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Assessing population performance of hunted impala and wildebeest in Simanjiro Plains, Northern Tanzania

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ABSTRACT

Human exploitation of wildlife is driving some species to severe population decline but, few studies examine the combined effect of hunting, environmental variability and demographic traits on population dynamics of hunted species, making it difficult to design sustainable hunting practices. In this study forty-five model scenarios defined by varying levels of hunting, female breeding and mortality rates, were used under Vortex population viability modelling program to assess performance of impala and wildebeest populations and to explore the management options to improve their population persistence. The resident impala population was predicted to suffer severe decline under most hunting scenarios when >2% per year of its population is killed, resulting in local population extinction within 15 years. In contrast, the wildebeest population did not decline at 5% current hunting rates due perhaps to its migratory behaviour that buffers the hunting impact but could go extinct within just 40 years when hunting rate in increased. Further, <10% environmental variability associated with the female breeding and mortality rates had considerable impacts on the population change and size under most hunting scenarios. Improving habitats and reducing hunting could improve female breeding rates thus ensuring the long-term survival of the ungulates in the Simanjiro plains, Tanzania.

Key words: Extinction risks - hunting pressure – poaching - population decline - population viability - savanna plains - Tarangire ecosystem - wild ungulates.

INTRODUCTION

Populations of large mammals in African protected and unprotected areas are experiencing declines caused by a range of factors including over-hunting and habitat conversion (Kideghesho *et al*. 2006, Craigie *et al*. 2010, Rija *et al*. 2020). There is a considerable debate whether commercial hunting is really benefiting conservation, with some supporting while others opposing. Legal trophy hunting has helped some populations to persist, increase or even recover after decline (IUCN 2016). On another hand, trophy hunting is known to harm hunted population locally, e.g., causing population decline and extinction in Saiga (*Saiga tatarica*) (Loveridge 2007; Milner-Gulland *et al.* 2001). The support for legal hunting particularly in some countries where the wildlife is still abundant, is based on the tenet that it generates revenues that are used to fund conservation especially in areas where conservation options are limited (Roe *et al*. 2020) and where protected species are still illegally harvested due to poverty (Rija *et al*. 2020). Revenues from legal hunting can protect wildlife against threats of habitat loss and poaching through financing law enforcement (Lindsey *et al*. 2012) and is useful for wildlife conservation particularly when carefully regulated (Lindsey *et al*. 2007). Further, legal hunting can also provide economic benefits to local communities and, therefore, become an incentive for them to support conservation efforts (Lindsey *et al*. 2007, Baldus and Cauldwell 2004,). However, illegal activities including poaching and habitat loss caused by illegal grazing and logging are a common problem facing many species including those subjected to legal hunting within protected areas (Rija *et al*. 2020). The impact of these threats together may affect population growth rates, mainly through reducing female breeding and survival rates of target species. Understanding the impact of poaching and variability of vital population parameters such as breeding and survival rates on a wild mammal population faced with the hunting pressure may be important for designing sustainable harvesting options in wildlife reserves.

The wildlife in less-strictly protected areas in Tanzania is managed with legal exploitation and yet is increasingly faced with pressures from illegal offtake and habitat fragmentation by humans (Bolger *et al*. 2008, Newmark 1996). There is limited information on illegal offtake, population size and trends of most hunted species as well as other contributing causes of animal mortalities in many wildlife reserves (Rija *et al*. 2020, Stoner *et al*. 2007). Moreover, decisions over the legal hunting are often made without considering the levels of offtake by illegal means as well as population growth of individual species under natural environmental conditions (Baldus and Cauldwell 2004). This poses a conservation dilemma and risks overhunting and, therefore, potentially causing population decline of exploited species.

The Tarangire ecosystem in northern Tanzania has sustained hunting activities for at least two decades. The ecosystem is made up of a network of protected areas and legal hunting reserves: national parks, game reserves and game-controlled areas (Rija and Hassan 2011). The Simanjiro plains in this ecosystem are wet season dispersal and calving areas for the wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) (Kahuranga and Silkiluwasha 1997). The Simanjiro plain lies within a game-controlled area - a category of less strict protected area designated for legal hunting of wildlife in Tanzania and that receives minimal protection from the wildlife authorities (Caro *et al*. 2009). The wildlife in this area, is under increasing pressure due to anthropogenic activities on wildlife habitats and illegal hunting (Bolger *et al*. 2008, Newmark 1996). These threats have caused marked decline in wildlife populations (Caro et al. 1998), yet the threats are increasing (Msoffe *et al*. 2011, Msoffe 2010), causing concerns over the sustainability of the wildlife species in these increasingly threatened wildlife areas.

