

*Effects of trophy hunting on Cape buffalo (*Syncerus caffer c.*) horn spread and population dynamics*

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Abstract

Trophy hunting is often put forward as a sustainable way to contribute to conservation measures in many African countries, but there is question about whether sustained trophy hunting has adverse effects on physical and demographical characteristics of hunted species.

To address this question, this research studied whether a relationship exists in Cape buffalo (*Syncerus caffer c.*) between horn spread, male age and the prevalence of males of breeding age, and distance from areas where hunting takes place. This was done in an area that encompasses Kruger National Park and the Associated Private Nature Reserves, some of which allow trophy hunting while others do not. Free movement is possible for buffalo in this area, so it is essentially one large population undergoing different hunting pressures at a gradient. Horn spread and age data was acquired by visually analysing photos of buffalo herds and individuals, and placing buffalo in horn spread and age categories. Linear mixed models and a t-test were performed to analyse this relationship. In total, over 4500 photos were analysed resulting in a sample size of 2380 unique buffalo.

Results show that there was no significant increase in horn spread or male age as distance from hunting areas increased. The chances of encountering a lone male or bachelor herd did increase significantly as distance from hunting areas increased.

This study concludes that there are no apparent effects of trophy hunting on horn spread, nor on population structure that could affect population dynamics in Cape buffalo.

1. Introduction

Trophy hunting is often put forward as a sustainable way to contribute to conservation measures in many African countries (Lindsey, Frank, Alexander, Mathieson, & Romanach, 2007). It provides a large portion of the tourism income, and is often considered more eco-friendly than other forms of tourism, although this is hotly debated (Di Minin, Leader-Williams, & Bradshaw, 2016; Ripple, Newsome, & Kerley, 2016) (see Background trophy hunting).

Despite its proposed merits in terms of species and ecosystem conservation, there is increasing worry that trophy hunting has adverse effects on both population genetics and population dynamics. Partly this worry arises from trophy hunting removing the animals with the biggest or most aesthetically pleasing trophy, essentially creating an artificial selection pressure. For trophy hunting to be considered ecologically and evolutionarily sustainable, it needs to support and sustain wildlife populations without having negative consequences on abundance and genetic diversity over many generations.

When these animals are removed from the population before they have had a chance to reproduce, these preferred traits might be lost from the population if they are

(highly) heritable (Chiyo, Obanda, & Korir, 2015; D. W. Coltman et al., 2003). This effect has been documented in several commonly hunted species, such as the African elephant (*Loxodonta africana*) and Stone's sheep (*Ovis dalli stonei*). In elephants tusks have significantly decreased in size, or sometimes even disappeared entirely, under severe hunting (legal and illegal) pressure for the ivory trade (Chiyo et al., 2015; Whitehouse, 2002). In Stone's sheep, under hunting pressure, horn size has significantly decreased (Douhard, Festa-Bianchet, Pelletier, Gaillard, & Bonenfant, 2016). Changes in these physical characteristics could feed through to population-level effects through changes in sexual selection, male-male competition (Garel et al., 2007), as well as potential genetically correlated traits. Research has

Background trophy hunting

Trophy hunting is legal in 23 countries in sub-Saharan Africa and generates approximately 201 million USD per year (Lindsey, Roulet, & Romañach, 2007). The area where hunting takes place consists of almost 1,500,000 km² of mostly private land, 22% larger than the area of national parks in this part of the world (Lindsey, Roulet, et al., 2007). It has been argued that, if it wasn't for trophy hunting, these areas might not be home to the many animals found there (hunted species and non-target species), and often these areas make up a relatively large area of a given species' total distribution (Lindsey, Roulet, et al., 2007). Although many trophy hunters target 'wild' and 'dangerous' game for the thrill of the experience, as a memento, or proof, of the hunt, a large majority of hunters have a goal of bringing home a trophy, and as such want a trophy for aesthetic properties, adhering to certain industry standards (Gandy & Reilly, 2004). Trophy size can be measured using several different methods, the two most popular being the Rowland Ward spread and the Safari Club International (SCI) spread (Gandy & Reilly, 2004). Many places have rules and regulations when it comes to hunting, primarily about whether animals of a specific age, sex or social status can be hunted, but there is always a chance that these are not adhered to.

Research has shown that hunters are not always accurate at determining the age or sex of an animal, (Balme, Hunter, & Braczkowski, 2012) and corruption is often present when clients wish to shoot an animal that is technically off limits. (Lewis & Jackson, 2005)

shown for example that body size in Soay sheep (*Ovis aries*) decreased under harvesting pressure, and that this decrease in body size was genetically correlated with a decrease in parasitic resistance (A. D. W. Coltman et al., 2013). Horn size was determined to be a reliable indicator of health in African buffalo, as horn size was negatively correlated with parasite richness and the likelihood of infection (Ezenwa & Jolles, 2013). As such, horn size was not the proposed cause of this parasitic resistance but a trait correlating with higher fitness in general, which may suggest that individuals have horn size related to genes correlating with higher fitness, which could disappear from the population if trophy hunting selects for larger horns. Alternatively, this correlation between horn size and health benefits could be due to environmental factors, such as quality and quantity of nutrition which has been proven to influence horn growth, and individuals who have access to adequate resources are hypothetically more likely to resist parasitic infection (Monteith et al., 2018).

As most desirable trophies tend to be on animals of a specific sex or age group, it is expected that individuals belonging to this sex or age group will be removed from the population at a higher rate than others. If this happens consistently over a longer period of time, this artificial change in population structure can affect the dynamics of a population (Milner, Nilsen, & Andreassen, 2007).

Whether trophy hunting affects the population dynamics depends on the selection effect that trophy hunting has on the population. This selection effect can be two-fold; 1) as a result of skewed sex ratios which is expected due to a sex bias in harvesting, and 2) as a result of a younger breeding male population which can be expected due to the harvesting of older, more phenotypically impressive males.

