

**Modelling population dynamics of the African Buffalo *Syncerus caffer* using data on
population estimates, harvest and rainfall from the Selous – Mikumi Ecosystem,
Tanzania**

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Abstract

Knowledge on the population dynamics of African buffalo is a prerequisite for developing its successful harvest strategy. Acquiring such knowledge requires among others the use of population models which reveals important demographic information and suggests some management actions to be taken. This study aims at developing an understanding on how to take population estimates and influences of rainfall into account when developing harvest strategy. I hypothesize that annual quota would be influenced by population estimates and that population estimates would be influenced by rainfall. I used data on the buffalo population estimates, annual quota, harvest, and rainfall as well as survival and fecundity rates obtained from different sources. The study employs the use of the package **Popbio** in the statistical program **R**, to construct and analyze an age-specific Leslie matrix population model. Tracing study on the increase phases of the Selous – Mikumi population estimates reveals that high annual average growth rates 1.16 and 1.34 could be explained by stable and unstable age distribution respectively. Results suggest population growth is sensitive to changes in survival and fecundity rate of adults and juveniles. Annual harvest level is controlled by the annual harvest quota, which is set independently on the amount of rainfall and population estimates. This study shows empirically that age-specific population estimates provide detailed demographic information, which could be used to make informed decisions. I recommend the use of the method that estimates detectability and is capable of providing age and sex specific demographic information, which would facilitate identification of the causal factors overriding population changes. Finally, in order to halt buffalo population decline it is important that harvest strategy should not allow harvesting of adult and juvenile age class, instead calf, sub-adult and senescent age classes could be harvested.

Introduction

The ultimate goal of successful management of harvested wildlife populations is to find a harvesting strategy that is sustainable and which result in annual yields, with little variation among years (Aanes, Engen, Sæther, Willebrand, & Marcström, 2002). Attaining this goal requires an in-depth knowledge of population dynamics, which is the science of describing and understanding changes in populations over space and time or analyzing why populations do not change but have reached some kind of equilibrium (Engen & Sæther, 1998). African Buffalo like other animals are subjected to population changes and are particularly sensitive to changes in weather (Douglas & Leslie, 1986; Owen-Smith, 1990 & Picton, 1984). Portier, Festa-Bianchet, Gaillard, Jorgenson & Yoccoz (1998) suggest that rainfall and population estimate data could be used in population models to make realistic projections of population changes.

African buffalo are gregarious animals forming groups of up to 1,000 individuals per herd (Winnie, Cross, & Getz, (2008). African buffalo are selective feeders in the rainy season and feed unselectively during dry season (Sinclair, 1977). They are categorized as a species of “least concern” and inhabit a wide range of habitats in sub-Saharan Africa (IUCN SSC Antelope Specialist Group, 2008; Simonsen, Hans, Siegismund, & Arctander, 1998). Their current range is fragmented and confined in protected areas (IUCN SSC Antelope Specialist Group, 2008). Their population size and distribution is primarily influenced by rainfall and diseases (Sinclair, 1977; Skinner & Chimimba, 2005). They normally produce one offspring after a mean gestation period of 340 days and can breed all year around, but when water is scarce their birth season is synchronized during the rainy season (Brocklesby, & Robertshaw, 1963; Carmichael, Patterson, Grager, & Breton, 1977; Sinclair, 1977; Skinner and Chimimba, 2005). The weaning period ranges from six months (Buchholtz, 1990) to 15 months (Skinner and Chimimba, 2005). During the weaning period the mother can remain anoestrus and

produces milk until the calf starts to live independently (Skinner and Chimimba, 2005). The inter-birth period ranges from 15.1 months (Sinclair, 1997) to 24 months (Kingdon, 1997). However, fecundity rates may vary between years depending on the prevailing weather conditions; reports show that under suboptimal conditions buffalo give birth every other year (Pienaar, 1969). They reach sexual maturity at the age of 3.5 to 5.5 years, but males become actively involved in breeding activity only when they reach 7-8 years old (Sinclair, 1977). African buffalo can live up to 20 years in the wild and up to 29 years in captivity (Jones, 1993). Sinclair (1977) found that the amount and distribution of rainfall influence the buffalo survival. Pienaar (1969) reported that calf survival rate is very low and only 30% to 45% will survive to maturity.

Ecologically, buffalo play important roles such as feeding facilitation, nutrient cycling and being hosts to a multitude of pathogens and parasites as well as a preferred prey to lions in many African savannah ecosystems (Jolles, 2005; McNaughton, Prins, 1996; Ruess, & Seagle, 1988; Sinclair, 1977). Economically, African buffalo is of paramount importance as far as tourist hunting industry in Tanzania is concerned. It is the highest ranked priority species for income generation contributing to about 13% of the total earned by the Wildlife Division. Buffalo is the most preferred game species to be hunted and approximately 1.5 animals are shot per client that visits the Selous Game Reserve (Baldus & Cauldwell, 2004). Baldus & Cauldwell (2004) reported that the future of the Selous Game Reserve as hunting destination depends on a healthy buffalo population.

The buffalo population is affected by droughts, diseases and poaching (Sinclair, 1977; Skinner & Chimimba, 2006). Buffalo is a favourite bush meat in many parts of Africa, making it susceptible to poachers (IUCN SSC Ungulate Specialist Group, 2008). Drought and its subsequent effect on food supply have been reported to be the main limiting factor

regulating the buffalo population (Sinclair, 1977; Skinner & Chimimba, 2005). The effect of drought seems to be most pronounced when it interacts with diseases (East, 1999). Previous reports have shown that, buffalo population are threatened by a number of diseases including pleura-pneumonia and rinderpest (Winterbach, 1998), bovine tuberculosis (Jolles, Cooper, & Levin (2005), Anthrax (De Vos & Bryden. 1996), Foot and mouth diseases (Vosloo, Bastos, Sangare, Hargreaves & Thomson, 2002)

The hunting history in Tanzania dates back to 1961, when Game Department opened up Game Controlled Areas to hunting with the objective to increase earnings from wildlife (Baldus & Cauldwell, 2004). In 1965, hunting was permitted for the first time in the game reserves, including Selous Game Reserve. However, in 1973 sport hunting was banned through Government Notice No. 210 of 1973 (Nshala, 1999), and in 1978 sport hunting was reopened and all hunting activities were put under the control of Tanzania Wildlife Corporation (TAWICO). In 1988, corruption and poor management were evident, which compelled the government of Tanzania to withdraw mandate over the hunting activities from TAWICO and handed it over to the Game department (Baldus & Cauldwell, 2004). In 1980s, Tanzania experienced a rampant poaching which contributed to decline of many wildlife populations (Baldus & Cauldwell, 2004). The situation necessitated the government of Tanzania in 1988/9 to conduct a countrywide joint antipoaching operation (Operation Uhai) involving the Wildlife Division, Tanzania National Parks, the police force and the army. The outcome of this operation was the recovery of wildlife populations in Tanzania (Baldus & Cauldwell, 2004).

In Tanzania hunting is regulated by the Wildlife Conservation Act number 5 of 2009, which permits three types of hunting to be practiced 1) local hunting for citizen and resident non citizen, 2) traditional hunting for few recognized societies as hunter-gatherer, and 3)

sport/trophy hunting for tourists. Hunting is conducted in designated hunting blocks from the 1st of July to 31st of December each year, and only mature males are allowed to be hunted (Wildlife Conservation Act [WCA], 2009). Any person aged 18 years or more with a valid hunting permit and a licensed firearm can hunt (WCA, 2009). There are more than 60 species of wildlife that can be hunted in Tanzania (Baldus & Cauldwell, 2004). Annual hunting quotas for buffalo and other species are based on population estimates, proposals from game reserve's managers, outfitters and Professional Hunters based on long-term knowledge and experience (Severre, 1996). Annual hunting quota is set each year before the hunting season by a committee appointed by the minister responsible for wildlife resources (WCA, 2009). Nshala (1999) and Majamba (2001) argued that Tanzanian quota setting system does not provide the Wildlife Division with reliable information. Similarly, Stephens, Frey-roos, Arnold & Sutherland (2002) mentioned that lack of biological knowledge on exploited species, population status and the consequences of current harvest strategy can result in unsustainable exploitation.