Elsewhere, population viability analysis (PVA) studies have been useful in assessing impacts of human exploitation on the viability of large mammals such as elephant (*Loxodonta africana*) in southern Africa (Selier *et al*. 2014), manatees (*Trichechus manatus*) in Florida (Marmontel *et al*. 1997) and dugongs (*Dugong dugon*) in Australia (Heinsohn *et al*. 2004) and, thus, providing information for improving conservation of species in the wild. PVA provides a unique opportunity to assessing how wildlife harvesting (through legal or illegal means) and habitat threats interact together to influence the dynamics of wild ungulates. Here, population models are built to examine the viability of two exploited ungulate species; impala (*Aepyceros melampus*), and wildebeest using VORTEX 9.93, a computer-based population viability analysis (PVA) model (Lacy and Pollak 2014). It was hypothesized that: (i) population growth rates of impala and wildebeest will show no decline trend under the initial level of poaching and environmental variability but the impact will be higher under increased hunting level causing severe population decline and extinction (ii) species demographic traits will have stronger effect on the growth rate of both modelled populations than the levels of offtake and environmental variability combined. Because habitat fragmentation and loss due to increasing human agricultural activities have severe impact on the species vital rates mainly through increasing variability on the demographic rates, then assessing factors that affect ungulate population change and size could be particularly interesting for the wildlife managers for designing necessary strategies to improving conservation activities within and outside core protected areas where wild animals still thrive.

MATERIALS AND METHODS

Study site

This study was conducted in the Simanjiro plains located between 3^o 52’ S - 4^o 24’ S and 36^o 05’ E - 36^o 39’ E on the eastern side of Tarangire National Park (Figure 1). The plains comprise non-protected areas plus the Lolkisale and Simanjiro Game Controlled Areas (GCAs); and are important dispersal and calving range for the migrant wildlife from the Tarangire and nearby Lake Manyara National Parks (Kahurananga 1981).

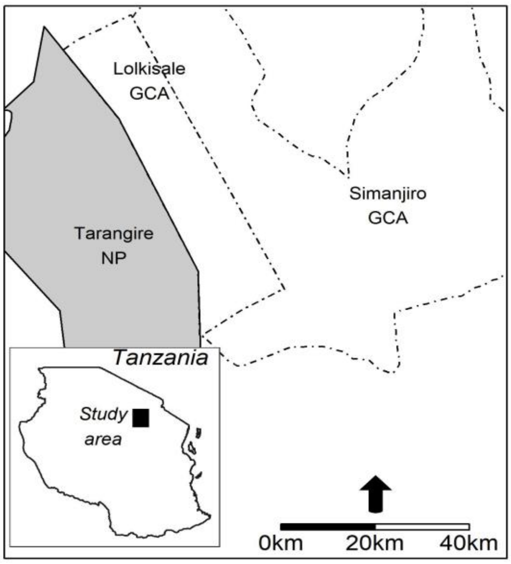

Figure 1. Map of the Simanjiro plains (Simanjiro and Lolkisale Game Controlled Areas) in the Tarangire ecosystem.

The wildlife species migrating seasonally into this area include, but not limited to, zebra, wildebeest, buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), and elephants. These animals spend over a half of the year grazing in this area. Resident game animals are impala, giraffe (*Giraffa camelopardalis tippelskirchi*), lesser and greater kudu (*Tragelaphus species*), Grant’s gazelle (*Nanger granti*) and warthogs (*Phacochoerus africanus*). The area is characterized by semi-arid savanna vegetation type with an average annual rainfall of 600 mm (Kahurananga 1979). The savanna trees in these areas are mostly of *Acacia* species mixed with *Combretum* species with characteristic short grasses forming extensive grass plains. Details of the vegetation type and structure have been described by Kahuranaga (Kahurananga 1979).

There are thirteen villages distributed in east outside of Tarangire National Park, all primarily inhabited by agro-pastoral Maasai communities. Extensive farming in these areas has shrunk important grazing areas for the wildlife, with potential negative impact on the population of wild mammals inhabiting these areas (Bolger *et al*. 2008, Newmark 1996). Further, the area serves as a hunting ground that has been divided into hunting blocks leased to licensed hunters by the Government. Formal licensed hunting for trophy and subsistence by tourist and resident hunters, respectively, is conducted each year during the hunting season - July to December and may extend time depending on reviews of hunting regulations. Illegal hunting is also common in the study area and extracts considerable numbers of animals per year (Rija 2009).

Study Species

Impala and wildebeest (Plate 1) are two antelope species that comprise wild mammal assemblage in the study area. The impala is mostly resident to the area while the migratory wildebeest annually move in and out from a strictly-protected area, Tarangire National Park, although some herds of wildebeest are resident in the study area (Rija pers. obs, 2020).

Impala (*Aepyceros melampus*)   Wildebeest (*Connochaetes taurinus)*

Plate 1: Images of wild ungulate species: impala and wildebeest, investigated in this study.

