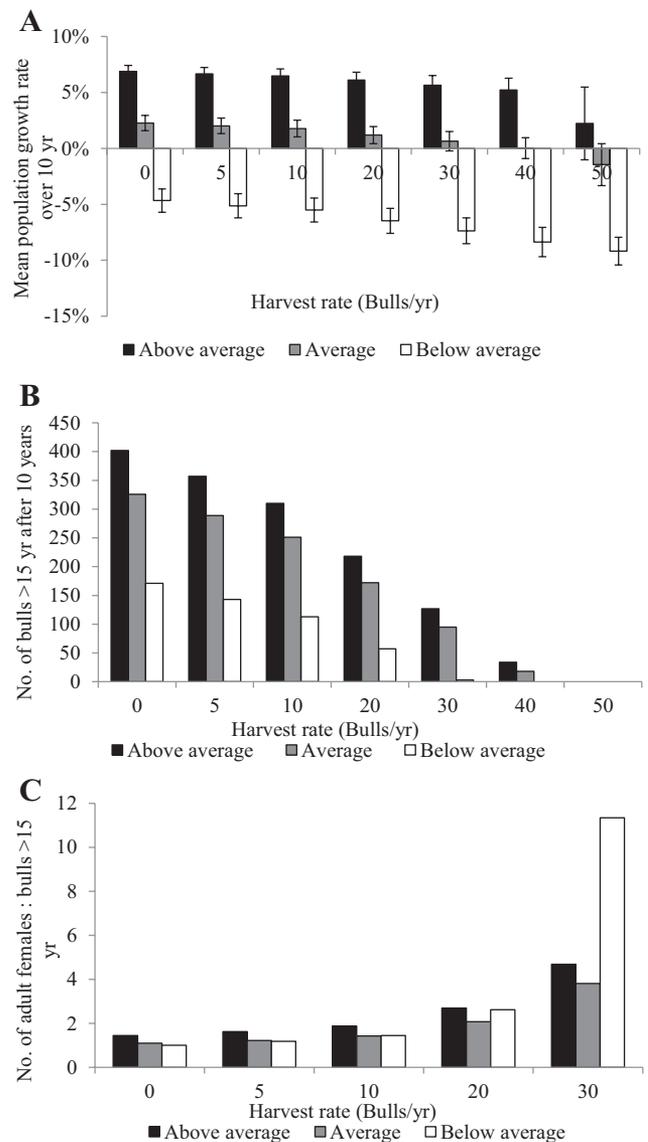

Figure 3. Comparison of (A) mean population growth rate, (B) number of bull >15 years old, and (C) changes in sex ratio of females to bulls >15 years old of elephants in the Greater Mapungubwe population under 3 environmental scenarios (above average, average, and below average) and 7 different adult bull harvesting rates after 10 years of harvesting at the specific rate. Outputs are from VORTEX modeling with 100 iterations run for 10 years. The ratio of breeding age females to bulls >15 years old for harvest rates of 40 and 50 bulls per annum are too large and are not reflected in the graph.

mately 6.76 $\pm$ 1.30% when 50 bulls per year were harvested. Under all 3 conditions, as harvest rate increased, the number of bulls >15 years in the final population declined steadily (Fig. 3B). After 10 years of harvesting under below average conditions, 18 bulls >15 years remained at the harvest rate of 30 bulls per annum, and under both average and above average conditions, no bulls >15 years were left at a harvest rate of 50 bulls per annum.