Challenges associated with estimating population size poses severe constraints on our ability to develop appropriate harvest strategy (Getz & Haight, 1989), but developing a scientific based quota setting system is necessary (Nshala, 1999). Many studies on African buffalo population ecology and behaviour have been conducted in various locations across sub Saharan Africa (Grimsdell, 1969; Macandza, Owen-Smith & Cross, 2004; Mloszewski, 1983; Owen-Smith & Cross, 2004; Pienaar, 1969; Prins, 1996; Sinclair, 1977; Turner, Jolles & Owen-Smith, 2005; Vidler, Harthoorn, Brocklesby, & Robertshaw, 1963). However, little effort has been made to develop harvest strategies accounting for uncertainties and with a human dimension aspect in mind.

This study aims at developing an understanding of how to take uncertain rainfall and population estimates into account when developing harvest strategies. In addition, the study seeks to develop an understanding on how a bottom up approach could help to change harvest strategies towards sustainability. I hypothesize that annual quota would be influenced by population estimates and that population estimates would be influenced by rainfall. Data on the buffalo population estimates, vital rates, harvest and rainfall were used in this study. The package Popbio in the statistical program R was used to construct and analyze the Leslie matrix population model. Findings from this study would provide information which could help to improve management decisions.

Methods

Study area

The Selous - Mikumi Ecosystem covers an area of approximately 71,000 km². It is located in South - Eastern Tanzania within Latitude 7°17' to 10°15' South and Longitude 36°04' to 38°46' East. The ecosystem includes three protected areas of different categories, namely Selous Game Reserve (ca. 50,000 sq km), Mikumi National Park (3,230 km²), Kilombero Game Controlled Area (ca. 6,912 km²) and some areas outside protected areas (ca. 10,440 km²) Figure 1.

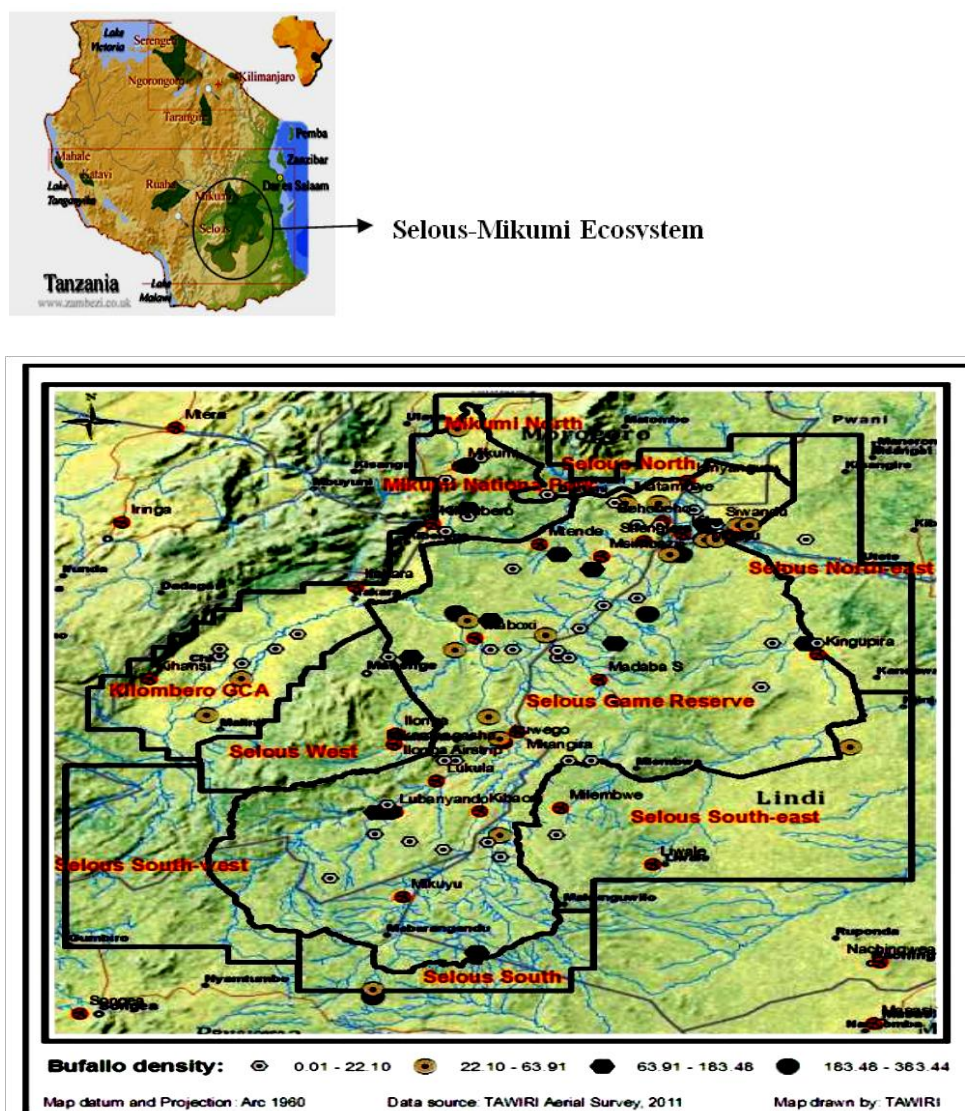


Figure 1. A map of the Selous –Mikumi Ecosystem showing buffalo distribution (Zambezi, 2008; TAWIRI, 2011)

The area is characterized by different types of habitats, including forests, woodlands and grasslands. In addition to that, the area has an extensive network of rivers and small lakes offering suitable habitat for buffalo. The area is considered to be the largest wilderness area under protection in Tanzania, with more than 2,000 plant species, 400 species of birds and 20 mammals and reptiles species (Tanzania Wildlife Research Institute [TAWIRI], 2011). It contains the largest populations of African elephant (*Loxodonta africana*), Puku (*Kobus vardonii*) and African buffalo in the world (TWCM, 1999; TAWIRI, 2002).

Population Monitoring

Buffalo population estimates were obtained from 8 aerial surveys conducted by TAWIRI in Selous – Mikumi ecosystem which is comprised of 10 census zones (Figure 1). These surveys were conducted during the dry season (post breeding surveys) from 1986 to 2011 using Systematic Reconnaissance Flight (SRF) method as described in Norton-Griffiths (1978). This method assumes that group detection probability consistently increases with the group size and that every individual in a group has an equal chance of being detected (Cook & Martin, 1974; Cook & Jacobson, 1979). These surveys aimed to assess population status, map their distribution, obtain population trend and estimating anthropogenic activities (e.g. farming, habitat destruction, encroachment and cattle grazing) over the ecosystem. The survey is made from an aircraft flying on a straight line at a constant altitude above the ground. The field of search is defined for the observers by two marks or streamers on the wing struts. Between these streamers, observers scan a strip of ground having a constant known width when an aircraft is at the surveying altitude (Table 1). Population size and density are then estimated; the latter is estimated as the numbers of animals seen on the strip divided by the product of strip width and transect length. During surveillance a single engine aircraft is flown by a crew of one pilot and three observers. As it flies along the transect line, 1 front seat observer and 2 rear seat observers record observations on the buffalo encountered in each sub

unit of the area, habitat characteristics, human activities, and the respective altitudes meter to the nearest 3 meters. The pilot is responsible for controlling height, navigate and record the beginning and end points of each transect by using GPS and flight lines drawn on maps using ArcView with coordinates written out for them to follow and mark as completed.

