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The influence of human induced factors on African elephant (*Loxodonta africana*) populations in Sub-Saharan Africa

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MSc in Biology

Submission date: June 2015

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Abstract

Numerous studies have been done on the conservation of the African elephant (*Loxodonta africana*) yet too few studies have focused on comparing the ultimate factors that influence the African elephant populations. Here, we looked at several human induced factors that reflect parts of the Human Elephant conflict and tried to find which one of those had the most important effect on African elephant populations in Sub-Saharan countries. Agricultural activity and deforestation together with increasing human population density and poaching all have a negative effect on elephant populations. However, we found that poverty, measured by *per capita* income, was by far the most significant factor affecting elephant populations. This variable translates in not only individual poverty that results in lucrative poaching, but also in national economical and political stability, which is essential for effective conservation management. Furthermore, our results show that, in order to protect the African elephant, tackling the poverty problem is more important than creating new protected areas.

Abstrakt

Flere forsøk har blitt gjort for bevaring av den Afrikanske elefanten (*Loxodonta africana*) men lite forskning har fokusert på sammenlikning av faktorene som påvirker den Afrikanske elefantens populasjon. Vi har sett på faktorer som er påvirket av mennesker, som reflekterer på deler av 'Human Elephant Conflict' (HEC) og prøver å finne ut hvilken av dem som hadde størst effekt på den Afrikanske elefant populasjonen i Sub-Sahariske land. Jordbruks aktivitet og avskoging sammen med en befolkings vekst og ulovlig jakt, har en negativ effekt på elefant populasjonen. På en annen side så har undersøkelsene vist at fattigdom målt etter hver innbyggers inntekt var betydelig den viktigste faktoren som påvirker elefant populasjonen. Denne faktoren skyldes ikke bare individuell fattigdom som resultat av lukrativ jakting, men også av en nasjons økonomisk og politisk stabilitet som er essensielt for effektiv bevaring. Videre viser våre studier at for å ivareta den Afrikanske elefanten, så er håndtering av fattigdom viktigere enn å skape nye vernende områder.

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1 Introduction

The African elephant (*Loxodonta africana*) has been an icon throughout human history and in modern times, belonging to the African ‘Big Five’, this species has arguably become even more known. With its amiable and majestic appearance, it has mesmerized young and old and inspired poets and painters alike. Apart from being inspiring, the African elephant serves many purposes, most of them only indirectly affecting the human population.

The African elephant has been graced with many names describing its ecological, economical and cultural importance. A “flagship species”, a “keystone species” and an “ecosystem engineer”, to name a few (Barua, 2011; Wright & Jones, 2006). The elephant’s ecological significance in an area cannot be underestimated. From creating habitat (Pringle R. M., 2008) and hindering succession of vegetation by uprooting trees and destroying bushes and shrubs (Haynes, 2011), to providing drinkable water for other species by digging wells in ephemeral river systems (Ramey, Ramey, Brown, & Kelley, 2013), the African elephant, with its huge body mass and posture, shapes the land around him and influences numerous other species in its direct proximity (du Toit, Moe, & Skarpe, 2014). An ecosystem engineer, coined by Jones et al. (1994), was originally defined as “organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing ... state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats” (Jones, Lawton, & Shachak, 1994). Apart from changing their direct environment in the advantage of other species, African elephants also do extensive damage to the vegetation and can, when populations grow too big, leave a trail of destruction (Jones, Lawton, & Shachak, 1997a; Cumming, et al., 1997; Pringle, Young, Rubenstein, & McCauley, 2007).

As the African elephant is a very intelligent and opportunistic species, which, when left alone, has an average per annum growth rate of 5% (Spinage, 1990), it comes a lot in contact with the ever-growing human population, which is invading the elephant's natural home range. This causes the Human Elephant Conflict (HEC), which includes any interaction between elephants and humans if either or both parties have a negative experience from that encounter (Inogwabini, Mbende, Bakanza, & Bokika, 2013). Elephants often raid the crops of local farmers in search of food and water. By doing so they do not only destroy the farmer's crops, but also often inflict damage upon buildings, humans or themselves (Amwata & Mganga, 2014). Various methods of mitigating this HEC have been proposed (Wiafe & Sam, 2014; Thuppil & Coss, 2012; Messer, 2010) but up until today, no universal method has been devised. Using several different methods, either at the same time or alternating, seems to be the best option (King, Soltis, Douglas-Hamilton, Savage, & Vollrath, 2010).