Assuming average conditions, the MSY would be below an annual harvest rate of approximately 40 bulls >15 years old (Fig. 4). This was approximately 2.60% of the total
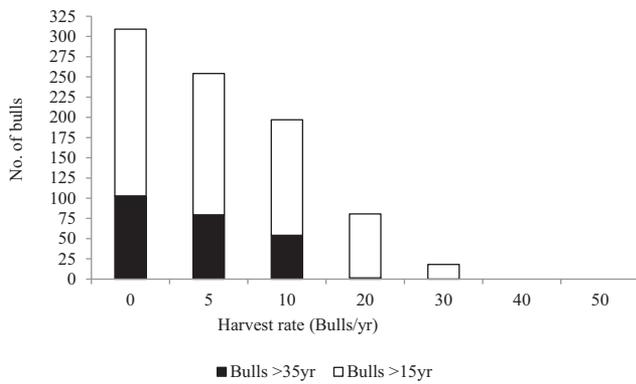
Figure 4. Predicted number of elephant bulls >35 years old and the number of bulls >15 years old remaining within the population after 10 years of hunting at different harvesting rates under average conditions in the Greater Mapungubwe population.

population or 12% of the initial adult bull population of 321. If hunter preference and the social structure of elephant bulls were taken into account (bulls 15–35 years are unlikely to mate under natural conditions), the maximum sustainable harvest rate of bulls was approximately 10 bulls >35 years per annum. Based on the recommendation of Martin et al. (1997), hunting quotas should ideally not exceed 0.7% of the total population and thus only 9 bulls >35 years could be hunted from the current population of 1,224 elephant. Based on Caughley's (1993) approach, only 6 bull elephants per annum could be hunted.

Even though relatively high hunting quotas were allocated to the 3 community trusts within the Central Bobonong District, Botswana, the annual kill rate within these hunting concessions was low. Of the 144 elephant on quota from 2006 to 2010, only 71 elephants were hunted (Fig. 2B). A similar trend was observed in Zimbabwe, where of the 54 elephants on quota since 2008, fewer than half the quota was harvested (Fig. 2B). Despite this low off-take, hunting in 2010 was 75% above the MSY levels suggested by the VORTEX model, 77.5% above MSY calculated using the formula of Martin et al. (1997), and 85% above that calculated using the formula of Caughley (1993).

Assuming a stable age structure, an initial population of 1,224 elephants should have included approximately 200–300 bulls >15 years old. Under average conditions, the model predicted 321 bulls >15 years old with no hunting. Harvesting led to an increasingly skewed sex ratio. Under no harvest, the model predicted a 1:1 bull >15 years old to breeding age female ratio but dropped to 1:25 bull >15 years old to breeding age females ratio at a removal rate of 40 bulls per annum under average conditions (Fig. 3C). Under average conditions, the number of bulls >35 years old dropped steadily with an increase in the harvest rate (Fig. 4). At a harvest rate of more than 20 bulls >35 years old per annum, no bulls would be left in this age class after 10 years of harvesting regardless of environmental conditions.