Table 1. Survey parameters used in aerial surveys in the Selous - Mikumi ecosystem for the 2002, 2006 and 2011 surveys (TAWIRI, 2008; TAWIRI, 2011)

Year	Aircraft Number	Flying Height (m)	Ground Speed (km/hr)	Transect spacing (km)	Transect length (km)	Mean Strip width (m)
2002	5H GNU	113	200	10	4.1	151
	5H MPK	120	198	10	3.57	181
	5H MPZ	120	220	10	3.1	169
2006	5H SGR	106	225	5	5.2	104
	5H MPK	112	192	5	7.3	90
2011	5H SGR	103	225	2.5-10	5.2	150
	5H TWR	110	192	2.5-10	7.2	159

Each transect was divided into sub units defined by 30 seconds of flying time, and the number of transects depended on shape of the area and wind direction. The pilot tried to avoid cross-wind flight lines which has effects on navigation, very short flight line or transects length which cause problems in statistical treatment of data, and very long (greater than 100km) flight lines/transects length that would cause observer fatigue. These recordings are then transcribed onto data sheets after each flight and finally data were entered in computers and analysed using special designed software developed at CIMU for SRF surveys (TAWIRI, 2011). In order to eliminate the effect of size differences in sampling units, population estimates were computed using the Jolly's Method (Jolly, 1969; Norton-Griffiths, 1978; TAWIRI, 2007; TAWIRI, 2011). The method computes total population size by multiplying

the area of the census zone and overall density of animals per unit area within the sample size (Jolly, 1969; Norton-Griffiths, 1978).

The **d-test** was used to test whether there was a significant statistical difference between two population estimates (TAWIRI, 2008; TAWIRI, 2011). The method is useful to determine whether the observed difference between two population sizes is probably due to actual change in animal numbers. This method assumes two estimates were drawn independently, and it is suitable for sample units greater than 30 (Norton-Griffiths, 1978). The method is based on degrees of freedom of the sample error and it does not take in to account any differences in bias between two estimates (Norton-Griffiths, 1978). Any resulting **d** greater than 1.96 confirms the two population estimates are statistically different from each other at 5% level (Norton-Griffiths, 1978).

The SRF method has a long history and has been widely applied in estimating animal abundance in East Africa (Gwynne & Croze, 1975). Jolly (1969) concluded the method allows collection of large quantities of data from extensive areas quickly and at a relatively low cost. However, the method is criticized for underestimating population size due to observation error caused by detectability, which is described as the failure to detect all animals in a given sampled area (Pollock & Kendall, 1987; Jolles, 2007). Caughley (1974) concluded that bias during aerial surveys is caused by aircraft speed, flying height and strip width that can reduce detectability. Additionally, Norton- Griffiths (1978) found that population estimates of the clumped or gregarious animals (e.g. buffalo) are also associated with sampling error. As pointed out by TAWIRI (2007), estimates of buffalo population size are problematic and difficult to use as a basis for quota setting.

Rainfall and food limitation

In order to assess the influence of rainfall on the buffalo population changes in the Selous - Mikumi ecosystem, rainfall data from 1991 to 2011 were used. These data were collected by Tanzania Meteorological Agency at different weather stations strategically positioned within the study area. Average annual rainfall was calculated and plotted against intrinsic rate of increase, $\log(\lambda)$ during the period intervening two counts.

The Leslie Matrix Population Model

The Leslie matrix is a model which assesses contributions of different age specific survival and fecundity rates in a population growth matrix (Leslie, 1945). The model provides useful insights which could be used to counteract population changes (Sinclair, Fryxell, & Caughley, 2006). In some literature the Leslie matrix is referred to as transition matrix (...). The model contains rows and columns in which survival rates and fecundity rates of different age classes are shown. The survival rates are arranged in a subdiagonal from one age class to another class across time interval and the fecundity rates are arranged on the top row of each age class in the matrix. Each column in the matrix represents age class. Columns represent the state of an initial time period t , rows represent the fate of an individual age class at time $t+1$. When constructing the Leslie Matrix you can assume either post birth pulse or pre birth pulse depending on the time where census estimates were taken. The matrix can be used to estimate stable and unstable age distributions, population growth rates and elasticities. At stable age distribution population grows geometrically and proportions of individual in each age class is constant (Sinclair et al, 2006). In this distribution population growth is a function of integrated combination of age dependent survival and fecundity rates (Sinclair et al, 2006). The function $eigen.analysis(A)$, is used to obtain stable age distribution (Stubben & Milligan, 2007). On the other hand, the Leslie matrix model can be used to obtain unstable age distribution before a stable age distribution occurs. Unstable age distribution is reached when

a population is exposed to perturbation, for instance a severe drought which kills all other age classes in a population, leaving a population with only mature individuals which have high survival and fecundity rates. When conditions are good after perturbation, a population originally will start grow with extremely large population growth rate and the rate drastically declines to low level, then goes up and down and finally stabilizes at a stable age distribution. A population can stay at unstable age distribution phase for 2 to 3 generations (Sinclair et al, 2006). Unstable age distribution can be obtained using the function *pop.projection()* (Stubben & Milligan, 2007). In addition to stable age distribution, the Leslie matrix model could be used to obtain elasticities which measures importance of proportional change in survival and fecundity rates on population growth (De Kroon, Croenendael, & EhrlBn, 2000). Summation of elasticities in a matrix gives a total of 1.

Therefore, I grouped individuals into 20 age classes and used the approach described in Jolles (2007). Since aerial surveys were conducted during the dry season (post breeding census) and buffalo population is assumed to exhibit a birth pulse, I constructed a post birth pulse Leslie matrix population model using survival rates (i.e. probability of a particular age class surviving to the next year) and fecundity rates (i.e. annual probability that a female buffalo of a particular age class produces a female calf as matrix elements. I assumed that the buffalo population is composed of 50:50 ratio of male to female. Results from this analysis were used to identify parameters which have strong effects on the buffalo population changes. The package **Popbio** in a statistical program **R** was used to construct and analyze the Leslie matrix model.

Parameterization

Survival

Previous studies of African buffalo across the region have been used to provide different survival rates (Sinclair, 1977; Getz, 1996, Jolles, 2007; Cross et al, 2005). These studies have

shown that survival rates for the buffalo vary within and between age classes, with calf survival rates being lower compared to juvenile and adult age classes. These rates progressively increase through juvenile age class and reach maximum and attain a relatively stable state at an adult age class and then drop down progressively through senescent age class. I decided to use Jolles (2007) estimates as a baseline in my study because the annual

Table 2: Age-specific survival and fecundity rates of buffalo obtained from various studies conducted in Africa. The minimum, baseline and maximum values were used in the Leslie matrix population model as matrix elements to obtain growth rates lambda (λ), age distribution and elasticities

Age class parameters	Minimum	Baseline	Maximum	Source
1. Survival rates				
Calves (0-0.5) a year	0.64	0.74	0.91	0.76 (Sinclair, 1977), 0.95 (Getz, 1996), 0.91 (Cross et al, 2005), 0.64 (assumed)
Juveniles (0.5-4.5) years	0.83	0.84	0.95	0.95 (Sinclair, 1977), 0.83 (Getz, 1996), 0.94 (Cross et al, 2005)
Sub-adults (4.5-5.5) years	0.83	0.97	0.98	0.93 (Sinclair, 1977), 0.83 (Getz, 1996), 0.94 (Cross et al, 2005), 0.98 (assumed)
Adults (5.5-14.5) years	0.83	0.97	0.98	0.85 (Sinclair, 1977), 0.83 (Getz, 1996), 0.84 (Cross et al, 2005), 0.98 (assumed)
Senescents (14.5-20) years	0.35	0.73	0.91	0.35 (Getz, 1996), 0.91 (Cross et al, 2005), 0.98 (assumed)
2. Fecundity rates				
Sub-adults (4.5-5.5) years	0.05	0.15	0.26	0.25 (Taylor, 1985), 0.26 (Getz, 1996), 0.05 (assumed)
Adults (5.5-14.5) years	0.29	0.37	0.43	0.29 (Carmichael et al, 1977), 0.35 (Sinclair, 1977), 0.43 (Mizutani, 1987)
Senescents (14.5-20) years	0.20	0.30	0.34	0.34 (Getz, 1996), 0.20 (assumed)

periods during which the counts data were collected in that study (1957 to 2004) to the great extent coincides with my study period (from 1986 to 2011). In addition to that, the method (distance sampling) used in the study to obtain density produces a less biased, sex and age specific estimates (Buckland et al, 1993; Norvel et al, 2003; Jolles, 2007). Furthermore, the amount of rainfall is almost similar in our study areas. In that regard, I defined minimum and maximum survival rate as the lowest and the highest values from previous studies relative to

Jolles', (2007) estimates respectively (Table 2). In situation where previous studies had no lower or higher values in a particular age class relative to Jolles', (2007) values which could be used as minimum or maximum value, I used 10% more or less than the survival rate provided in Jolles', (2007), in that particular age class to get the maximum or minimum value respectively.