The demographic characteristics of these species vary considerably, from reproduction, mortality, population structure to the life span in the wild (Tables 2 and 3). Both species are classified as being of least concern on the IUCN red list book, however due to increasing pressures from hunting and alteration of their key habitats, they are increasingly prone to local extinction (Rija *et al*. 2020, Borger *et al*. 2008). Further, the study area is a crucial calving range for the wildebeest especially during the wet season when the species migrate outside of the park for breeding.

Sources of data

The initial population sizes were derived from field estimations by Rija and Hassan (2011) (Table 1). Illegal offtake levels used in this study were n = 178 for the wildebeest and n = 226 for the impala hunted per annum from the study area as estimated from results of previous studies by Kahurananga (1981), TAWIRI (1994 and 2001),and Rija & Hassan (2011). In the absence of life history parameters for the Tarangire ungulate populations, the simulation models used data published for these species from Serengeti ecosystem (Heinsohn *et al*. 2004). The Serengeti ecosystem closely matches Tarangire-Simanjiro ecosystem (Lamprey 1964) because they are similar in terms of plant phenology, local climatic conditions (rainfalls) and existing land-use types. Both Tarangire and Serengeti are protected areas and are in similar ecological regions receiving relatively similar annual rainfalls of 500 mm and 600 mm for Serengeti (south-east) and Tarangire, respectively (Grange and Duncan 2006, Mduma *et al*. 1999).

Table 1: Wildebeest and impala population estimates (with SD) in the Simanjiro plains from previous studies conducted using aerial census and ground distance sampling.

Species	1970*	1971*	1972*	1994**	2001**	2011
Wildebeest	977± 194	2146 ± 385	2873 ± 478	6976 ± 1863	4189 ± 2754	5199 ± 2670
Impala	164±84	105 ± 43	275 ±106	1298 ± 304	1546 ± 549	4534 ±1393

***Sources of data**:* * Kahurananga (1981), ** TAWIRI (1994 and 2001), ∞Rija and Hassan (2011*)*

The wildebeest population in Serengeti is regulated mostly by food supply (Mduma *et al*. 1999, Dublin *et al*. 1990, Sinclair and Norton-Griffiths 1982) suggesting that important population parameters may be similar to the Tarangire populations that is regulated by similar factors (Lamprey 1964). Data on the mortality of wildebeest from Serengeti (Grange *et al*. 2004) were used to derive the age mortality rates for the Tarangire population following Heinsohn *et al*. (2004). Fecundity data for the wildebeest were also derived from the data given by Grange and colleagues (Grange *et al*. 2004) and were used as surrogates for the Tarangire-Simanjiro populations. Further, for the impala population the vital parameters were derived from Ginsberg and Milner-Gulland (1994), Jarman and Jarman (1979) and Jarman (1973). The data on population characteristics sourced from the literature used in the population modelling are shown in Table 2.

Table 2. Life history parameters of the wildebeest from eastern Africa

Parameter	Range/values	Survival rate[c]
Age at 1st reproduction males	3-4 years	calf(1 year- 0.75
Age at 1st reproduction females	1.5-2 years[a]	Yearling - 0.85
Inter-birth interval	1.5-2 years	2- year old- 0.87
Mating system	Polygynous[a]	3-5 year old- 0.89
Number of young	1	mature female- 0.79
Sex ratio of young	63%[a]	old female- 0.78
Sex ratio of adult	32.8%[a]	
Annual mortality -juveniles	16-20%[a,d]	Fecundity rates[c]
Yearling mortality	1.3%[a]	2 - year old - 0.37
Annual mortality adult males	1.4-5%[d]	3-5 year old- 0.89
Annual mortality adult females	1.4-5%[b,d]	Mature female- 0.95
Maximum age	20a	old female- 0.95

Sources of data: a- Talbot & Talbot (1963), b- Mduma *et a*l. (1999), c- Grange *et al*. (2004), d- Baptist & Fink (1992)

Model Construction and assumptions

The life history parameters used for the wildebeest models are shown in Table 3. Fourteen models simulating the population dynamics of wildebeest were built in which the first model which allowed no harvest used all values presented and assumed the female fecundity rate to be 80% (Grange *et al*. 2004). In this and subsequent scenarios the population model assumed a stable distribution of age class because no data were available on the age structure of the Tarangire ungulates. However, the available data elsewhere indicate that fecundity for the Serengeti wildebeest is constant at age classes for females above five years old (Grange *et al*. 2004), perhaps supporting the assumption of a stable age distribution as it corresponds to the females' age of first reproduction of 3 years. To model this population, female breeding was reduced to 70% (Model 2) and increased the mortality values at age class one and two (yearlings) in Table 2 by 20%. This was because calf survival in Tarangire is approximately 20% lower than in the Serengeti wildebeest (cited in Talbot and Talbot 1963) perhaps due to high predation pressure on young in Serengeti (Grange *et al*. 2004).