Most ungulate populations are strongly sex and age structured, and these different age and sex classes are subjected to different stressors, and have correspondingly different survival rates (Gaillard, Festa-bianchet, & Yoccoz, 1998; Milner et al., 2007). Because of the different survival rates for each of the age classes, there is a difference between populations of similar size but different structural makeup, both in temporal dynamics and responses to environmental variation. Populations that are subjected to trophy hunting have a far higher mortality rate among potentially reproductively active aged males than non-hunted populations (Milner et al., 2007). This is generally due to female biased populations being the most productive (Milner et al., 2007), and it therefore makes sense to remove males over females, but also because a large amount of species is sexual dimorphic, and trophy hunters prefer male trophies, due to the presence of characteristics that may be smaller or absent in females (Milner et al., 2007).

Populations that are subjected to hunting often also have a lower mean age for males, as the older and more fully-grown males are selected and removed from the population. This affects natal sex ratios, as well as overall male survival. Both observational and experimental studies show that older males sire more male offspring than younger males (Holand et al., 2006; Sæther et al., 2004). They hypothesized this is due to female hesitance to mate with younger males, and that the delayed mating and resulting parturition leads to more female offspring as this would maximise fitness as predicted by the Trivers-Willard model, which hypothesises that parents in better physical condition would be expected to show a bias towards male offspring (Trivers & Willard, 1973). It is therefore to be expected that a lower mean male age as a consequence of trophy hunting will lead to fewer male offspring, potentially affecting population dynamics even further.

Additionally, overall male survival can be diminished in cases where young males are more involved in mating (due to the absence of prime age males), as males increase their engagement and investment in mating behaviour (Milner et al., 2007) leaving them in bad physical condition.

This likely leads to increased winter mortality, when lack of food and water and dropping

Cape buffalo

Cape buffalo (Syncerus caffer c.) are one of the famous "Big Five", and extremely popular with trophy hunters. They are common throughout sub-Saharan Africa, although currently they are mostly found within the confines of national parks and protected areas. Buffalo are hunted in several countries in Africa, and between 2005 and 2014 over 17,000 were imported as trophies to the US alone. Buffalo hunting can bring in revenue of between 15,000 and 18,000 USD depending on length of the hunt and cost of the accommodation, and as such can be a sizable source of revenue for game reserves (The Humane Society Of The United State, 2016). The aim of many buffalo hunts is to shoot an animal that will make it into the record books. The Rowland Ward scoring system measures Cape buffalo trophies based on only the greatest outside spread, where a minimum of 42 inches is required for a record book entry (Gandy & Reilly, 2004). The SCI scoring system measures the length along the outside of the horn, from tip to tip, added to the measurement of width of the boss. A minimum of 100 inches is required for a record book entry. These scoring systems are troublesome as buffalo horns wear down, and thus decrease in width, with age (Gandy & Reilly, 2004). This has led to the top 10 record book SCI entries being young, pre-breeding or breeding bulls, who likely have had no opportunity to pass on these record genes. While the Rowland Ward scoring system also incorporates the boss width, which increases with age, the bulls most often found in their record books are still in their prime (Gandy & Reilly, 2004). There is increasing pressure from experts to establish a new scoring system where age is incorporated, decreasing the amount of (pre) breeding bulls that are hunted (Robertson, pers. comm, January 2018).

In most countries, there are rules and regulations concerning the practice of trophy hunting of buffalo, but these are based on precise assessments of age and trophy size.

IUCN has listed Cape Buffalo as 'Least Concern', but this assessment is 10 years old, and the population is decreasing. This decrease is most likely due to droughts becoming more common, but also due to habitat loss, poaching and diseases. While trophy hunting might not yet be a main contributor to their decreasing number, with other known factors likely to be exacerbated in the future it is vital to know any negative permanent influences it might have (IUCN SSC Antelope Specialist Group, 2008).

temperatures add stress which animals in poor conditions are less well equipped to survive (Milner et al., 2007). Survival is also affected by the fact that high adult (male) mortality leads to a higher proportion of young animals, which are more susceptible to winter mortality in general. This leads to greater population variability in hunted populations than in non-hunted populations.

The male bias in harvesting regimes has been found to result in extremely biased sex ratios, such as in North American Elk (*Cervus elaphus canadensis*) and Saiga antelope (*Saiga tatarica*) where the sex ratio was 0.05 adult males per female in both populations after harvesting pressures (Milner-Gulland et al., 2003; Noyes, Johnson, Bryant, Findholt, & Ward, 1996). While many species have female biased populations, and therefore would be expected to not suffer diminished fecundity, or even experience an increase under a more skewed sex ratio, research has shown that there are sex ratio thresholds where populations crash due to reduced fecundity, and these differ between species. This reduced fecundity appears to be largely attributed to a shortage of males in rut and a low mean male age (Milner et al., 2007; Solberg, Loison, Ringsby, Sæther, & Heim, 2002). Younger males have shown to be capable of inseminating females successfully, but there is question whether they can inseminate the same large number of females prime aged males can (Mysterud, Coulson, & Stenseth, 2002). Moose (*Alces alces*) experience reduced fecundity at mild female biased sex ratios (0.25-0.7) (Solberg et al., 2002), while it has been observed in elephants (*Loxodonta africana*) at a sex ratio as skewed as 0.013 (Dobson & Poole, 1998).

Although not all sex ratios lead to population crashes, less extremely skewed sex ratios have been shown to affect birth timing and synchrony (Milner et al., 2007). Several studies have shown that parturition timing is earlier, and synchrony is greater when sex ratios are more balanced. (Noyes et al., 1996; Sæther et al., 2004). Lower mean male age seems to be the cause, as it affects female choice and female distribution. Females tend to be more spatially dispersed when there is a skewed sex ratio, which leads to a less synchronous rut (Mysterud et al., 2002). Additionally, females being choosy about which male to mate with when there is a lack of prime aged males delays conception (Mysterud et al., 2002). This delayed conception and parturition date can also affect subsequent generations. Female ungulates who are born later often need an extra year of growth before they are in adequate physical condition to reproduce (Langvatn, Albon, Burkey, & Clutton-Brock, 1996; Mysterud et al., 2002). Birth timing and synchrony have important ramifications on demography as they affect survival and bodyweight of offspring. Higher synchrony of births leads to increased survival in species that are subjected to heavy new-born predation (Sinclair, Mduma, & Arcese, 2000), and later parturition leads to decreased bodyweight and survival in offspring (Clutton-Brock, 2018; Holand et al., 2006).