Fecundity rate

Similar to the survival rates, I used fecundity rates from previous studies (Carmichael et al, 1977; Sinclair, 1977; Taylor, 1985; Mizutani, 1987). I also defined minimum and maximum fecundity rate as the lowest and the highest values from previous studies relative to the (Jolles, 2007) estimates respectively (Table 2). In situation where previous studies had no lower or higher values in a particular age class relative to Jolles', (2007) values which could be used as minimum or maximum value, I used 10% more or less than the fecundity rate provided in Jolles', (2007), in that particular age class to get the maximum or minimum value respectively. Both survival and fecundity rates were then entered in the Leslie to obtain different growth rates (λ), age distribution and elasticities.

Tracing buffalo population changes in the Selous – Mikumi Ecosystem

The buffalo population has previously been reported to exhibit growth rates and annual average growth rates for 1.16 and 1.36 respectively (Sinclair, 1977). On the other hand, Jolles (2007), reported three growth rates 1.04, 1.05 and 1.12. The annual average growth rate of 1.04 and 1.05 seemed to be very low for a buffalo population, while a growth rate of 1.12 was observed only during years of high rainfall (Jolles, 2007).

I used the Leslie matrix model to trace maximum growth rates observed in the Selous Mikumi ecosystem estimates from 1986 to 2011 in three different scenarios. In the first scenario, I used the highest age dependent survival and fecundity rates when a population is in its

unstable age distribution, containing only mature females. The end of the first scenario (i.e. unstable age distribution) automatically marks the beginning of the second scenario in which a population reaches a stable age distribution at the highest age dependent survival and fecundity rates. However, when the population is in its stable age distribution subadults, adults and senescents contributes to population changes. These highest survival and fecundity rates were chosen from previous studies (Table 2). On the other hand, the third scenario was used to trace the decrease phase in two main categories based on the age dependent survival and fecundity rates of the baseline model. The first category was divided into two sub categories in which population was assumed to be affected by food limitation and poaching. Therefore I changed fecundity and survival rates to reflect the effects of food limitation and poaching in each age class based. The fecundity and survival rates used were assumed rates on based age class characteristics and poachers selectivity. In the second category percentage change at $\pm 5\%$ in population parameters, the percentage change were made in relation to the survival and fecundity rates of the baseline model, i.e. using values provided by Jolles', (2007). Finally, growth rates produced in this tracing analysis were compared with growth rates suggested by Selous - Mikumi population estimates from 1986 to 2011 to draw my conclusion.

Results

Population Monitoring

The Selous - Mikumi buffalo population estimates revealed a 52% decline from 225,000 individuals in 1986 to 108,830 individuals in 2011. During this period buffalo population estimates reveal periods with large differences in population growth. From the year 1986 to 1991 the population showed a decline at an annual average growth rate of 0.83 followed by an increase from 1991 to 1994 at an annual average growth rate of 1.34. A decline was also observed from 1994 to 1998 at an annual average growth rate of 0.93 followed by an increase from 1998 to 2002 at an annual average growth rate of 1.16. From the year 2002 to 2006 and 2006 to 2009 buffalo population progressively declined at an annual average growth rate of 0.80 and 0.72 respectively and finally showed a rapid growth from 2009 to 2011 at an annual average growth rate of 1.63 (Figure 2).



Figure 2. Buffalo population estimates in the Selous - Mikumi ecosystem based on the aerial surveys conducted in the dry season from 1986 to 2011. The filled points represent population estimates from 8 aerial surveys conducted in the ecosystem from 1986 to 2011. The open circles represent the unknown estimates filled up in the years between counts assuming a steady increase or decrease.

Results indicate a general population trend in different protected areas forming the Selous-Mikumi ecosystem. Out of six sub areas, four (1, 2, 3 and 6) showed a decline in population density from 2002 to 2006 and a slight different trend from 2006 to 2011. No data were available for sub area 6 beyond 2006. In contrast, two sub areas 4 and 5 showed an increase in density from 2002 to 2006 and no data were provided beyond 2006 (Figure 3).

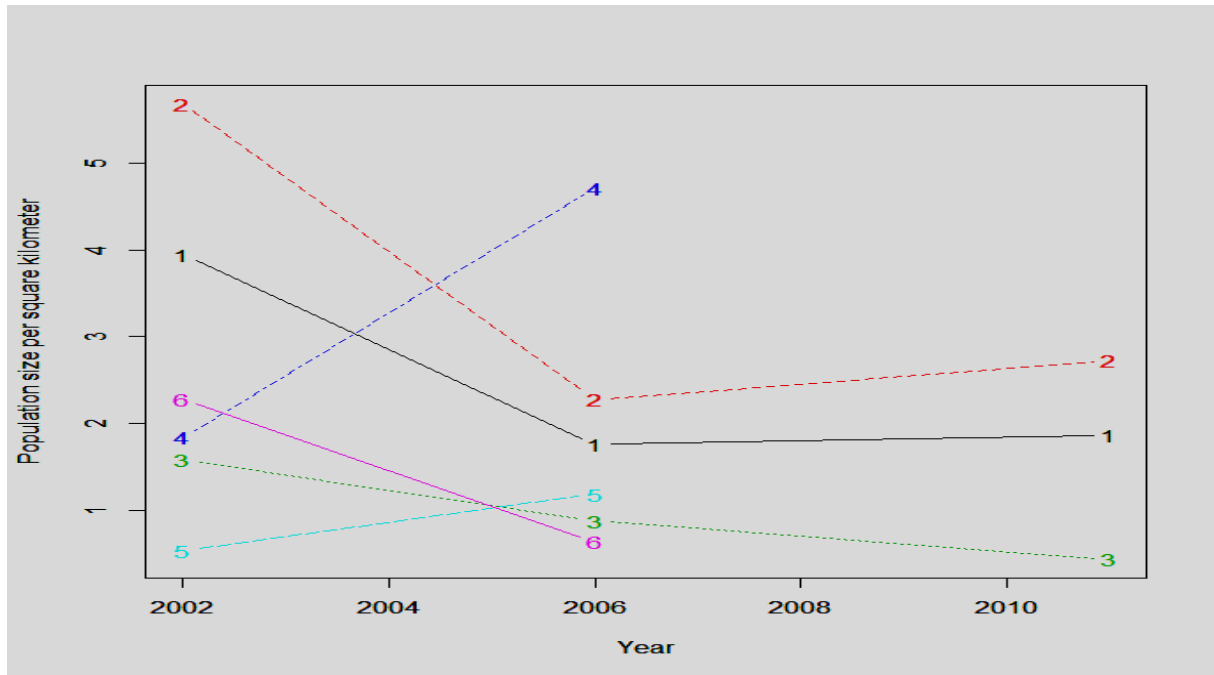


Figure 3. Buffalo Population size per square kilometer in protected areas forming the Selous-Mikumi ecosystem from 2002 to 2011. Different areas in the Selous-Mikumi ecosystem are described by numbers as follow, Area number 1 - Selous game reserve, 2 - Mikumi national park, 3 - Kilombero game controlled area, 4 – Open area on the northern part of the Selous game reserve, 5 - Open area north east of the Selous game reserve and 6 - Open area south east of the Selous game reserve).