Table 3: The life history parameters of wildebeest as recorded in literature, and the values used in models in this study.

Parameter	**Range/value**	**Values used**
Age at first reproduction for males (yr)	3.0 - 4.0	4
Age at first reproduction for females (yr)	2.0 - 3.0	2
Mating system	Polygynous	Polygynous
Number of young	1	1
Fecundity rate	0.37-0.95	0.7,0.8
Sex ratio of young (M/F)	0.5	0.5
Annual mortality (first year)	0.16 - 0.25	0.21
Annual mortality (yearling)	0.11	0.11
Annual mortality (2 year old)	0.13	0.13
Annual mortality (3-5 year olds)	0.11	0.11
Annual mortality (6-10 year olds)	0.21 - 0.28	0.21
Annual mortality (adults)	0.22 - 0.37	0.22
Maximum age (yr)	20	18

In subsequent models (Models 5-14), hunting was introduced into the model under varying female breeding and mortality rates as explained above. In these models, hunting was first set at the assessed kill of 178 individual wildebeest per year from illegal hunting under the maximum possible female breeding rates of 80% and 70% (Models 5, 6). Mortality rate was increased by 10% across all age classes and kept constant all other parameters as in the previous models to test the effect of mortality on the population change and overall size with potential extinction levels (Models 7, 8). In models 9 and 10, the models assumed the hunting level to increase by 50% of the current rate to reflect increased demand for bushmeat due to increased human population size and when legal hunting quota is potentially increased (Msoffe 2010, Baldus and Cauldwell 2004) and modelled the target wildlife population under the two levels of female breeding rates.

In the succeeding models (Models, 11 and 12) an additional 10% mortality was imposed across all age classes and breeding rates also to simulate an increase in demand for wildebeest bushmeat and trophy by both legal and illegal hunters in the area. In the last models (Models 13, 14), the impacts of hunting were examined by doubling the current hunting rate under the two levels of female breeding rates. In these models, the wildebeest population was simulated by increasing mortality (as above) on initial mortality rates similar to other models above.

To understand sensitivity of the modelled population to environmental variability, 5% and 10% variability rates were set on the initial population parameters. This reflects effects of rainfall variability and recurring droughts in Simanjiro, respectively (Msoffe 2010) on the life history parameters such as birth, breeding, recruitment and mortality rates. These levels also introduce some variability into the model simulations as most estimates of vital parameters do not provide variability estimates. Furthermore, there are no estimates of carrying capacity for any of the Tarangire wild mammal species. For this species, the carrying capacity was set at twice its initial population size following previous studies (Selier *et al.* 2014, Heinsohn *et al.* 2004). The population was thus modelled under density independence and the initial population size set at 5199 wildebeest (Rija and Hassan 2011) because the population is currently large for inbreeding to occur. Notable catastrophes in the study area include severe droughts (Msoffe *et al.* 2011) which, as observed in the -Serengeti-Mara ecosystem (Ogutu *et al.* 2008; Serneels *et al.* 2001) may lead to marked population decline of wildlife and delayed recovery due to drought-induced insufficient food resources. Field observations in Tarangire-Simanjiro ecosystem indicated a usually lowered calf dropping rate by wildebeest due to food shortages associated with severe droughts (Rija 2009).

Accordingly, 5 and 10% variability were set to simulate reduced reproduction and recruitment of wildebeest because of catastrophes. Further, sex ratio at birth was considered to be uniform i.e., 50% following previous studies (Talbot and Talbot 1963). Furthermore, the effect of supplementation on population dynamics was assessed due to natural migration of wildebeest from and to Tarangire National Park during the calving period (Kahuranga and Silkiluwasha 1997). The wildebeest population simulation started with an initial population size of 5,000 animals using an annual time step. All simulations were run for 100 years and for 200 iterations each. The simulations started in year 2020 onwards for a maximum of 100 years.

For impala, a density-independent model characterising the population dynamics was constructed using data in Table 4. Fecundity in impala is considered to be 70% and 90% in the first and later years, respectively (Ginsberg and Milner-Gulland 1994). Males were assumed to start breeding at the age of five with only 30% of them participating in the process (Jarman 1979, Jarman and Jarman 1973). The model assumed a maximum of 80% fecundity on average for all females and an alternative fecundity rate of 70%, 50%, 30%, 10%. Yearling males (1-3 years old) experience twice as high mortality as females (Jarman and Jarman, 1973, Dasmann and Mossman 1962), so in the model input, the mortality of males at this age class was double that of females. A similar procedure as that described for the wildebeest above was used to build fifteen simulation models for the impala population. A 10% increase in the mortality rates was imposed across all age classes to examine its impacts on the population dynamics. However, in models 8-14 inclusive, hunting was varied in a decreasing order of magnitude - 6%, 4% and 2% of the current population size. This simulated hunting options likely to sustain this species in the area. The impala population model incorporated catastrophes as explained for the wildebeest model analyses. Similar to the wildebeest, the impala population simulations used an annual time step, with an initial population size of 4500 animals (Rija and Hassan 2011). The simulations started in year 2020 onwards for a maximum of 100 years. Across the simulation, a population was considered extinct when it died at any time along the simulation process and showed extinction probability of one. Also, model results showed mean population change (r), probability of extinction (ranging from 0-1), time to species extinction (i.e., when a population indicated potential for extinction and overall population size at the end of the simulation time