Although the elephant's obvious biological importance, somehow humankind has been ignoring this for decades and has instead focused on its natural products such as meat, skin, bones and of course, ivory (De Boer & Baquete, 1998). The ivory crisis in the 1970's had a devastating effect on all African elephant populations (Parker & Amin, 1983). All over Sub-Saharan Africa populations decimated due to an extreme increase in illegal killing or poaching. The economical basis for and implications of poaching are complex, and however essential they may be for efficient and effective conservation strategies, too few conservationists have studied this matter (Wittemyer, 2011; Bulte & van Kooten, 1999). Monitoring and controlling poaching, however, is something else entirely; Gavin *et al.* (2009) have looked into several methods of how to control poaching but again "no method is a panacea". Poverty often leaves local people no other option than to poach for food or money through the trade in natural products; this is, however, only of marginal importance compared to the organized ivory poachers (Lemieux & Clarke, 2009). Trying to combat the black market in ivory trade and to discourage poachers with shoot-kill-policy has not yet yielded the desired effect (Messer, 2010). More and more, in addition to stopping the black market, conservationists are trying to reduce the demand for ivory by influencing the consumer market in e.g. China (Martin & Vigne, 2014; Stiles, 2004).

Poaching aside, elephants have to cope with several other issues such as increasing human population, deforestation and habitat destruction (Lindenmayer, Cunningham, & Pope, 1998; Haines-Young, 2009), agricultural activities and tourism. Habitat fragmentation, which is one of the more important consequences of habitat destruction, is caused by various factors such as increasing road infrastructure, increasing logging activities and transformation of forest to farmland (Cumming, 1994). The (edge) effects on the species residing in those fragmented areas can be significant (Murcia, 1995). All these human induced factors have been driving this unique species to the verge of (local) extinction and despite extensive research in this area, there is still need for a better understanding in what the fundamental factors are that affect the elephant populations, be it natural or human induced. Luckily, after the Ivory ban (1989) (Bulte & van Kooten, 1999), which was a response on the Ivory crisis, several populations of African elephant have been recovering (Lemieux & Clarke, 2009). Some countries have even been forced to implement culling in their conservation management plan to mitigate the negative effects of a too large elephant population in one area (Skarpe, et al., 2004).

There is a need to conserve the African elephant and to do so, we need sound scientific research that management officials can use to base their decisions on. From species specific animal welfare to handling trans-boundary migration routes and from surveys with local people to proposing new concepts for conservation (Ahlering, Maldonado, Eggert, Fleischer, Western, & Brown, 2013; Berger, 2003); a lot has been done and accomplished yet still most of the African elephant populations decline and the Human Elephant Conflict is far from solved. A relatively new array of conservation concepts puts the local community and its collaboration in a central position (Hackel, 1999). By trying to manage wildlife populations in such a way that the local community profits from the preservation of their wildlife, conservationists hope to achieve a more durable way of management. Revenue from culling, tourism and selling of natural products should compensate for the 'reward' locals get from poaching (Nyahongo, 2010a). Several programs in Southern and Eastern Africa have been implemented with varying success (Fischer, Muchapondwa, & Sterner, 2010; Nyahongo, Community Participation in Management and Sustainable Use of Wildlife: Advantages and Disadvantages, 2010; Holmern, 2010).

Especially for species like the African elephant, which need huge areas and often migrate over long distances, trans-boundary policies and national parks can be very beneficial. They remove the artificial borders, which allows wildlife to roam within their natural home ranges. Unfortunately, this causes humanitarian

and political issues as seen in the Greater Limpopo Transfrontier Park between South Africa and Mozambique (Marshall, 2007), where, by opening up the country border between the two countries, there has been a significant increase in illegal migration of people.

Although most research focuses on very specific topics, it is sometimes useful to return to the ultimate sources of a problem. The aim of this study, was to look at which human induced factors influence African elephant populations in Sub-Saharan Africa and which of those are of higher importance to the elephant populations in terms of effects on total elephant population sizes. In order to analyze these ultimate factors, we selected several variables of which scientific results show, have a negative (or positive) influence on wildlife populations, and African elephant populations in particular. As described above, factors such as agricultural activity influence the elephant in various (in)direct ways. When these factors are quantifiable, we can use them for a general analysis.

We included agriculture, deforestation, total protected area, poverty variables, poaching and variables for human population density. We hypothesized that (1) all of the previous variables except the total protected area would have a negative effect on elephant populations and that (2) the total protected area would have a positive effect on elephant populations. Additionally, we hypothesized that (3) deforestation and poaching would be the most influential and that (4) the total protected area would have only a marginal effect on the elephant populations. Lastly, we hypothesized that (5) poaching would be highly positively correlated with poverty.

2 Methods

2.1 Study species: the African elephant

The African elephant (*Loxodonta africana*) is a large herbivorous mammal in range now confined to Sub-Saharan Africa. It is considered a keystone species (Owen-Smith, 1988; Shoshani, 1993) and has an important influence on its surroundings; while providing niches for other species and opening up areas (Pringle R. M., 2008), it also does extensive damage to vegetation (Pringle, Young, Rubenstein, & McCauley, 2007; Cumming, et al., 1997).