These mechanisms can all follow on from sustained offtake and can affect populations at the demographic level as well as at the genetic level. This calls for studies that address the combined effects of these population pressures.

This study aims to establish whether a relationship exists between physical characteristics, population dynamics and trophy hunting. This is achieved by studying the changes in horn spread and mean male age in a wild population of Cape buffalo (*Syncerus caffer c.*) in South Africa. To date, there is no conclusive evidence for effects of trophy hunting in Cape buffalo, with some research showing there is no change in horn spread under persistent hunting pressure (Muposhi, Gandiwa, Bartels, Makuza, & Madiri, 2016) while other sources suggest a decline in average horn spread (Robertson, pers. comm, January 2018). As such, there is still doubt on how trophy hunting affects Cape buffalo. In order to properly address this relationship, this study will test whether horn spread and mean male age differs between hunted and non-hunted areas. Specifically, in this study

we aim to answer the following questions:

1. Does horn spread increase with increased distance from areas where trophy hunting takes place?
2. Does mean male age increase with increased distance from areas where trophy hunting takes place?
3. Are lone males and bachelor herds more common in areas where they are less likely to be hunted?

To answer these, we used data from the non-hunted Kruger National Park area and the (hunted) private reserves bordering it.

2. Methods

2.1 Study Area: Greater Kruger National Park

The Associated Private Nature Reserves (APNR) are located in the province of Limpopo, South Africa, west of Kruger National Park. Their combined area covers over 1800 square kilometres. (Fig 1.)

The APNR consist of several private game reserves such as Klaserie Game reserve, Timbavati Game reserve and Balule Game reserve. There are no internal fences between these game reserves, nor between the APNR and Kruger National park. This allows for total freedom of movement for all wildlife in these areas. Buffalo numbers in the APNR therefore vary. There were an estimated 8000 buffalo before the four-year drought period, but at the time of this study these numbers have decreased to approximately 2000 individuals based on annual aerial game counts. Hunting is permitted in most of the private nature reserves, with the exception of Manyeleti, which is not part of the APNR as it is a provincially owned

reserve. As Manyeleti borders Kruger National Park directly, and the other private game reserves are more or less situated on a west to east line, it was decided to take buffalo data from the furthest west datapoint as the starting point and calculate the distance (using latitude and longitude) from there as a proxy for a hunting pressure gradient. The actual border between areas where hunting is and is not allowed is not clearly marked, and with no internal fences, intermingling between hunted and non-hunted populations is expected. Although all game reserves and Kruger national park are interconnected, it is impossible for animals to move from Manyeleti to Timbavati as there is a road in between, so they must go through Kruger National Park. Therefore, the shortest

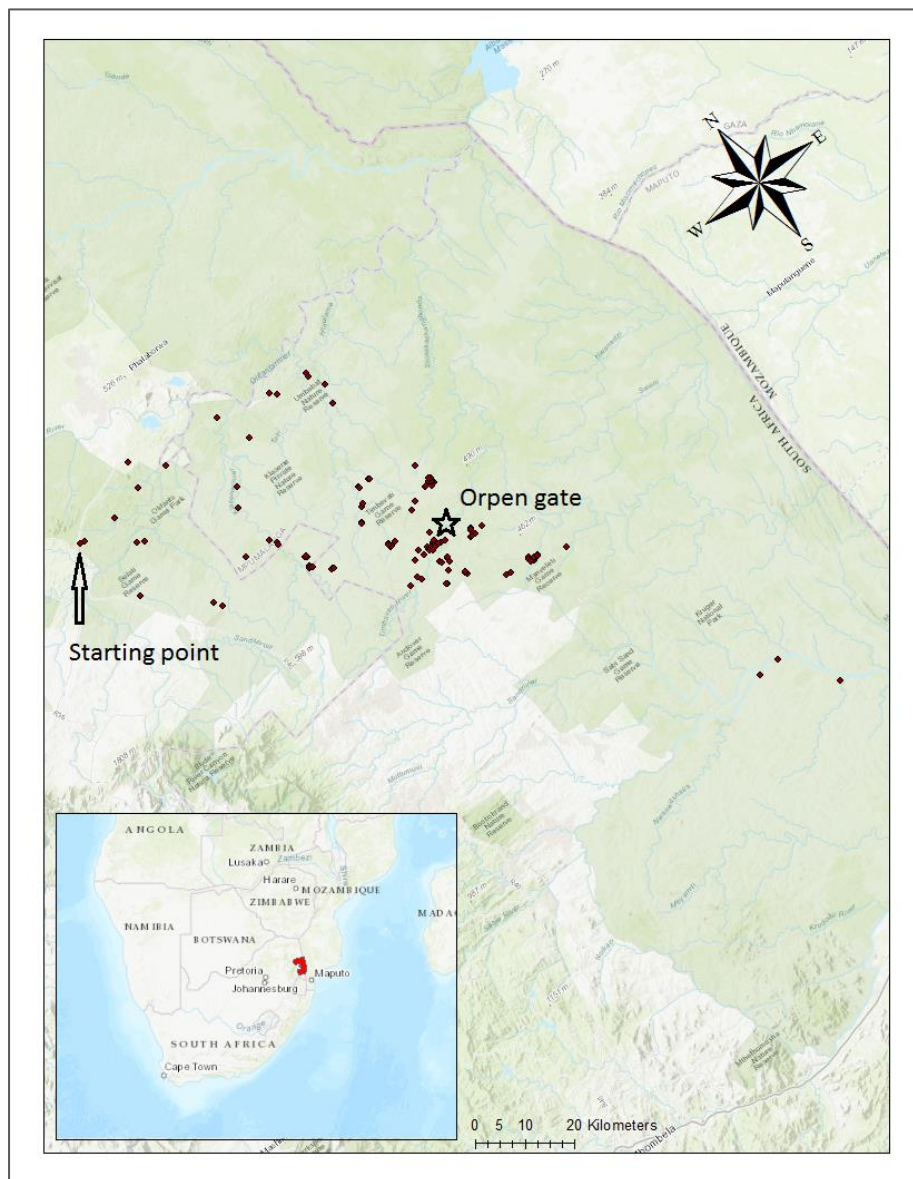


Figure 1- Map of buffalo data locations. GPS coordinates for all used photos are plotted (squares). Starting point is indicated by an arrow and Orpen gate is indicated by a star.

distance from buffalo data in Manyeleti to the closest Kruger Gate, Orpen, was incorporated in the total distance to the starting point. This is considered to be the shortest distance buffalo would have to travel to get from Manyeleti to Timbavati and vice versa. While there is no reason to assume hunting pressure is highest at the starting point, it is the furthest away from the boundary. One can therefore assume that the chance of crossing the boundary, or even exchanging genes with buffalo from the other side of the boundary, is smallest at the starting point, and increases as the buffalo are found further away from the starting point.