Table 4: The life history parameters for impala as recorded in literature and the values used in models in this study (See text for data sources).

Parameter	Range/value	Values used
Age at first reproduction for males (yr)	2	5
Age at first reproduction for females (yr)	2	2
Mating system	Polygynous	Polygynous
Number of young	1	1
Fecundity rate	0.7-0.9	0.7, 0.8
Sex ratio of young (M/F)	0.5	0.5
Annual mortality (first year)	0.4	0.4
Annual mortality (2 year old)	0.1 - 0.2	0.1
Annual mortality (3 year olds)	0.05	0.05
Annual mortality (4-5 year olds)	0.03	0.05
Annual mortality (6-8 year olds)	0.05	0.25
Annual mortality (adults)	0.2 - 0.6	0.25
Maximum age (yr)	13	11

RESULTS

Pattern of population dynamics and effect of hunting

The models performed as expected that, in the absence of harvest, the simulated populations of wildebeest and impala would survive for 100 years under models 1-4 inclusive (Tables 5 and 6). The mean population sizes for both species would stabilise under a ‘no hunting’ regime and would remain just below the assumed carrying capacity but above the initial population sizes for all the species. The population of wildebeest would grow at a significantly higher rate than impala.

The introduction of harvest into the model systems resulted in considerable changes of mean population sizes to all the species (Models 5-14 inclusive, Tables 5 and 6, Fig 2). Under initial harvest levels, only one of the simulated wildebeest populations became extinct (after 26 years) under the current hunting rate of approximately 5% of the initial population size (Model 8, Table5).

Table 5: Vortex simulation models for wildebeest population under different hunting scenarios showing the population growth (r ± SD), probability of extinction, mean extinction time and mean final population (±SD). FB= female breeding rate (%), M= mortality rate (%).

Model	Description	Mean population change (r)	Probability of extinction	Mean extinction time (yr)	Mean final population size
1	no hunt, 0.8 FB	0.095 ± 0.062	0	-	10301 ±536
2	no hunt, 0.7 FB	0.071 ± 0.063	0	-	10260 ± 498
3	no hunt, 0.8 FB,+10%M	0.076 ± 0.064	0	-	10212 ± 554
4	no hunt, 0.7 FB,+10%M	0.053 ± 0.065	0	-	10037 ± 544
5	hunt=271, 0.8 FB	0.078 ± 0.063	0	-	10267 ± 566
6	hunt=271, 0.7 FB	0.054 ± 0.064	0	-	10110 ± 539
7	hunt=271,0.8 FB,+10%M	0.059 ± 0.065	0	-	10137 ± 570
8	hunt=271,0.7 FB,+10%M	0.034 ± 0.066	0.01	26.0	9833 ± 1193
9	hunt=407, 0.8 FB	0.070 ± 0.065	0	-	10247 ± 531
10	hunt=407, 0.7 FB	0.043 ± 0.068	0.04	22.0	9551 ± 2080
11	hunt=407,0.8 FB,+10%M	0.050 ± 0.067	0	-	10049 ± 687
12	hunt=407,0.7 FB,+10%M	0.015 ± 0.082	0.34	24.4	6456 ± 4741
13	hunt=542,0.8 FB,+10%M	0.034 ± 0.081	0.27	14.0	7143 ± 4406
14	hunt=542,0.7 FB,+10%M	-0.029± 0.122	0.85	16.1	1369± 3355

Table 6: Vortex simulation models for the impala population under different hunting scenarios showing the population growth (r ± SD), probability of extinction, mean extinction time and mean final population (±SD). FB= female breeding rate (%), M= mortality (%).