Effects of Hunting on Movement

In all but 1 region, increasing or constant numbers of bulls were hunted each year between 2006 and 2011 (Fig. 2B). In those regions where more than 3 bulls were hunted each year, the numbers counted ranged between 0 and 11 animals (Zimbabwe and Mapungubwe; Fig. 5A). However, where 6 or more animals were shot in a year, the number in the census was never greater than 13, whereas when hunting occurred less often, up to 25 bulls occurred in the region and where hunting was absent, up to 35 bulls were counted. Female numbers and bull numbers were not correlated in any region for the 6 years counted (South Africa: $r^2 = 0.674$, $P = 0.142$; Northern Tuli: $r^2 = 0.137$, $P = 0.796$; Tuli Block: $r^2 = 0.714$, $P = 0.111$; Zimbabwe: $r^2 = 0.137$, $P = 0.796$; $n = 6$). The number of bulls hunted in a particular year negatively affected the number of females observed within each region in the same year ($F_{1,22} = 5.564$; $n = 24$; 1-tailed $P = 0.015$). Where 1 or no animals were shot in a locality per year, more females (>320) occurred, and conversely where hunting of
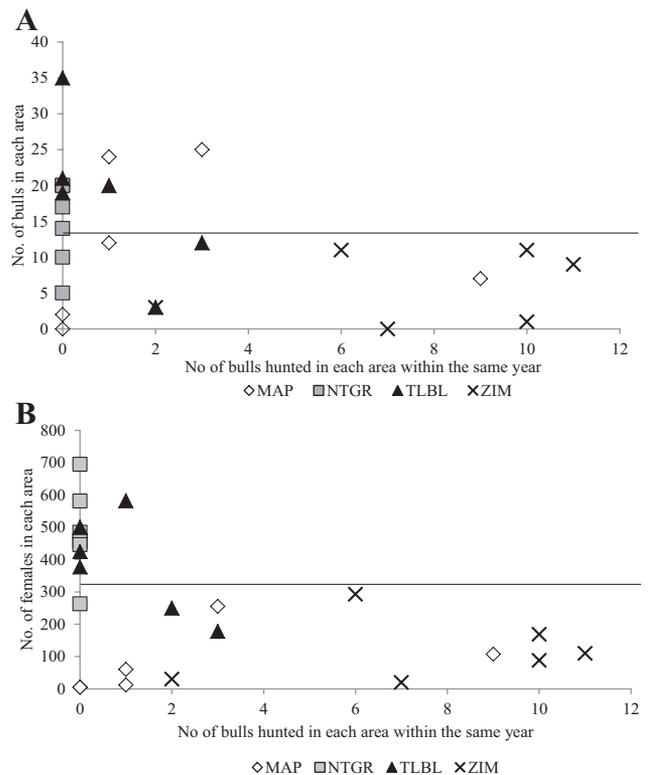

Figure 5. Effect of hunting of bulls in the hunting season immediately prior to the aerial survey in each of the 4 regions of the Greater Mapungubwe Transfrontier Conservation Area on the number of bulls counted (A) and the number of females in each region (B). Each point represents a count in a different year and the symbols indicate different localities (MAP, the South African section, including Mapungubwe National Park and private properties bordering the Limpopo River where elephants had access; NTGR, Northern Tuli Game Reserve; TLBL, Tuli Block from the Motloutse River to Baines Drift; and ZIM, the Zimbabwean section along the Limpopo River, including Maramani, Sentinel Ranch, and Nottingham Estate up to the Umzingwane River). The horizontal line in A indicates the maximum number of bulls counted (13) when 6 or more animals were shot in a year. The horizontal line in B indicates the maximum number of females counted (320) when ≥2 bulls were hunted in a year.

bulls was greater, fewer females occurred (Fig. 5B). Since habitats were almost identical, and no other factors limited distribution, these differences can be ascribed to the disturbance effects of hunting bulls on females.

DISCUSSION

Wildlife resources in Africa have long been hunted for sport, subsistence, and to control population size (Festa-Bianchet 2003). Trophy hunting targets the largest males or those with impressive horns, tusks, or antlers (Ginsberg and Milner-Gulland 1994, Milner et al. 2007). Even though it is generally restricted to a few individuals, where controls are lacking a high proportion of those individuals that qualify can be removed annually (Coltman et al. 2003, Crosmary et al. 2013). High levels of hunting are thus often not a sustainable use of wildlife resources (Baker 1997, Milner et al. 2007). This is especially true of long-lived or large species, such as elephant, with low intrinsic rates of increase (Archie et al. 2008, Fa and Brown 2009).

Several factors, including environmental conditions, influence the number of elephant that can be hunted per annum. Our model showed that selective hunting under all 3 environmental conditions tested, not only can have a direct effect on reducing population size (Milner et al. 2007, Allendorf et al. 2008) but also can bias the sex-ratio in favor of females and heavily skew the age structure towards younger animals. Undisturbed elephant populations have only a slightly skewed sex ratio favoring females (Poole and Thomsen 1989, Wittemyer 2001). Thus selective hunting consequently could have an effect on reproduction (Ginsberg and Milner-Gulland 1994, Milner et al. 2007, Allendorf et al. 2008). In several species, including saiga antelope (*Saiga tatarica*; Milner-Gulland and Bennett 2003) and elephant (Dobson and Poole 1998), a sex-ratio threshold may exist (77 females per male for elephant), below which fecundity decreases as a result of insufficient male breeding capacity.