Annual quota and annual harvest levels of mature male buffalo

Data showing the annual harvest levels of mature male buffalo in the Selous game reserve were consistently below the annual quota throughout the study period (Figure 4), and removes less than 2% of the buffalo population. Data also suggest that annual quotas set independently of harvest level and population estimates. Data also show that annual quotas are consistently

increased from 1996 to 2001 while annual harvest level shows some up and down variation in the same period. In 2004 annual quota and harvest level significantly decreased, levels increased again in 2005. From 2005 to 2011 annual harvest level consistently declined, while annual quota was quite stable until 2010 and declined in 2011. In 2004, 2008 to 2011 annual harvest levels were below 50% of the respective annual quotas.

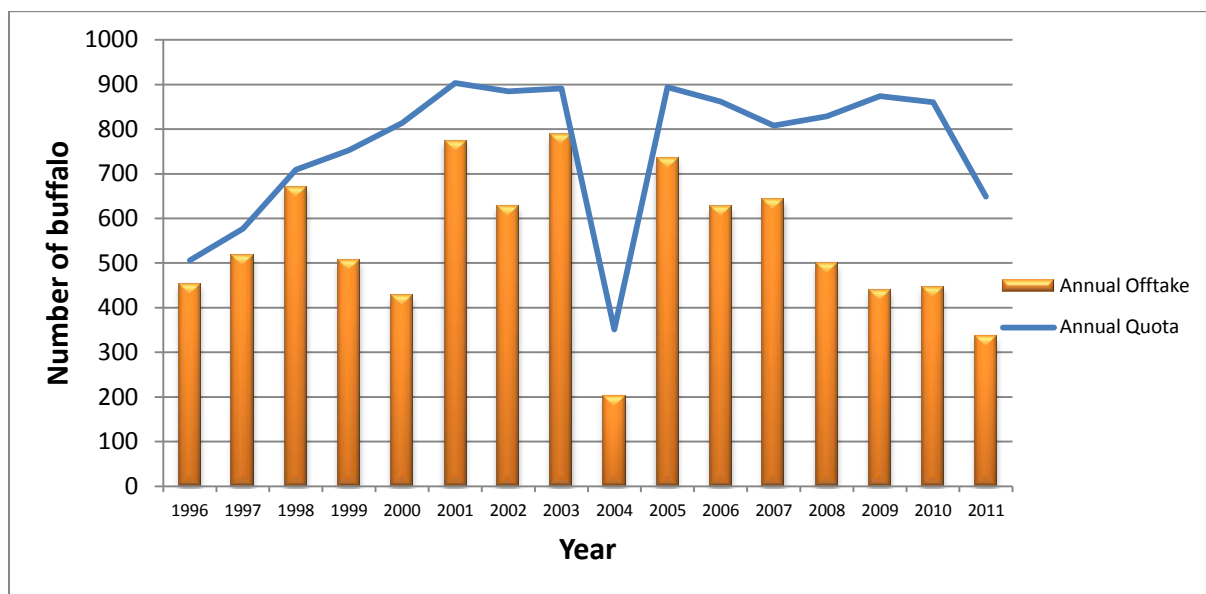


Figure 4. Annual quota and annual offtake/harvest levels of mature male buffalo only in the Selous game reserve from 1996 to 2011.

Outside Selous, annual harvest levels were generally below the annual quotas except in 2000, when annual harvest surpassed the annual quota (Figure 5). There is no data on the harvest levels of mature male buffalo from 1996 to 1999 in areas outside Selous game reserve. However, available data on annual quota during the same period show that annual quota was fairly constant. From 2001 to 2004 annual harvest was reduced to very low level whereas annual quota showed minor up and down variations from 2000 to 2003, and then reduced significantly to very low level in 2004. In 2005 and 2006 both annual quota and annual harvest levels increased, and from 2006 to 2011 annual harvest consistently declined while annual quota showed some variation but was generally declining.

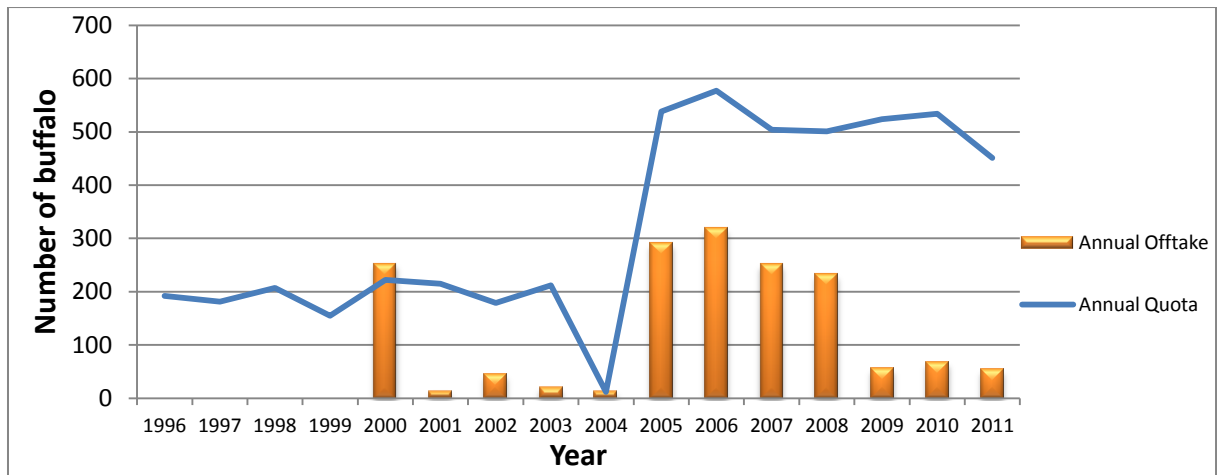


Figure 5. Annual quota and offtake/harvest levels of mature male buffalo outside the Selous Game Reserve from 1996 to 2011.

Rainfall and food limitation

Average annual rainfall in the Selous - Mikumi ecosystem from 1991 to 2011 is 809.5 mm. The lowest annual rainfall observed was 447mm in 2005 and the highest was 1189.2mm in 2006. The highest $\log(\lambda)$ was 0.44 observed when rainfall was above the average annual rainfall and

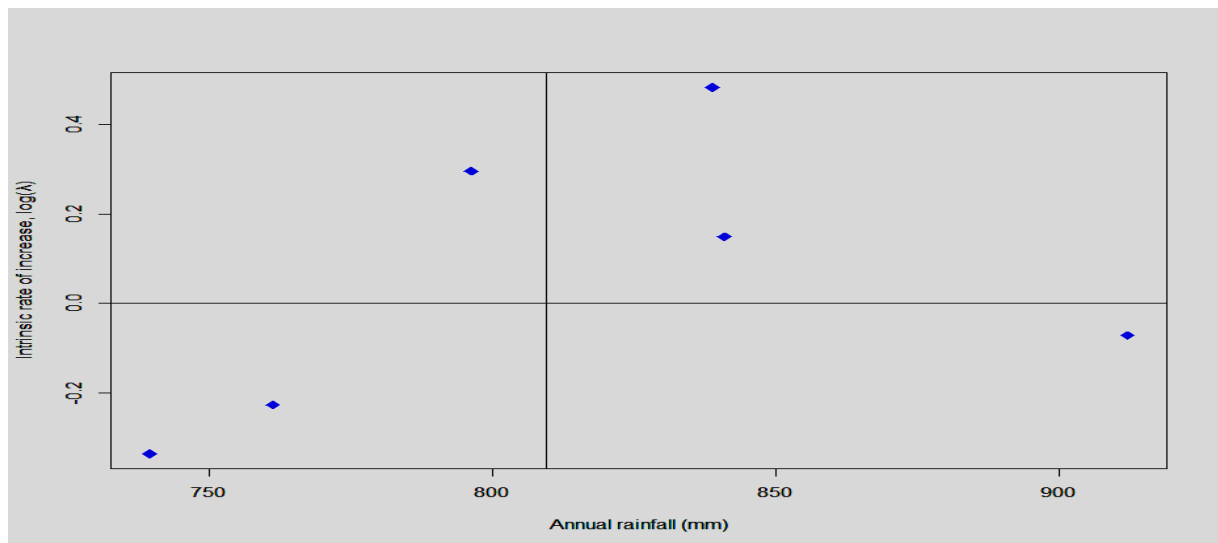


Figure 6. Relationship between intrinsic rate of increase, $\log(\lambda)$ and annual rainfall in millimetres.