2.2 Data acquisition

Individual buffalo data was acquired through means of photographs. The majority of photos used were taken from a Savannah S aircraft, usually at an altitude of approximately 400ft. Photographing at this altitude meant that larger herds were easier to spot than lone males or bachelor herds, and as such one has to take into account that this method is not exhaustive, and that these photos represent a subsample of the buffalo in this area. It also minimized the disturbance. Photographs were taken between June 2017 and February 2018, using a Canon 6D. This camera recorded the latitude and longitude for each photo, which allowed for GPS positioning of each assessed buffalo (see fig 1). There was no fixed pattern to the timing of photographs, as weather and personnel varied. Whenever a herd was encountered the pilot usually circled the herd several times to ensure that the majority of the buffalo in that herd were photographed. In total, over 4500 photos were taken, containing many duplicates. Whenever possible, multiple photos of one area were stitched together to create one large photograph, which minimized the chance of duplicate buffalo assessments. In the end, 158 photos were deemed to contain 2380 unique buffalo and were used as the sample. About 50 photos were not taken from the aircraft, but rather from a vehicle whilst driving through Kruger National Park.

2.3 Data analysis

All photographs underwent the following procedure. First, buffalo photos were checked for obvious duplicates, and individual buffalo were numbered. These buffalo were then assigned an approximate age for males and horn spread for both males and females. After instruction by Dr. Kevin Robertson, age and horn spread assessments were done by the same student to minimize observational error. Assessments were done in a way that if there was any doubt in which age or horn spread category a buffalo belonged, the most conservative category was recorded. If there was any doubt on whether a buffalo was being assessed twice, it was removed from the sample.

Horn spread, which was defined as the greatest outside spread, was divided into 10 categories:

- U3 – under 30 inches
- L3 – low 30's (30-33 inches)
- M3 – mid 30's (34-36 inches)
- H3 – high 30's (37-39 inches)
- L4 – low 40's (40-43 inches)
- M4 – mid 40's (44-46 inches)
- H4 – high 40's (47-49 inches)
- L5 – low 50's (50-53 inches)
- SC – scumcap (both horns broken off)
- N/A – spread cannot be assessed for calves

Based on their estimated age, bulls were categorised into breeding classes:

- BB – before breeding (aged 7 and younger)
- CB – currently breeding (aged between 8 and 12)
- PB – post breeding (aged 13 and older)

Age and breeding class is not relevant for calves and cows when looking at the effects of trophy hunting, and as such weren't categorised.

2.4 Current hunting regulations

The current hunting regulations regarding buffalo bulls in the Greater Kruger National Park, as stated in the "Greater KNP Hunting Protocol for Reserves where hunting takes place" are as follows (Sowry, 2018):

Buffalo

The following categories of Buffalo bulls may be hunted:

- **'Classic buffalo bull – unlimited spread'**, no limit on Rowland Ward spread **must be a minimum of 12 years of age.**
- **'Classic Buffalo bull – sub 38'**, must be a minimum of 10 years old.
- **'Management buffalo bull – sub 34'**, (Rowland Ward) spread, minimum 6 years old, not a scrum cap or broken horn bull

2.5 Statistical analysis

All statistical analyses were performed using R Studio version 3.3.1.

Horn Spread

R (R Core Team, 2012) and lme4 (Bates, Maechler, Bolker, & Walker, 2015) were used to perform a linear mixed effects analysis of the relationship between horn spread and distance from the hunting areas. The assessments placed buffalo in categories of horn spreads, but this statistical analysis needed continuous data, so the mean horn spread per category was used. As fixed effects, distance and sex (without interaction term) were entered into the model. As random effects, intercepts for which reserve the herd buffalo appeared in, unique herd identifier and which photographer collected the data were obtained. Random slopes did not appear to improve the model fit, and as such were left out. Visual inspection of residuals did not reveal any obvious deviations from homoscedasticity or normality. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. Marginal and conditional r^2 values were obtained using the MuMIn package (Barton, 2018). An independent t-test was also performed using buffalo data from two reserves where trophy hunting was allowed, namely Klaserie and Timbavati, and from reserves and parks where trophy hunting is not permitted, Manyeleti and Kruger National Park. All assumptions were adhered to, including homogeneity of variance despite unequal sample sizes.

Age Classes

The relationship between male age classes and distance was also analysed by using a linear mixed model. The dependent variable consisted of average male ages indicating the 3 different age classes. As with the previous analysis, buffalo analysis provided categorical data for age. This was transformed to numerical data by taking age 7 for pre-breeding males, age 10 for currently breeding males and age 13

for post breeding males. Fixed effects were distance and herd ID (bachelor herd, lone male or mixed herd) without interaction term, and random effects intercepts were included for unique herd identifier, reserve and photographer. Visual inspection of residuals did not reveal any obvious deviations from homoscedasticity or normality. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. Marginal and conditional r^2 values were obtained using the MuMIn package (Barton, 2018).