For a harvest system to be sustainable, consideration of its effect on age-dependent or size-dependent fecundity, growth, and survival rates of individuals, and the growth rate and age structure of the population is warranted (Fa and Brown 2009). For most species, older, high-value trophy animals are past breeding, and form approximately 10% of the total male population (Hurt and Ravn 2000). When considering that the majority of mating in an elephant population is done by bulls >35 years old (Poole 1989, Hollister-Smith et al. 2007), and that loosing these bulls can lead to social problems (Slotow et al. 2000), the maximum sustainable yield for social stability within the study area was predicted by the VORTEX model to be about 10 bulls >35 years old per annum. The models of Caughley (1993) and Martin et al. (1997) both suggest even more conservative rates. Harvesting quotas should further take into account other sources of mortality, such as problem animal control and natural mortalities (Baker 1997). These are rarely included in the calculation of quotas (Baker 1997, Caro 1999). The current levels of trophy hunting are thus unsustainable and far exceed the MSY of the population. Even though hunting brings in revenue to local communi-

ties, the overall value to the area is relatively low, and at the present harvest rate, hunting is not sustainable.

During the 6 biennial aerial surveys, the greatest number of bulls counted was 88 in 2001 (Selier 2010). Several factors could contribute to the fewer number of bulls counted. Lone bulls are difficult to spot and a few were likely missed during the counts. Further younger bulls associated with breeding herds might have been assumed to be part of the breeding herd. These errors, however, do not account for the large difference between what the model predicted and what was observed during the aerial counts. Therefore, hunting over the past 10 years had likely already depressed bull numbers.

Old bull elephant also have greater reproductive success, and their longevity may further reflect greater fitness (Hollister-Smith et al. 2007, Ishengoma et al. 2008). In populations recovering from poaching, the lifetime reproductive output of dominant male elephants in the population increased (Ishengoma et al. 2008). Whether this has an impact on reducing genetic diversity in the population is still unclear (Ishengoma et al. 2008). Removing the primary male breeders in a population not only hampers reproduction and recruitment but could also disrupt the social organization (Milner et al. 2007, Whitman et al. 2007). In elephant, older bulls have a social network with high centrality and strong bonds (Archie and Chiyo 2012). Consequently, the elimination of older bulls from elephant populations may negatively affect social cohesion in bull elephant groups (Ishengoma et al. 2008, Archie and Chiyo 2012). Further, the selective removal of adult males over an extended period could result in a greater proportion of younger males (Milner et al. 2007), which may increase the reproductive tenure of these males (Poole 1989, Archie and Chiyo 2012). In the absence of older bulls, young bulls increase the frequency and duration of their musth period (Slotow et al. 2000). Abnormal behaviors in these young males, such as elevated aggression, killing people, and killing white rhino (*Ceratotherium sinum sinum*) have been the result of distorted male age hierarchies (Slotow et al. 2000, 2001; Slotow and van Dyk 2001; Bradshaw et al. 2005).

Where communal areas occur on the periphery of protected areas, the open borders between protected and communal lands create a source-sink effect with animals constantly being removed from the periphery of the protected areas (Hoare 2000, Balme et al. 2010b). High human densities and conflicting land use practices (crop farming) draw elephant, especially bulls, towards community areas, primarily during periods of low natural food availability, thereby creating an ecological trap (Hoare and Du Toit 1999, Chiyo et al. 2005). Elephants can move from tourism areas where they may be wanted, to areas where they are unwanted such as community crop fields. Ongoing killing of problem animals on the periphery of protected areas erodes the quality of the remaining animals in terms of trophy quality (Hoare 1995) and genetic diversity (Archie and Chiyo 2012).