Model	Description	Mean population change (r)	Probability of extinction	Mean extinction time (yr)	Mean final population size
1	no hunt, 0.8FB	0.061 ± 0.062	0	-	8888 ± 483
2	no hunt, 0.7FB	0.036 ± 0.061	0	-	8635 ± 491
3	no hunt, 0.8FB, + 10%M	0.038 ± 0.065	0	-	8705 ± 621
4	no hunt, 0.7FB, + 10%M	0.013 ± 0.064	0	-	7770 ± 1188
5	hunt=301, 0.8FB	0.034 ± 0.069	0.06	34.8	8123 ± 2158
6	hunt=301, 0.7FB	-0.029 ± 0.118	0.76	35.9	1706 ± 3206
7	hunt=301, 0.8FB, +10%M	-0.027 ±0.130	0.75	36.5	1896 ± 3400
8	hunt=301, 0.7FB, +10%M	-0.108 ± 0.154	1.00	9.3	0
9	hunt=208, 0.8FB	0.038 ±0.065	0.01	72	8699 ± 1046
10	hunt=208, 0.7FB	-0.038 ± 0.167	0.69	49.7	1947 ± 3188
11	hunt=208, 0.8FB, +10%M	-0.011 ± 0.133	0.45	57.4	4169 ± 4026
12	hunt=208, 0.7FB, +10%M	-0.124 ± 0.257	1.00	32	0
13	hunt=104, 0.7FB, +10%M	0.1027 ± 0.065	0	-	8498 ± 639
14	hunt=104, 0.7FB, +10%M	-0.033 ± 0.137	0.6	67.3	1911 ± 2816

By contrast, the impala populations struggled under the current hunting rates. Six percent of the simulated impala populations became extinct under the present hunting regime of 6% of population size (Model 5; Table 6) and, alarmingly, a small reduction in female breeding rate (from 80% to 70%) resulted in 76% of the simulated populations crashing. The addition of a further 10% mortality resulted in total population collapse (Models 7, 8; Table 6).

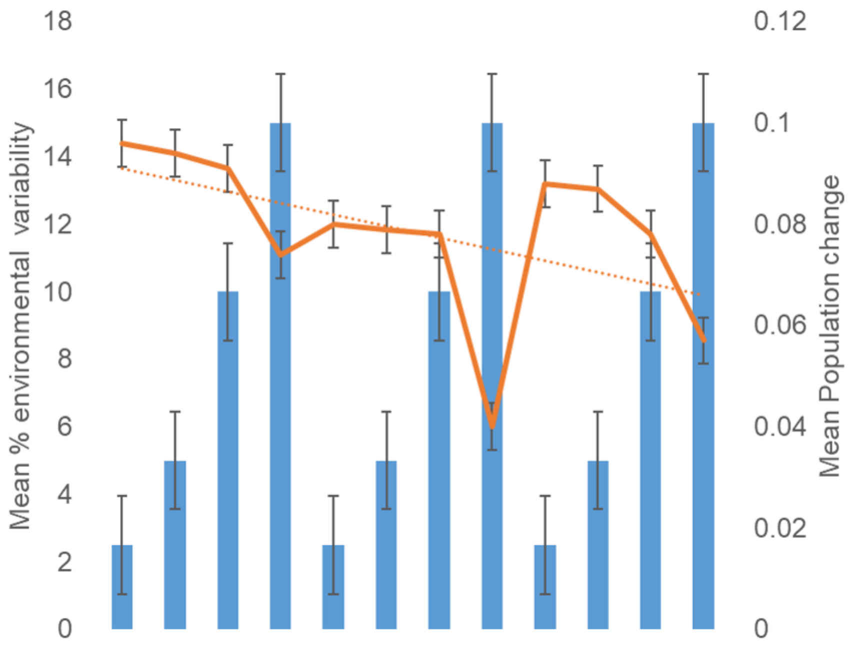

Figure 2. Mean (+ error) population change of wildebeest showing effect of environmental variability on the population faced with harvesting rates. Line graph shows mean population change under different levels of variability (blue bins).

Furthermore, when the harvest levels were changed to simulate an increase or decrease in offtake for these species, their populations responded differently. For the wildebeest whose hunting was simulated to increase above the present offtake, 4% of the populations became extinct in the mean time of 22.0 years (Models 9-12, Table 5). The populations of impala still declined to extinction when the hunting rates were reduced to 4.6% of its current population size (Models 9-12 inclusive; Table6). The population of all species changed considerably with a further increase or decrease in the levels of offtake. The probability of extinction was high (*P*=0.85) for wildebeest when the hunting rate was doubled, about 10.4% of its population size (Models 13-14, Table 5). Even if the offtake of impala was reduced to approximately 2% of its population size, 60% of the simulated populations would still become extinct.

Influence of mortality and fecundity rates on population dynamics

The simulated populations of both species appeared to be strongly influenced by the fecundity and mortality rates used. In wildebeest and impala, the 10% variation in their fecundity and mortality rates had little effect in the absence of harvest (Models 5, 3; respectively, Tables5 and 6). The mean final population sizes for these models decreased by 0.4 and 2.8% from model four to model three for the wildebeest and impala, respectively. Furthermore, under the same hunting regime (Models 3 and 4, Tables 5 and6) an increase in mortality rate by 10% across all the age classes decreases the population sizes of impala but not wildebeest.