Herd Identity

To test whether lone males and bachelor herds are more prevalent as distance increases, a binomial GLMER was used. The dependent variable was either a TRUE value, if the animal was a lone male or part of a bachelor herd, and a FALSE value if the animal was part of a mixed herd. Distance was entered as a fixed effect, and as random effects intercepts for photographer and reserves were created, as well as a random slope for reserves. Multicollinearity was assessed and resulted in the variable "Sex" being removed from the model. All other assumptions were adhered to. Marginal and conditional r^2 values were obtained using the MuMIn package (Barton, 2018)

3. Results

In total, 2380 buffalo were analysed, of which 664 were males, and 1716 were females. A horn spread of 44 to 46 inches (M4) was the largest encountered. The majority of males had a horn spread in the mid 30's category, while for females the low 30's was most frequent. Almost all of the buffalo that had a horn spread smaller than 30 inches were female, while horn spreads over 40 inches were mostly found in males. See table 1. All 664 males were sorted into age groups, with before breeding (BB) males being the most numerous, followed by currently breeding (CB) males and then post breeding (PB) males. See table 2.

Table 1: Horn spreads counts and percentages for all assessed buffalo males, females as well as total number of buffalo.

	M		F		Total	
	n	(%)	n	(%)	n	(%)
SC	1	0.2	0	0.0	1	0.0
U3	15	2.3	332	19.3	347	14.6
L3	156	23.5	841	49.0	997	41.9
M3	378	56.9	454	26.5	832	35.0
H3	86	13.0	82	4.8	168	7.1
L4	27	4.1	6	0.3	33	1.4
M4	1	0.2	1	0.1	2	0.1
Total	664	100.0	1716	100.0	2380	100.0

Table 2: Breeding class counts and percentages for all buffalo males.

	M	
	n	(%)
BB	550	82.8
CB	103	15.5
PB	11	1.7
Total	664	100.0

3.1 Horn Spread

Results indicated that there was no increase in horn spread with increased distance from the hunting start point. This held true when males and females were analysed separately, as well as combined (see fig 2-4.) The average horn spread for males was 34.69 inches (S.D. = 2.93, N=664), which corresponds to the M30 category, while the average horn spread for females was 32.19 inches (S.D. = 2.64, N=1716). This corresponds to the L30 category. The combined average horn spread was 32.89 inches (S.D = 2.85, N=2380).

Adding "Distance" ($\beta = 0.0051$) did not improve the model ($P=0.345$), whereas "Sex" ($\beta = 2.5332$, $p<0.0005$) did significantly improve the model. The marginal r^2 was 0.157, while the conditional r^2 was 0.178. This indicates that the random effects of reserves, photographer or unique herd ID did not increase the model fit substantially.

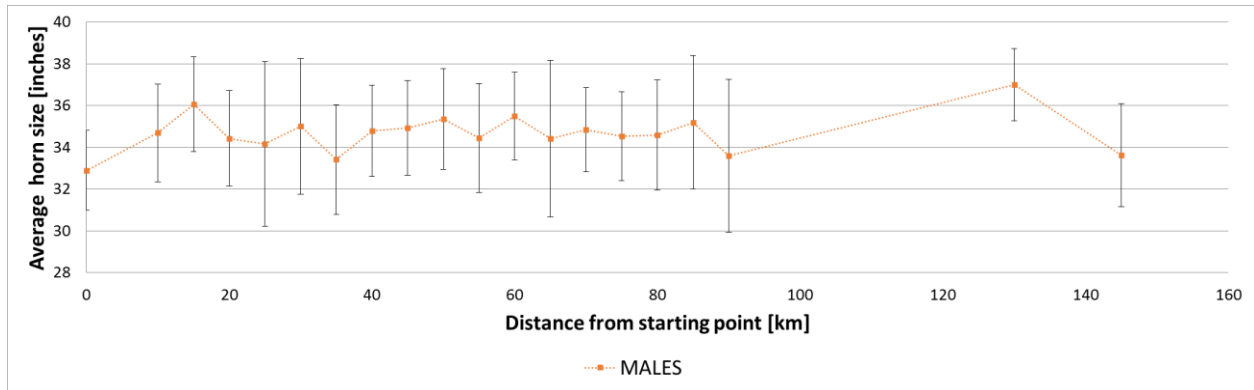


Figure 2 : Average male horn spread over distance in 5 km increments. Error bars represent the standard deviation

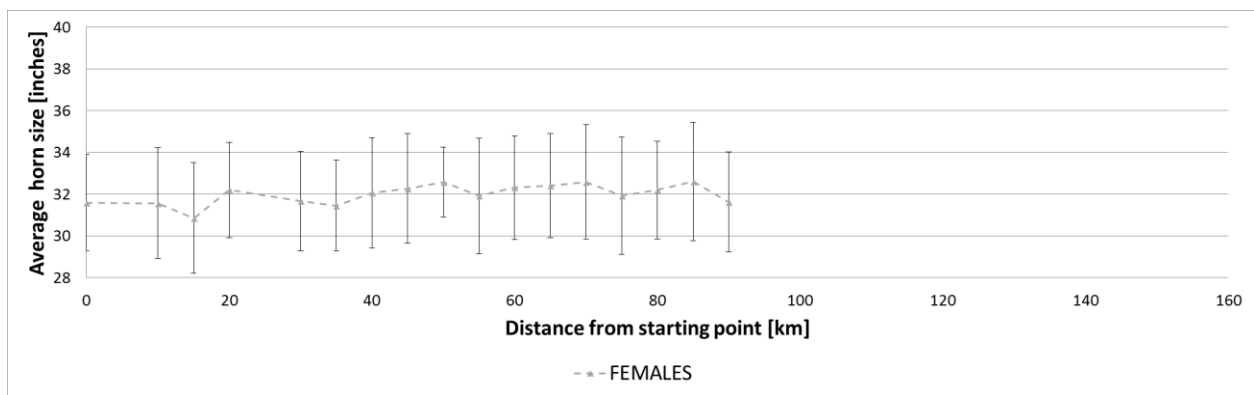


Figure 3 : Average female horn spread over distance in 5 km increments. Error bars represent the standard deviation