the lowest $\log(\lambda)$ observed was -0.27 observed when rainfall was below average annual rainfall (Figure 6). Data show that out of six estimates, three estimates had $\log(\lambda)$ below the average annual rainfall and three estimates had $\log(\lambda)$ above the average annual rainfall. Out of three estimates which are below average annual rainfall, two have a negative $\log(\lambda)$ and one have a positive $\log(\lambda)$. On the other hand, out of three estimates which are above average annual rainfall, two have a positive $\log(\lambda)$ and one have a negative $\log(\lambda)$.

Leslie Matrix Population Model

Population growth rates, age ratios and elasticities of λ

In assessing how high a buffalo population can increase I got an average annual growth rate of 1.14, which was obtained when assumed biologically optimum age class survival and fecundity rates at a stable age distribution were used. However, data from previous studies showed that three growth rates of 1.02, 0.89 and 1.12 could be obtained when age specific survival and fecundity rates at the baseline, minimum and maximum levels are used, respectively (Table 3). On the other hand, data show that juveniles and adults age classes have higher elasticities of λ and age ratios than other age classes. Data also show that sub adults age class has the lowest elasticities while senescents age class has the lowest age ratios.

Table 3. Growth rates, age ratios and elasticities when baseline, minimum and maximum survival and fecundity rates were used.

Vital rates used	Lambda (λ)	Elasticities					Age ratios				
		Calves	Juveniles	Sub-adults	Adults	Senescents	Calves	Juveniles	Sub-adults	Adults	Senescents
Baseline	1.02	0.15	0.34	0.05	0.35	0.10	0.09	0.35	0.08	0.37	0.02
Minimum	0.89	0.12	0.32	0.07	0.43	0.05	0.09	0.38	0.09	0.34	0.00
Maximum	1.12	0.15	0.39	0.06	0.31	0.09	0.09	0.35	0.08	0.33	0.03

Tracing buffalo population changes in the Selous – Mikumi Ecosystem

a) Increase phases

The Leslie matrix population model reveals that the highest annual growth rate a buffalo population could have is 1.40 (Figure 7). This annual growth rate could only be obtained when a population is in unstable age distribution, with high survival and fecundity rates of 0.98 and 0.43 respectively. However, a population can stay at such extreme growth rate only once after which the growth rate drastically declines to 1.11 followed by some fluctuates around 1.16 and finally stabilizes from the 15th year with an annual growth rate of 1.16 at a stable age distribution.

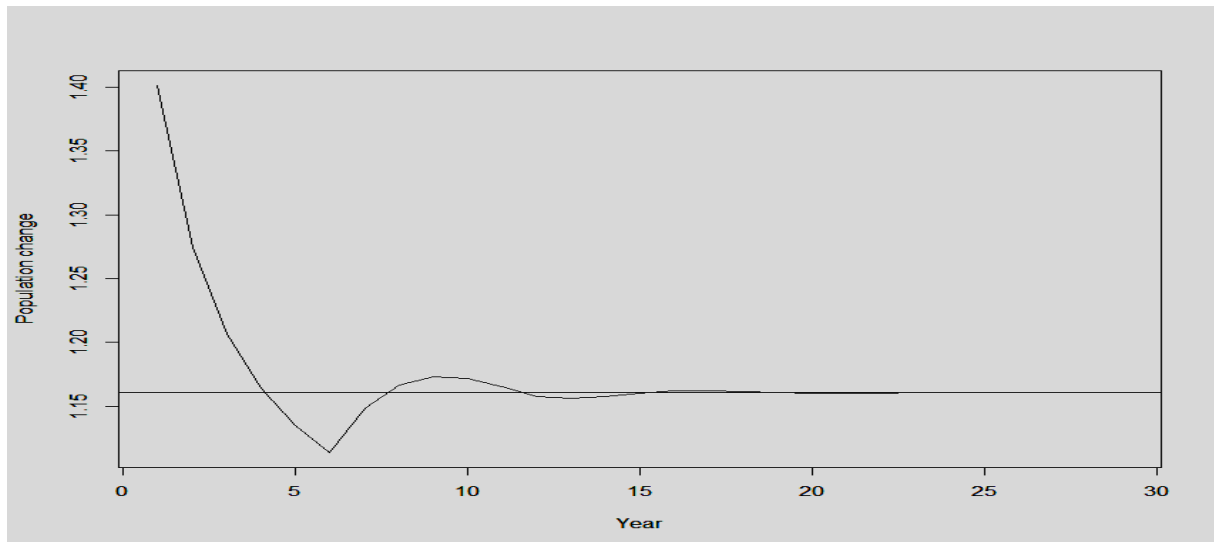


Figure 7. Population changes when buffalo population is at an unstable age distribution.

b) Decline phases

Selous – Mikumi population estimates suggest four decline phases with average annual growth rates of 0.72, 0.83, 0.80 and 0.93 observed between from 1986 to 2011. However, when baseline fecundity and survival rates were reduced to some biologically reasonable values to reflect the effects of food limitation and poaching on the population, different average annual growth rates were observed (Table 4). Data reveal that the effect of food

limitation on fecundity rates of sub adults, adults and senescents age classes could reduce average annual growth rate from 1.02 to 0.91. Whereas the effect of food limitation and poaching on survival rates of all age classes could reduce average annual growth to 0.49 and 0.52 respectively.

Table 4. Effects of food limitation and poaching on average annual growth rates

Scenarios	Lambda (λ)	Fecundity rates				
		Subadults	adults	Senescents		
Baseline	1.02	0.15	0.37	0.30		
Food limitation	0.91	0	0.10	0.05		
Poaching	0.92	0.10	0.10	0.05		
		Survival rates				
		Calves	Juveniles	Subadults	adults	Senescents
Baseline	1.02	0.73	0.84	0.97	0.97	0.73
Food limitation	0.49	0.1	0.35	0.6	0.6	0.35
Poaching	0.52	0.5	0.4	0.5	0.5	0.35

Percentage change in population fecundity and survival rates

Data on $\pm 5\%$ changes from the baseline survival and fecundity rates show that buffalo population is more sensitive to changes in survival rates than fecundity rates. The sensitivity of the population to changes in either survival rates or fecundity rates is reflected on the slopes of the two lines (Figure 8).