To date, there is still no consensus on whether or not there is only 1 species of African elephant. Some consider the savannah elephant *Loxodonta africana africana* and the forest elephant *Loxodonta africana cyclotis* as different species (Comstock, et al., 2002; Roca & O'Brien, 2005; Roca, Georgiadis, & O'Brien, 2005). In the International Union on Conservation of Nature's (IUCN) African Elephant Database (AED), only one African elephant species is recognized and in this study, too, the African elephant will be considered 1 species: *L. africana*.

2.2 Study area

This study includes 31 African, Sub-Saharan countries for which elephant population data was available; only 14 countries were used in the separate poaching data analyses. These countries differ strongly in environment, culture and history (Lewis, 1996) and the way a country handles its inevitable Human Elephant conflict (HEC). Big differences are also observed in country size, total elephant count and elephant range area. Some countries with bigger populations and a significant tourism based economy often have a more elaborate and uniform ways of counting elephants and monitoring populations (Blanc, et al., 2007).



Figure 1 Map of study area in Sub-Saharan Africa. Countries in grey are included in the elephant data 1998 - 2012 (31); countries marked with diagonal lines provided data on PIKE (14). (*modified from http://www.oucom.ohiou.edu/tdi/Topics_International_Health/Dracun_1.htm*)

Although several countries had a total African elephant population count of only a few individuals, which would not count as a viable population (Armbruster & Lande, 1993), they were still included in this study in order to have enough observations for the statistical analyses.

2.3 Data collection

Data was collected from online sources; the IUCN AED provided most data related to elephants such as total count per country, amount of protected area per country and elephant range area, The World Bank provided data on e.g. Forest

cover, Income *per capita* and agricultural activity and the Human Development Index was obtained from the United Nations Development Program's (UNDP) Human Development Reports (HDR). The poaching data was obtained from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) conference report in Bangkok, 2013 (CoP16 Doc. 53.1, 2013).

2.4 Statistical analyses

Although this study focused on explaining the variation in population data of the African elephant (2.4.5), a brief analysis on available poaching data was also performed (2.4.6). The analyses are thus split in two sections, which will be handled accordingly, but first I elaborated on the model selection protocol used in these analyses (2.4.1 - 2.4.4) (Grueber, Nakagawa, Laws, & Jamieson, 2011). Analyses were done in the statistical program R (R - A Development Core Team, 2015).

2.4.1 Variable selection

Explanatory variables were chosen based on relevant and sound previous scientific research. I focused on human related factors that have a direct or indirect effect on African elephant populations in Sub-Saharan countries. The variables chosen in this study attempt to represent several facets of the Human Elephant conflict in Africa.

Elephant population counts and the IQI

The data in the AED is collected from many different sources and methods have not been standardized. The African Elephant Status Report (AESR) 2007 elaborates on a protocol on how to handle this variety of data (Blanc, et al., 2007); they devise 4 categories of elephant numbers based upon data quality and survey type. In this study, only the '*definite*' and '*probable*' numbers of African elephant have been used to limit the amount the error in the data. Because of this specific way of handling these multiple sources, the elephant population data cannot be used for trends over time at continental level (*more info p.13* (Blanc, et al., 2007)) The AED also includes an Information Quality Index (IQI), which is based on elephant data quality and the fraction of elephant range assessed (Blanc, et al., 2007).

Range area (RA) & Protected area (PA)

Range area is calculated as the areas defined as '*known*' and '*possible*' range in the AED. These categories, used in the AESR2007 report (Blanc, et al., 2007), include areas with suitable habitat that most likely contain elephants and areas in

historical range that still have suitable habitat but have a human population density of 15p/km² or less, respectively. It does not contain data from areas considered ‘*doubtful range*’, which are areas that likely do not have elephants but where this hasn’t been confirmed (Blanc, et al., 2007).

Forest area (FA) & Agricultural activities

The forest area is calculated as the total area of land (hectares), which is spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10%, or trees able to reach these thresholds *in situ*. It does not include land that is predominantly under agricultural or urban land use (The World Bank, 2014).

Agricultural land refers to the share of land area that is arable, under permanent crops, and under permanent pastures. Arable land includes land defined by the Food and Agricultural Organization (FAO) as land under temporary crops. Land abandoned as a result of shifting cultivation is excluded. This category includes land under flowering shrubs, fruit trees, nut trees, and vines, but excludes land under trees grown for wood or timber (FAO, 2014).

Human population density (HPD) & Urbanization

Human population density is calculated as total amount of people (Lidgren & Gapminder, 2013) divided by total country area (Blanc, et al., 2007).