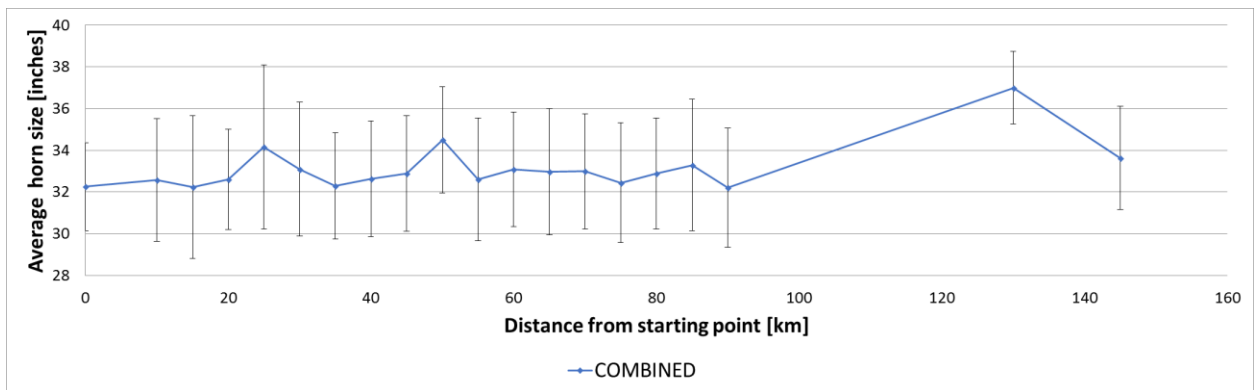


Figure 4 : Average horn spread of males and females combined over distance in 5 km increments. Error bars represent the standard deviation

The unpaired t-test also showed no significant difference in average horn spread between reserves that allow hunting, and areas that do not ($p=0.223$). The average horn spread from the hunted area in this analysis was 32.8 inches ($n = 630$), while the average horn spread in the non-hunted area was 32.9 inches ($n = 1197$). See figure 5.



Figure 5: Boxplot showing the average horn spread in areas with trophy hunting ($n=630$, $\bar{x} = 32.8$ inches) and areas without trophy hunting ($n=1197$, $\bar{x}= 32.9$ inches).

3.2 Age classes

Average male age was not found to increase as distance increased, as is evident in figure 6.

Before breeding (BB) males were more prevalent overall ($n = 550$), while currently breeding (CB) and post breeding (PB) were far less common ($n = 103$ and $n = 11$ respectively). The variable “Distance” did not significantly improve the model fit ($\beta = 0.0059$, $p=0.600$), while “Herd ID” did ($p<0.005$). The mean age for males in bachelor herds was 8.175(S.D. = 0.38), which contrasts to lone males, which were on average 1.25 years older (S.D.= 0.54), and males in herds were on average 1.28 years younger (S.D.=0.25). The marginal r^2 was 0.152 and the conditional r^2 was 0.567, indicating a large contribution of the random effects of photographer, unique herd ID and reserves to the model fit.

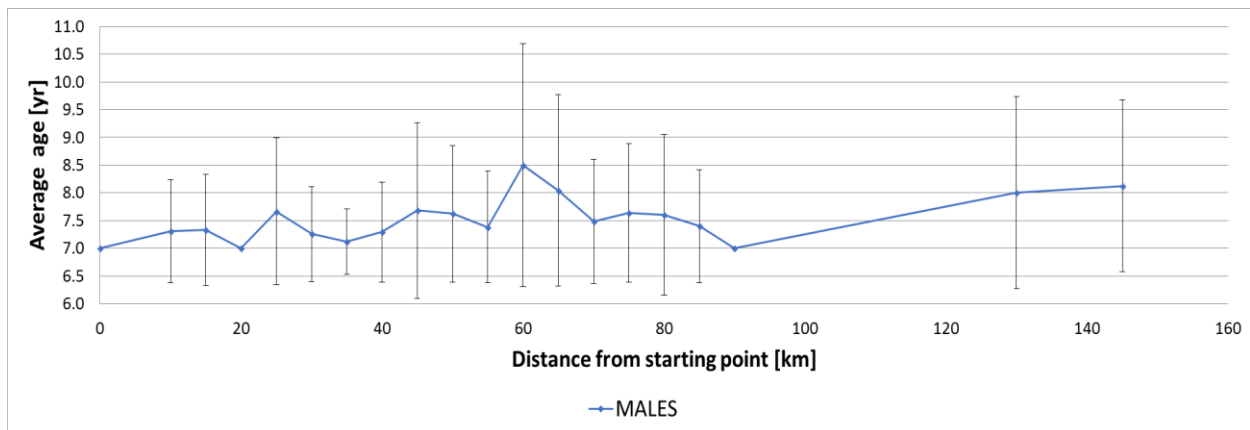


Figure 6 : Average male age over distance in 5 km increments. Error bars represent the standard deviation

3.3 Herd identity

Distance was a significant explaining factor for herd identity, with bachelor herds or lone males being 1.26 more likely to be encountered for every increase in distance unit. (Log odd = 0.23755, odds ratio = 1.2681, z value = 3.697, 95 % CI= 1.1422 – 1.5816). The intercept was also significant at log odd of -21.89, indicating the chance of finding lone males or bachelor herds at distance zero being almost nil. The probability of encountering a lone male or bachelor herd is plotted in figure 7. The marginal r^2 was 0.1724, suggesting that the fixed effects alone did not fit the model very well. The conditional r^2 was 0.9769, indicating the importance of the addition of the random effects of photographer and reserve where buffalo were found.

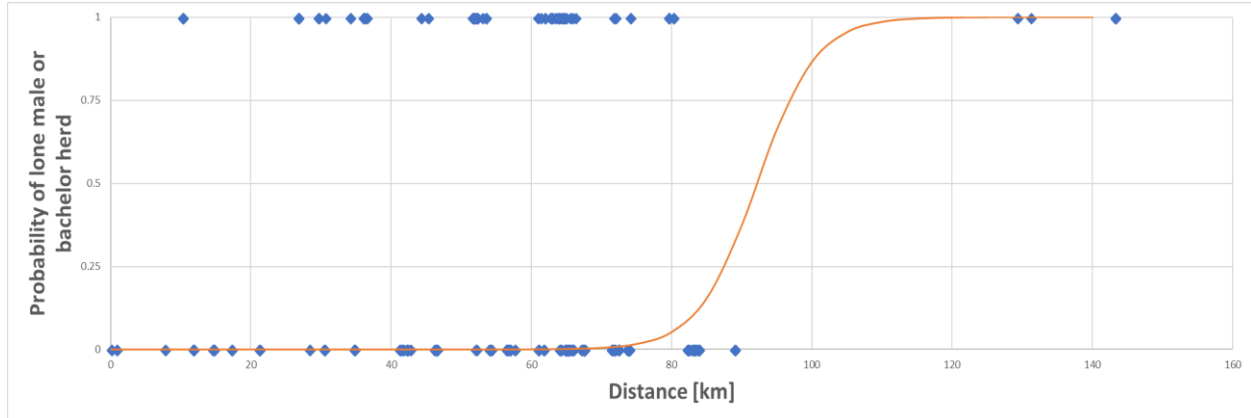


Figure 7 : The probability of encountering a lone male or bachelor herd over distance from hunting areas.