Sensitivity test

Unlike impala, the population of wildebeest did not change under the lower levels (i.e., 2.5 and 5%) of these variations and the population survived to the last year of simulation (Table 7). The probability of survival decreased markedly at higher levels i.e., 10-15%. Increase of calf and yearling (2-years old) mortality rates by 10, 20 and 30% on initial levels did not affect the rate of survival of the wildebeest population (Table 7). However, the mortality affected growth rate of this population, – showing decreasing trend with every increase of the mortality rates (λ = 1.072, 1.064 and 1.053, respectively) and, therefore, making this population more prone to extinction (Figure 3).

Table 7: Sensitivity of survival rates to increases of mortality (calf and yearling) and variation of mortality and fecundity rates in wildebeest. CM= calf mortality (%).

Model	Description	Mean population change (r)	Probability of extinction	Mean extinction time (yr)	Mean final population size
1	No hunt, 2.5% variation	0.096 ± 0.031	0	-	10367 ± 275
2	No hunt, 5% variation	0.094 ± 0.063	0	-	10271 ± 488
3	No hunt, 10% variation	0.091 ± 0.129	0		9656 ± 1362
4	No hunt, 15% variation	0.074 ± 0.211	0.01	57	8115 ± 2619
5	hunt =271, 2.5% variation	0.080 ± 0.033	0	-	10389 ± 241
6	hunt = 271, 5% variation	0.079 ± 0.064	0	-	10343 ± 551
7	hunt = 271,10% variation	0.078 ± 0.069	0.03	15	9271 ± 2240
8	hunt = 271, 15% variation	0.040 ± 0.233	0.4	52	4407 ± 4267
9	hunt = 90, 2.5% variation	0.088 ± 0.032	0	-	10419 ± 269
10	hunt = 90, 5% variation	0.087 ± 0.062	0	-	10237 ± 473
11	hunt = 90,10% variation	0.078 ± 0.133	0	-	9250 ± 1272
12	hunt = 90, 15% variation	0.057 ± 0.215	0.07	72	7411 ± 3537
13	No hunt, +10% CM	0.086 ± 0.063	0	-	10324 ± 327
14	No hunt, +20% CM	0.077 ± 0.064	0	-	10307 ± 319
15	No hunt, +30% CM	0.069 ± 0.064	0	-	10234 ± 336

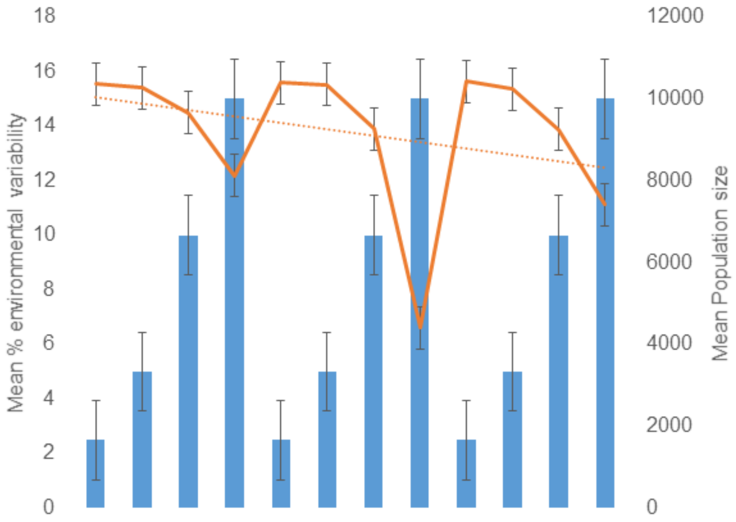

Figure 3. Effect of environmental variability and harvest rates on the population decline of wildebeest based on models interacting hunting rate and variability in resources. Mean expressed with standard errors, bins are environmental variation, and line indicate population data.

DISCUSSION

The simulation models suggest that the impala population is susceptible to present levels of harvest and is at great risks of severe decline. Even for wildebeest whose simulated populations appeared to withstand the current levels of hunting, severe population declines would occur if harvesting is increased above their current levels, though immigration still reduces the severity of population decline. If these models are, or nearly correct, then the impala population will decline towards extinction within a relatively short time (15 years) in the Simanjiro plains. These results corroborate recent findings in the Serengeti National Park on increased risks of decline for giraffe and buffalo populations (Rija 2017). Illegal and legal hunting have been implicated in causing declines of large wild mammal populations across large parts of Tanzania including the study area (Caro *et al.* 1998).

Although legal hunting is meant to be highly selective for adult males, in the presence of high offtake by residents and trophy hunters, this strategy may be flawed. Without supervision and with opportunistic poaching, both males and females would be hunted, thereby, increasing total offtake and directly reducing the number of animals in the area. Skewed sex ratio among the populations of impala and wildebeest in the Serengeti National Park has been associated with increased stresses of illegal hunting (Marealle *et al*. 2010). Further, as reported in the present study, sex ratio may have far reaching impact on the reproductive ability and population growth of these species.