The aim of allocating hunting quotas in terms of problem animal control laws are to deter elephants from entering communal areas and to compensate local communities for damage to crops and property with the aim to improve the

tolerance of communities towards elephants (M. Mamani, personal communication). We show, however, that hunting bulls is not an effective deterrent, as elephant return to the region within a year of the hunts. Similar results have been reported from Kasungu (Malawi) where high levels of poaching, of mainly bulls, led to additional males continuously moving into the area (Bell 1981). Younger bulls are more often responsible for crop raiding (Chiyo et al. 2005, Ahlering et al. 2011), but the older bulls are required for a good trophy income (Hurt and Ravn 2000, Festa-Bianchet 2003, Milner et al. 2007, Slotow et al. 2008). Regulations on damage causing animals differ between Botswana and South Africa. Botswana applies a clear and systematic process in dealing with damage causing animals (Wildlife conservation and National Parks Act no 28 of 1992), whereas South Africa at present, uses a more ad hoc and less systematic approach, which does not deal sufficiently with migratory cross-border movements of elephant (National Environmental Act 1998 and the National Norms and Standards for the management of elephants 2007).

A further consequence of hunting bulls, not taken into account in the model is the disturbance factor. For levels of hunting much greater than or close to the numbers counted in each year to be sustained over the 5-year period, immigration into the areas where greater hunting pressure occurs is necessary. These results indicate that although bulls do not completely avoid areas with greater hunting pressure, fewer bulls entered these areas, than areas where less or no hunting occurred. Thus, sustained high levels of hunting in a region do not appear to cause bulls to avoid that region and shooting trophy bulls will not alleviate the problem of conflict within Botswana. Given the systematic approach of Botswana towards problem animals, this approach would not likely be effective within South Africa. However, high levels of hunting of bulls caused a disturbance effect within breeding herds, possibly because of the high stress levels observed throughout the population during hunting disturbances (Burke et al. 2008). In a system where both consumptive and non-consumptive use is made of elephants, disturbance has major ramifications.

Photographic tourism is at present the main economic driver within the region (Evans 2010) and elephant are 1 of the main draws. Habituated viewable elephants, including large bulls with trophy size tusks, are important to the tourism industry (Blignaut et al. 2008, Slotow et al. 2008). Excessive hunting will therefore affect photographic tourism within the Limpopo Valley through significantly reduced numbers of big bulls, and could affect the chances of viewing elephants in general (Slotow et al. 2008, Di Minin et al., 2012). Furthermore, because of its selective nature, trophy hunting may decrease the number of large tusked individuals (Festa-Bianchet 2003). However, it is important that all stakeholders within transboundary areas benefit from wildlife, and a consultative process, which includes all stakeholders, is required to develop a sustainable non-consumptive and consumptive use plan with cost-benefit sharing for the area.

MANAGEMENT IMPLICATIONS

Current hunting quotas within the GMTFCA are unsustainable, and an urgent revision is required within each country with the establishment of a single multi-jurisdictional (cross-border) management authority regulating the hunting of elephant (and other cross-border species). The allocation of hunting quotas should be based on current data, taking into consideration the environmental conditions as well as the population dynamics and social structure of the species under consideration. Based on our results taking into consideration the social stability of the population and the current environmental conditions, the maximum sustainable yield is 10 bulls >35 years old per annum. Cooperation between countries, increased landscape connectivity, and the ability to generate income from tourism have been shown to work successfully in increasing wildlife numbers elsewhere (Plumptre et al. 2007).

A conservation planning assessment with the objective of enhancing biodiversity protection, while promoting sustainable development and improved quality of life for communities within the GMTFCA, is urgently required and should include all stakeholders. Where communities are included in the process and directly benefit from wildlife, either through consumptive or non-consumptive means, they are more likely to take ownership and the incentives to develop the land for arable purposes or livestock herds will be removed, thus benefiting biodiversity conservation (Hanks 2003).

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Associate Editor: John Daigle.