4. Discussion

This research aimed to establish whether there was a relationship between trophy hunting and genetic and demographic changes in a population of wild cape buffalo. Results indicate that distance was not a significant indicator of horn spread or male age, but the chances of encountering a lone male or bachelor herd did significantly increase with every kilometer increase away from hunting areas. These results will be further discussed in the following paragraphs.

4.1 Results

Horn spread

The results obtained in this study suggest that there is no obvious relationship between hunting pressure and horn spread, as there was no gradient in horn spread across distance and no significant difference in average horn spread between areas with and without trophy hunting. This result corroborated that of Muposhi et al, which found no measurable effects on trophy size due to hunting (Muposhi et al., 2016). The only variable that significantly affected horn spread was sex, which is to be expected in a sexually dimorphic species (Ruckstuhl & Neuhaus, 2000). However, neither males nor females separately, nor when combined, showed any change as distance increased. As there were so many more females analyzed than males, they influenced the average horn spread substantially, lowering the combined average. The marginal and conditional r^2 are both fairly low, indicating an ill-fitting model, and implying that there are other explanatory variables that were not included in this research.

Male age

Average male age did not increase with increasing distance, thus suggesting that hunted areas did not have fewer currently breeding and post breeding males than areas without hunting.

However, whether a male belonged to a mixed herd, a bachelor herd or was a lone male significantly affected the predicted age. This makes sense as most males found in mixed herds are too young to breed or be without the herds protection (Wray, n.d.). Although population dynamics were not studied directly, the fact that no changes in male age were found would seem to indicate that trophy hunting would not cause any changes in population dynamics regarding natal sex ratio or overall male survival not directly related to harvesting. The conditional r^2 value for this model, while still not very high, indicated a large contribution by random effects of photographer and reserve. It is possible that some photographers were better at spotting lone males and bachelor herds, or that some reserves had better watering holes, where lone males and bachelor herds are often found (Wray, n.d.).

Chance of lone males or bachelor herds

The chance of encountering a bachelor herd or lone male was 1.26 times more likely for every kilometre away from the start point in the hunting area. Again, although significant, the marginal r^2 was quite low, indicating a less than perfect fit, and the random effects increased the fit substantially. The fact that bachelor herds and lone males are found more frequently as distance increases, and have a significantly higher mean age than mixed herds, is at odds with the fact that mean age does not increase as distance increases. This could be due to the fact that there appears to be no difference in how likely mixed herds are to be encountered, regardless of distance, and that these mixed herds bring down the average age, compensating for these apparent trends. Whether lone males and bachelor herds are more likely to be encountered in areas further away from hunting pressures could have several explanations. It can be hypothesized that, due to a behavioural adaptation, that as they are more likely to be hunted they have learned to stay away from these high-risk areas, something which has been shown in several species, but not yet studied in buffalo (Stillfried, Belant, Svoboda, Beyer, & Kramer-schadt, 2015). It could also be

that because they are in smaller groups and of the desired trophy quality, that they are hunted more and that there are fewer lone males and bachelor herds left in hunting areas.

All things considered, some of the results obtained in this study vary from some results obtained in similar studies, albeit on different species. If the results in this study represent the actual processes occurring under sustained hunting, then there are several theories that might explain these varying results, and the lack of overt effects of trophy hunting. It is possible that gene flow, environmental factors or hunting pressure influence population genetics and dynamics more than previously anticipated. These theories will be explored further in the following paragraphs.

4.2 Explanations for the lack of effects of trophy hunting on horn spread

Large gene flow between hunted and non-hunted populations

One of the reasons why the expected effects of trophy hunting were not found in this study could be because there is more gene flow than anticipated. Research into fission fusion (the breaking apart and formation of herds) events in buffalo has shown that buffalo form fluid groups, and that adult males in particular separate from one herd and join another randomly (Cross, Lloyd-Smith, & Getz, 2005; Wielgus et al., 2018). Fission fusion effects are more frequent during the rainy season, which took place during the period data was collected. A four-year drought preceded this study period, which could have exacerbated these fission fusion events, as diminished rainfall and the ensuing lack of water and deficient nutritional resources might have caused buffalo to increase their range and daily movement patterns. Buffalo are dependent on daily water, and as such must cover large areas if water is scarce. While herd home ranges typically vary between 100 km²-200 km², and their mean daily movement tends to be approximately 6.1 km, it is not outside the realm of possibility that this increased due to lack of resources. While the overlap between herd home ranges vary between 15-50% of their total ranges, one can imagine that with increased migration this will be closer to the higher estimate, with increased fission and fusion events, and subsequent mixing of herds and increased geneflow as a result (Conybeare, 1980). This potential increased migration might also have impacted the results by analyzing buffalo in areas where they are not usually found, if they had moved there due to drought related reasons. Waterholes are better tended to and are more numerous in the APNR than in Kruger, which might have drawn buffalo with larger horns from Kruger to reserves in the APNR. This could have confounded any gradient that might have been apparent otherwise by mixing separate populations into one large population.