Adoption of selective hunting as a way of sustaining the breeding potential of exploited populations is still debated. Selective hunting of adult males has caused retarded female conception and reproductive collapse in Saiga antelopes (*Saiga tatarica*) (Milner-Gulland *et al*. 2003; Milner-Gulland *et al.* 2001). Further, disproportionate hunting of prime males of sable antelope (*Hippotragus niger*) in northern Zimbabwe has also been associated with the reduced survivorship of the young animals due to extended parturition period and for causing a population decline (Fergusson 1990 in (Ginsberg and Milner-Gulland 1994)). In impala population, Ginsberg and Milner-Gulland (Ginsberg and Milner-Gulland 1994) reported unsustainable hunting to have resulted from selecting adult males. Furthermore, the term ‘adult male’ is a loose term especially during the actual hunting process in the field. Due to the difficulty of ageing animals in the field, active prime males would almost certainly be killed as has been observed in the Simanjiro area (Rija 2009). This could result in retarded female conception and young survival, although it is still unclear as to what level, this may apply in the hunted populations. However, these hunting models strongly suggest that the manipulation of sex ratio occurring in hunted populations could lead to reduced fecundity and high probability of population collapse. This is consistent with previous findings from elsewhere (Ginsberg and Milner-Gulland 1994; Gruver *et al*. 1984).

Environmental variability (EV) associated with the female breeding, recruitment and mortality rates showed considerable effect on the population change and overall size. Habitat loss, drought and diseases may impose strong constraints on the breeding, recruitment and overall mortality of young and adults. Habitat loss reduces food and cover required for reproduction and survival of most wild animals, thereby affecting population size. In the study area, habitats for most species have shrunk due to agricultural farming expansion into their grazing range (Bolger *et al*. 2008). Loss of rangelands will first impact on the migratory wildebeest negatively, while when coupled with increased illegal and legal hunting will mostly hasten both species into the extinction pit (Kidegheso *et al.* 2013). It is thus necessary to prioritize on improving habitat conservation in these areas lest the wildlife in them will continue to decline with impunity.

The results of this study highlight the need for immediate policy interventions to regulate hunting of impala population in the Simanjiro plains. The current harvest level of 5% for impala is unsustainable and needs to be reduced to at most 2% of its present population size to avoid any risks of local extinction. The current simulation models suggest that this species would persist to 100 years and beyond when the harvest is stopped or kept below 2% of population size. Reduction of total harvest of wildebeest is also recommended. However, reducing the harvest levels alone will not serve these species for longer times. Instead, efforts should be made to greatly reduce habitat loss for these species as increasing extensive farming will block dispersal corridor for the wildebeest, reduce their size or wipe them out (Bolger *et al.* 2008). Therefore, policies pertinent to land ownership and agriculture should be reviewed to include measures targeted at retaining wildlife habitats and the dwindling movement corridors for the migrant wildebeest (Caro *et al.* 2009), this will ensure the sustainability of the wildlife in the Simanjiro plains and across the greater Tarangire ecosystem. Furthermore, poaching appears to remove large numbers of animals many times more than the legal harvest (Rija 2009). This is the case since legal harvest, unlike poaching, involves setting hunting quotas and is conducted during the specified hunting season. While it may be difficult to completely halt poaching as poachers do not identify themselves, it is essential to combat this problem. Even complete banning of legal hunting will not lower the offtake to the level that these populations might be able to sustain. Banning of hunting may be more detrimental to populations of species given its role in generating revenues which are used to fund conservation activities along with providing economic incentives to local communities. Essentially, grass-root environmental awareness raising supported with improved livelihood strategies, enforcement of protection rules, and community involvement in conservation of wildlife should be employed, and should include the areas that are not formerly protected. Policy shift in favour of protecting the wildlife on such areas needs more emphasis.

CONCLUSION AND RECOMMENDATIONS

This study has identified that the simulated populations of these species are mostly sensitive to fecundity and natural mortality rates across all age class and to the annual variability associated with them. This study recommends improving the wildlife habitats that have strong influence on the population demography of various wild mammal species. Also, regulating hunting by the relevant authorities and improving law enforcement to reduce the levels of animal offtake from both legal and illegal causes are likely going to reduce the species risks to population decline. Further, the wildlife managers will need to have an up-to-date information on the population size and trend of the wildlife species to enable the appropriate decisions on the allocation of the hunting quota for each species. Such data will be generated easily by the wildlife rangers themselves using ground survey methods such as Distance sampling. Population monitoring will thus require building the capacity of the field rangers to conduct ground counts of the game species on their protected areas.

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