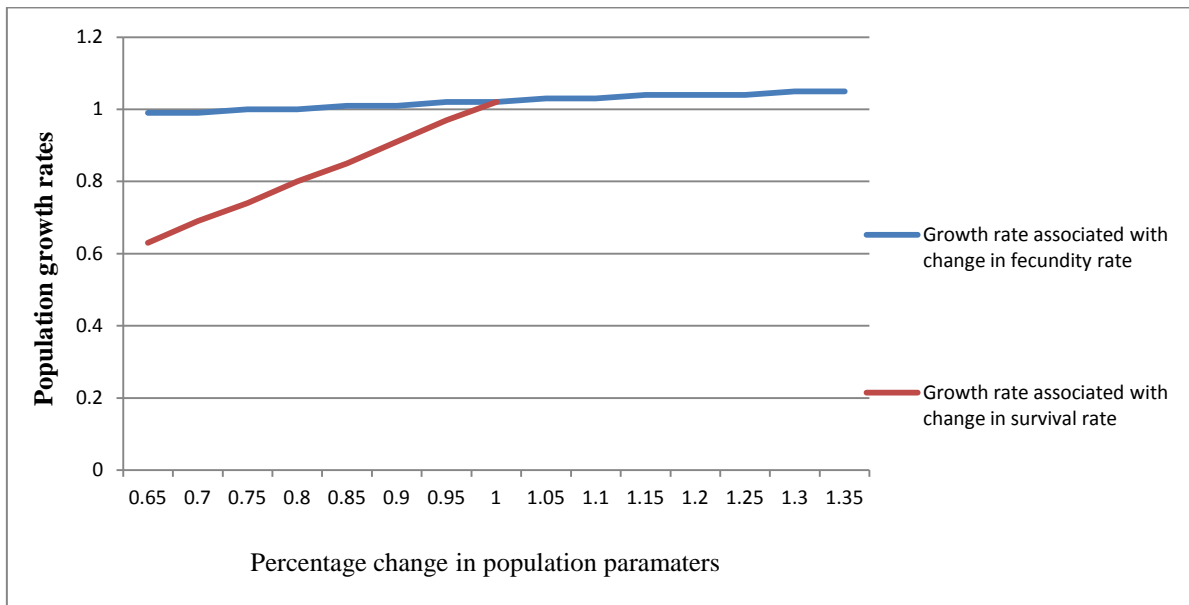


Figure 8. Relationship between percentage change in population parameters (survival and fecundity rates) and population change.

Discussion

Findings from my study suggest that the amount of rainfall influenced the annual population estimates; this observation is in line with my hypothesis. The amount of rainfall determines amount of food availability, which in turn determines population changes. In addition to the limitation posed by the amount of food availability effects, findings suggest that poaching had some influence on the buffalo population changes. On the other hand, data suggests that annual quotas are set independently of population estimates and annual harvests; this observation is contrary to my hypothesis.

Population Monitoring

The Selous - Mikumi buffalo population estimates reveal periods with large differences in population growth (Figure 2). Annual average growth rate of 1.16 at a stable age distribution was observed between 2000 and 2006. This growth rate was also documented before (Sinclair, 1977). Jolles (2007) reported that annual growth rate of 1.12 is high for a buffalo population and could only be achieved when there is high rainfall. In addition to that, Selous – Mikumi population estimates suggested annual population annual growth rate of 1.34 between 1991 and 1994. This growth rate was close to the annual growth rate of 1.36 observed by Sinclair in 1977. Such high annual growth rate could probably be achieved when a population is in its unstable age distribution. For a buffalo population unstable age distribution phase may span for 15 years. This phase is observed when a population is affected by a perturbation (e.g. severe drought) which has removed all immature and senescent age classes in a population leaving a population with only mature individuals. The remained mature individuals are characterized by high survival and fecundity rates, resulting to a high population increase once conditions are optimum after perturbation. However, this high growth rate is observed in only one year, thereafter a growth rate drastically decline followed by some fluctuations

around a certain equilibrium level and the population reaches a stable age distribution (Figure 7). However, Sinclair et al (2006) reported that long-lived populations may remain in unstable age distribution phase for 2 to 3 generations. The Selous – Mikumi population estimates also suggested an annual growth rate of 1.63 between 2009 and 2011. This study suggests that it is biologically not very likely for a buffalo population to grow at such high annual growth rate. However, I suspect that such high growth rate may be caused by measurement errors as suggested by TAWIRI (2011).

On the other hand, the Selous-Mikumi population estimates results suggested four decreasing phases in which buffalo population declined from 1986 to 1991, from 1994 to 1998, from 2002 to 2006 and from 2006 to 2009, with annual average growth rates of 0.83, 0.93, 0.80 and 0.72, respectively (Figure 2). These declines could be explained by food limitation and poaching, all of which cause population declines. Skinner & Chimimba (2005) reported that food supply is the most limiting factor limiting to a buffalo population. Similarly, Jolles (2007) and Sinclair (2002) also observed that a buffalo population is likely to be affected by food supply which is influenced by the annual variation rainfall. On the other hand poaching has been reported as a major cause of population declines in Tanzania (Dublin et al, 1990; IUCN SSC Ungulate specialist Group 2008; Mbugi 2013; Mshale (2008); Ndibalema & Songorwa, 2007; Siege & Baldus, 2000; Baldus, 2003; Baldus, 2009; Sincalir, 1977).

However, the trend described in the Selous Mikumi ecosystem is not a full representation of what is happening in individual protected areas within the ecosystem (Figure 4). While the population size of buffalo in the ecosystem showed a progressive decline between 2002 and 2009; in contrast, open areas on the northern and north eastern part of the Selous Game Reserve showed a population increase between 2002 and 2006. The increase of buffalo population size in these two areas is probably explained by major changes made in Tanzania's

wildlife policy aiming at involving rural communities and private sector in wildlife protection, utilization and sharing of revenue accrued from wildlife (Wildlife Policy of Tanzania, 1998). The policy change led to enactment of the Wildlife Management Areas regulations in 2002 and establishment of Wildlife Management Areas for the purpose of involving local communities in managing wildlife on the village land (Wildlife Management Areas regulations, 2002). Therefore the increase in buffalo population from 2002 to 2006 in the two areas is probably explained by improved habitat quality (and hence increased food supply) as a result of increased protection. Caro et al (1998) observed a positive correlation between population densities of large bodied herbivores and protection.

Caughley (1972) reported that variation in aircraft speed, flying height above the ground as well as transect width is the main sources of observation error in aerial surveys. Aerial survey parameters provided in Table 1 vary considerably between years and between aircrafts, this suggesting that the Selous - Mikumi estimates are affected by measurement errors. In addition to that, the gregarious nature of buffalo presents another potential source of sampling error (Norton-Griffiths. 1978). In that regard, these estimates are likely to be either overestimated or underestimated both of which can mislead managers in making decisions. However, because the same method has been used to estimate population sizes throughout study period, I speculate there could be other factors explaining population changes. Generalizing that large estimate differences between succeeding estimates may be attributed only to errors, or low population estimates are primarily attributed by poaching, as suggested by TAWIRI in 2011, may be misleading. This study recommends detailed studies to ascertain these two facts.

However, some of the biases could be minimized by use of a method that estimates detection probability. Because of the methodological problems and biases associated with aerial

surveys, distance sampling could be used as an alternative as it provides less biased estimates, sex and age specific population information (Buckland et al, 1993; Norvel et al, 2003). Although this method is laborious, it's assumptions are realistic and can be fulfilled by providing a proper training to field staff and by using appropriate procedure and effective design (Norvel et al, 2003).

Annual quota and harvest levels

Harvest is regulated by hunting quotas and is unlikely to affect buffalo population in the ecosystem as it selectively removes mature males account for less than 2% of the population annually (Figure 5). In addition to that, harvest quota did not reflect population changes and the preceding year harvest level. Severre (1996) reported that, annual quota are set based on population estimates only if estimates are available in that particular year. This suggests, if in a particular year no population survey has been conducted, annual quota will be set based on other information. In most cases proposals from game reserve's managers, professional hunters and outfitters are used (Severre, 1996).