Heredity and environmental factors as a driver of horn spread

Previous research has shown that horn and antler size in many animals is not just determined by genes, but that age and nutrition, and their potential interactions with genes, play an equal or sometimes even bigger role (Monteith et al., 2018). Age is of importance as in bovids, horn growth is a cumulative process over an animal's lifetime, and therefore their horns are largest when they are oldest (Monteith et al., 2018). This does not take wear into consideration, which is something that is especially relevant for buffalo (Robertson, pers. comm, January 2018). One of the most distinctive ways to tell a bulls age is by assessing how sharp the horn tips are, as they become blunter with increasing age (Pienaar, 1969). There are two ways in which nutrition can influence horn size structure, through direct environmental effects, and through maternal effects. The consequences of improved direct environmental effects have been demonstrated in a study by Hoefs and Nowlan (1997), where horn size of a captive and wild herd of Dall's sheep were compared. Although both originating from the same initial herd, the captive population received high quality feed, while the wild population did not. At the age of 7, overall horn size was 57% greater for the captive population than that of the wild population. The captive population also obtained a maximal basal circumference (33 cm) at age 4, while the free ranging males reached that

circumference at age 11. If resources differed enough over the study area so that different herds received different quality nutrition, some herds might have experienced faster and larger horn growth than herds and individuals that had access to nutrition of lesser quality. This could also be seen in maternal effects.

Maternal effects can be classified as a direct influence of the phenotype of the mother on the offspring's phenotype, and unrelated to the inherited genes (Monteith et al., 2018). Allocation of resources to their offspring during gestation have a large effect on offspring's later phenotype, and it is rare that individuals can compensate for a nutritionally deprived early start (Monteith et al., 2018). If buffalo cows consume food of lesser nutritional value, this affects their offspring even if their offspring moves to areas with better resources later in life, and thus can affect horn size and growth (Monteith et al., 2018). Heritability (the proportion of variability among individuals of genetic origin) of horn length for bighorn sheep has been estimated to be anywhere from 0.39 to 0.69, while red deer have an estimated heritability of antler traits ranging from 0.35 to 0.81. It is possible that heritability of buffalo horn spread is lower than expected, or that the nutritional value varied a lot over the study area, compensating for any selection for smaller horn spreads, or a combination thereof (Monteith et al., 2018).

Critical hunting pressure

It is possible no effects due to hunting were found because the hunting pressure was not high or consistent enough. Research has shown that for changes in parturition date (for example) a critical hunting pressure threshold needs to be reached before any measurable effects occurred (Gaillard, Servanty, Baubet, Brandt, & Gimenez, 2011). As access to hunting records was not granted for this area, this study had no clear and compiled data on how many buffalo have been hunted in each reserve, let alone on horn spread and age at the time of shooting. As such, there is no way to know for sure what intensity of hunting pressure these populations have been subjected to. Alternatively, it is possible that the hunting pressure has been constant over such a long time that the effects encompass the entire population and area. Local experts are adamant that bulls with horn spreads in the mid to high 40's range use to be far more common than it is now (Robertson, pers. comm, January 2018). Perhaps effects of trophy hunting on horn spread would be more apparent if comparing to historical data on buffalo populations. Nevertheless, given the large size of this population it is entirely conceivable that the hunting pressure as a means of selection was too weak to have any effect on the resulting horn spread.

4.3 Research limitations

As mentioned previously, the main limitation of this study was the lack of distinct populations undergoing different levels of hunting pressure. Given that Kruger and the ANPR constitute an open area, there is free movement possible between areas where buffalo are hunted and where they are not. This implies that there is no single population that is under consistent hunting pressure, although one can assume that the further away a herd is from the hunting boundary the smaller the odds are of them changing between these treatment areas. There were a number of other limitations to this study. Because there were occasions where there was a substantial amount of time between the gathering of data, and because the animals in question are not tagged or tracked, the possibility exists that some individuals have been photographed and assessed twice. Although the utmost has been done by the student to prevent this (and animals excluded if there was a possibility it was being doubly assessed) the possibility remains. Finally, the data acquisition method used (photographs) leaves a lot of room for assessment error, as well as a personal bias. As such, this research should be considered exploratory, and further research is needed to quantify what hunting pressures if any will have effects on buffalo, as further outlined below.

4.4 Future perspective (suggested research)

Further work is certainly required to disentangle these varying theories as to why there seems to be no effect on horn spread or population structure and dynamics due to trophy hunting. Based on the limitations of this study, one would suggest an experimental design.

To properly address any changes sustained hunting might have, it is imperative that there are properly defined and separated populations, preferably all coming from one original naive population and of a similar size and demographic. This ensures that all populations have similar baseline genetic variation and population dynamics. Secondly, it is vital to keep track of hunting pressures in the hunted areas, and changes in hunting pressure over time. This ensures that if there is a critical hunting pressure it can be determined, as well as the effects on genetic and population factors at differing hunting pressures. Thirdly, horn spread and population demographics must be analyzed frequently while animals are still alive so that any changes can be established on a more detailed timeframe.

Finally, as there is a possibility that no effects were found in this study because trophy hunting had already affected the entire studied population, a longer timeframe for follow up studies, or comparing to historical population data, might be necessary.

This should prevent any limitation that plagues this study, and as such provide a more definite grasp of the potential negative effects of trophy hunting.

4.5 Conclusions

Our data indicate that trophy hunting in an open system such as the Greater Kruger National Park does not necessarily lead to smaller horn spread, nor decreased mean male age; a result that casts a new light on current and future hunting regulations in the area. As mentioned previously, the APNR implement new hunting regulations at the beginning of 2018 (Appendix I). These state that any bull over the age of 12 may be shot, assuming it has fulfilled its reproductive potential. Bulls that have not yet contributed to the gene pool may be shot if they are under a certain horn spread range. While these regulations are a good way to preserve the genes that are in part responsible for larger horn spread, they are basically a form of artificial selection against smaller horned bulls. This is undoubtedly beneficial for the trophy hunting industry but might have unknown adverse effects if smaller horns increase fitness in ways not yet known. Although this research suggests that the current hunting pressure is not high enough to affect horn spread, it is possible this hunting pressure could increase with these new regulations as management might believe it will have controlled for any negative effects. As such, artificial selection against smaller horn spreads may occur. There are of course also ethical benefits of increasing the age at which animals are shot, allowing them to live in the wild for as long as possible might be considered a compromise by those who oppose hunting on moral grounds, while still acknowledging the conservation benefits associated with such practices. This study indicates that at current hunting pressures in the Greater Kruger National Park, there are no effects on either population genetics, nor changes in population demographics that could affect population dynamics.

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