Rainfall and food limitation

The amount of rainfall below the annual average (809.5mm) influenced a decrease in $\log(\lambda)$, whereas the amount of rainfall above the threshold influenced an increase in the $\log(\lambda)$. Similar findings were reported in previous studies (Coe et al, 1976; Sinclair, 1977; East, 1984; McNaughton, 1985; Mills, et al 1995). In contrast, Bell (1982) only observed a positive correlation between rainfall and animal density in areas where rainfall was assumed to interact with high soil fertility. Sinclair (1974) suggested that buffalo could not be able to live in an area receiving annual rainfall below 500mm. However, Sinclair (1974) noted some exceptions in which buffalo were observed to survive in areas receiving annual rainfall of 250mm but

with access to permanent water sources. On the other hand, data suggests that when the amount of rainfall is well above the average rainfall buffalo population declined. Sinclair (1977) found that in areas dominated by tall grasses "elephant grass", rainfall only correlates positively with food supply before these grasses mature, when the grasses have matured further rainfall correlated negatively with food supply. This suggests that the buffalo will only have food when these grasses sprout and before they mature. Once they mature food availability for buffalo declines and this will show a relatively similar effect as when there is no rainfall. In addition to that, Sinclair (1977) noted high calf mortality in years when there is high amount of rainfall particularly in waterlogged conditions during which calves are affected by infectious disease causing hoof to rot. Sinclair (1977) concluded that rainfall can act indirectly as density dependent factor by varying the amount of food supply or acts directly as density independent factor by causing direct effects on a population. The former happens during times of food shortage when intraspecific competition is likely to be intensified; the interspecific competition is further exacerbated by population group size and food selectivity (Sinclair, 1977). The latter could be explained by effect of rain to mortality as a result of flood or caused occurrence of a diseases causing hoof to rote in waterlogged conditions (Sinclair, 1977).

When a buffalo population experiences strong intraspecific competition, the outcompeted individuals become weak and eventually will die causing a decline in the λ . Therefore, food supply is a limiting factor which regulates λ of buffalo population (Dublin et al., 1990; McNaughton & Georgiadis, 1986; Sinclair 1974; Sinclair, 1977).

Leslie Matrix Population Model

Population growth rates, age ratios and elasticities of λ

Data revealed that maximum growth rate which could be achieved when biologically optimum values are used is 1.14. This growth rate was close to a growth rate of 1.16 observed from the Selous – Mikumi population estimates. Similarly, Sinclair (1977) observed a growth rate of 1.16 in Serengeti national park. Jolles (2007) observed a growth rate of 1.12 in years when the amount of rainfall was high. This suggests that, when there is high rainfall a buffalo population could grow at such growth rates. However, when I used minimum, baseline and maximum growth rates from other studies I got growth rates of 1.02, 0.89 and 1.12 (Table 3). The growth rate 1.02 is below the growth rates of 1.04 and 1.05 observed by Jolles (2007), who concluded that these annual growth rates are fairly low, suggesting that a buffalo population may be subjected to human induced mortalities environmental perturbations. On the other hand, a growth rate of 0.89 could be explained by periods of high mortalities as a result of rampant poaching, diseases occurrence or prolonged dry season resulting to food shortage. The explanations of Jolles (2007) could also be used to explain the occurrence of 1.12.

On the other hand, elasticities of λ to changes in survival and fecundity of juveniles and adults were consistently higher than for other age classes. High juveniles' survival rate accounts for the highest buffalo population growth rate (Table 3). Juveniles are characterized by low fat reserves since most of their dietary protein intake during weaning period is used for growth (Sinclair, 1977), and their survival is highly sensitive to fluctuations in food supply. So variation in juveniles' survival is important for annual population variation. Sinclair (1977) pointed out that the sensitivity of juveniles to variations in food supply is explained by variation in environmental factors particularly amount of rainfall. However, in places where

there is permanent water supply low juveniles mortality rates were reported even when the amount of rainfall was low (Sinclair, 1977). This suggests that annual variations may as well be explained by the interactive effect of rainfall and availability of water in a particular area. On the other hand, elasticities of λ to changes in survival and fecundity of adults were higher because, adults are the the most important reproductive age class and therefore reduction in their survival or fecundity rates would have a greater effect in a population growth. Also results show that, age ratios of adults and juveniles were consistently higher. This is explained by the fact that, these two classes have wider range than others. For instance, adult age class combines individuals from 5.5 to 14.5 years and juvenile from 0.5 to 4.5 years while calves age class combine individual from 0 to 0.5 a year. Therefore results suggest a decrease or increase in survival rate of adults and juvenile age classes will affect annual average growth rate of a population. Therefore in order to halt buffalo population size decline it is important that harvest strategy should not allow harvesting of adult and juvenile age class instead, calves, subadults and senescents age classes could be harvested.

Tracing buffalo population changes in the Selous – Mikumi Ecosystem

a) Increase phases

Selous – Mikumi population estimates suggest three increase phases with average annual growth rates of 1.16, 1.34 and 1.63 observed from 1986 to 2011. The annual average growth rate of 1.16 could be obtained when survival rate of 0.98 and fecundity rate of 0.43 are were used in the Leslie matrix at a stable age distribution. These rates are very high for buffalo population and could be reached when there is high rainfall which increases food availability which is important for keeping a population at good health. Sinclair, 1977 observed similar growth rate in Serengeti national park, while Jolles 2007 observed a growth rate closer to that i.e. 1.12. On the other hand, data suggests that a growth rate of 1.34 could only be achieved when a population is at unstable age distribution. When I entered survival rate of 0.98 and

0.43 at unstable age distribution, I obtained an annual growth rate of 1.40 (Figure 7). Therefore, 1.34 could be obtained when a population is at unstable age distribution in exhibiting high survival and fecundity rates. For a buffalo population unstable age distribution phase may span for 15 years. This phase is observed when a population is affected by a perturbation which has removed all immature and senescent age classes in a population leaving a population with only mature individuals. The remained mature individuals are characterized by high survival and fecundity rates resulting to a high population increase once conditions are optimum after perturbation. However, such high annual growth rate is observed only at the initial stage of unstable age distribution. However, Sinclair (1977) observed a growth rate of 1.36 which is close to 1.34 obtained in the Selous- Mikumi game reserve and 1.40 obtained from the Leslie matrix. This suggests that though under special circumstances, buffalo population could grow at such high annual growth rate. Data failed to trace a growth rate of 1.63 observed in the Selous game reserve. Such high growth rate is less likely to happen considering biology of the buffalo. Therefore, I suspect measurement errors could account for such high growth rates as suggested by (TAWIRI, 2011).

b) Decline phase

Selous – Mikumi population estimates suggest four decline phases with average annual growth rates of 0.72, 0.83, 0.80 and 0.93. Tracing study from the Leslie matrix suggests that, these growth rates could be achieved when a population survival rates and fecundity rates are reduced. Based on the available information, I speculate poaching and food limitation as the main factors which could cause a population to decline with such growth rate. When I reduced growth rates of each age class reflecting poaching and food limitation scenarios in the matrix, I obtained growths rates lower than those obtained in the Selous- Mikumi Ecosystem. Despite the fact that fecundity and survival values were reduced equally, data show that percentage change in survival rates had large effect on annual average growth rate than

similar change in fecundity rate. This suggests that, large population fluctuations are caused by changes in survival rates than fecundity rates.

Management Implications

The buffalo harvest strategy in Tanzania is based on a limited understanding of the population dynamics and with little consideration of local knowledge; this probably leads to less informed decisions than would be when using detailed demographic information and local knowledge. Scandinavia provides a good example where information from hunters' observations on Moose *Alces alces* calf per cow is used in showing how much of variation is explained by annual variation in fecundity and rainfall. Adopting this strategy would help to improve the quota setting system in Tanzania.

Aerial survey is the common method which has been used for decades to estimate population sizes; however, the method is unable to provide reliable, sex and age-specific demographic information. These shortfalls compelled me develop a Leslie population projection matrix model using age specific survival and fecundity rates obtained from a study conducted in South Africa (Jolles, 2007).

Results suggest population growth is sensitive to changes in survival and fecundity rate of adults and juveniles. Therefore in order to halt buffalo population decline it is important that harvest strategy should not allow harvesting of adult and juvenile age class instead, calves, subadults and senescents age classes could be harvested.

Generalizing that large estimate differences between succeeding estimates may be attributed only to errors, or low population estimates are primarily attributed by poaching, as suggested

by TAWIRI in 2011, may be misleading. This study recommends detailed study to evaluate present population estimates.

This study shows empirically that age-specific population estimates provide more detailed demographic information which could be used to make informed decisions. I recommend the use of a method that estimates detectability and which produce less biased population estimates. In addition the method should have ability of providing age and sex specific demographic information which could be used to produce detail population information.

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