Urban population refers to people living in urban areas as defined by national statistical offices. It is calculated using World Bank population estimates and urban ratios from the United Nations World Urbanization Prospects (The World Bank, 2014). The total number of urban inhabitants was divided by the total country population to get a percentage of total population living in urbanized areas.

Poverty & Human Development Index

This measurement is presented as the Gross Domestic Product (GDP) per capita in constant 2000 US\$. The inflation but not the differences in the cost of living between countries has been taken into account (The World Bank, 2014).

Human Development Index (HDI) is based on income *per capita*, life expectancy at birth and expected years of schooling and ranges from 0 to 1 (UNDP HDR, 2014).

Poaching

The Monitoring of Illegally Killed Elephants (MIKE) program evaluates relative poaching levels based on the Proportion of Illegally Killed Elephants

(PIKE), which is calculated as the number of illegally killed elephants found divided by the total number of elephant carcasses encountered by patrols or through other means. The PIKE can range in value from zero (no illegally killed elephants encountered) to one (all elephant carcasses encountered were illegally killed) (CoP16 Doc. 53.1, 2013).

2.4.2 Analyses structure

Analyses on elephant population data were performed separately for each year (1998, 2002, 2006, 2012) according to the same protocol. In following text, when mentioning values, the dataset of 2006 is used as reference. The 2006 dataset is complete for all variables but for 1 observation (HDI of Eritrea). The data of 1998 and 2002 lacks several observations in the elephant population variable and the 2012 dataset uses the 2006 data of PA, and the latest available data on Agriculture, Urbanization, Income and HDI (resp. 2009, 2011, 2011 and 2011). The hierarchical partitioning is done similarly, yet presented together.

Data on poaching, due to lack of data, covers only data from 2006 and 2012 and has only 14 countries included, versus 31 countries included in the elephant population data.

2.4.3 Accounting for correlations between explanatory variables

To abide to the assumptions of multiple regression analyses, the variables were tested for normality. All spatial variables, HPD and the Income variable were log-transformed. All variables thus were normalized within a 5% confidence interval except PA ($p < 0.01$).

The correlations between variables were examined to account for the problem of collinearity (Graham, 2003). All spatial variables were significantly correlated ($r > 0.60$, $p < 0.05$, $n = 31$). Similarly, the welfare variables HDI, Income and Urbanization were also inter-correlated. Correlations were tested using Pearson correlation analyses (Best & Roberts, 1975; Hollander & Wolfe, 1973).

2.4.4 Multi-model inference based in AICc

Based on previous implications due to multi-collinearity, 9 models were proposed with a unique combination of spatial and welfare variables. Akaike's Information Criteria accounting for small sample sizes (AICc) was calculated for each model (Hurvich & Tsai, 1989). The models with the lowest $\Delta AICc$, which represent the best model given the data and the proposed models, were selected for further analyses (Burnham & Anderson, 2002).

Including only a limited amount of observations has potential problems concerning the power of the proposed models. To this effect, Harrell (2001) has stated a 1/10 ratio, variable/observation, is a limit. Further AICc selection was thus performed on the 3 remaining models to limit the amount of variable to 4 or less, as to not compromise the output value of said models. This was done with the *dredge* function in R from the package MuMIn (Barton, 2015).

2.4.5 Variation in abundance of *L. africana*

In this first section I analyzed the African elephant population data and its underlying influencing factors. Models were proposed following previous model selection protocol for each year of data collection. I used linear regression models in R and used the variable IQI to correct for data quality, using the function *weights* (Chambers, 1992; Wilkinson & Rogers, 1973). Models were tested for normalized residuals using Shapiro-Wilk Normality Test (Royston, 1982; Royston, 1995). When the models did not comply with the assumptions, outliers were statistically identified and removed (this occurred only in the 2002 data, where the country Angola was removed).

Hierarchical partitioning analyses (Chevan & Sutherland, 1991) were done with the R package *hier.part* (Hatt, Fletcher, Walsh, & Taylor, 2004). This reveals the independent effects of the explanatory variables on the response variable. Hierarchical partitioning considers all possible models in a multiple regression setting and attempts to identify the most likely causal factors (Fossøy, et al., 2014). The method partitions the variance in the global model and estimates the total independent contribution of a given explanatory variable on the variance of the dependent variable (Mac Nally, 2000).

2.4.6 Variation in the proportion of illegally killed elephants (PIKE)

Data on illegally killed elephants is hard to get. The PIKE estimate used in this study is based on all the elephant carcasses found in all assessed areas of a country. However, only countries that had data in both 2006 and 2012 were selected. The quality of the PIKE data depends on the total amount of carcasses inspected; similarly to the IQI, I used a variable to correct for data quality in these models (total amount of carcasses found).

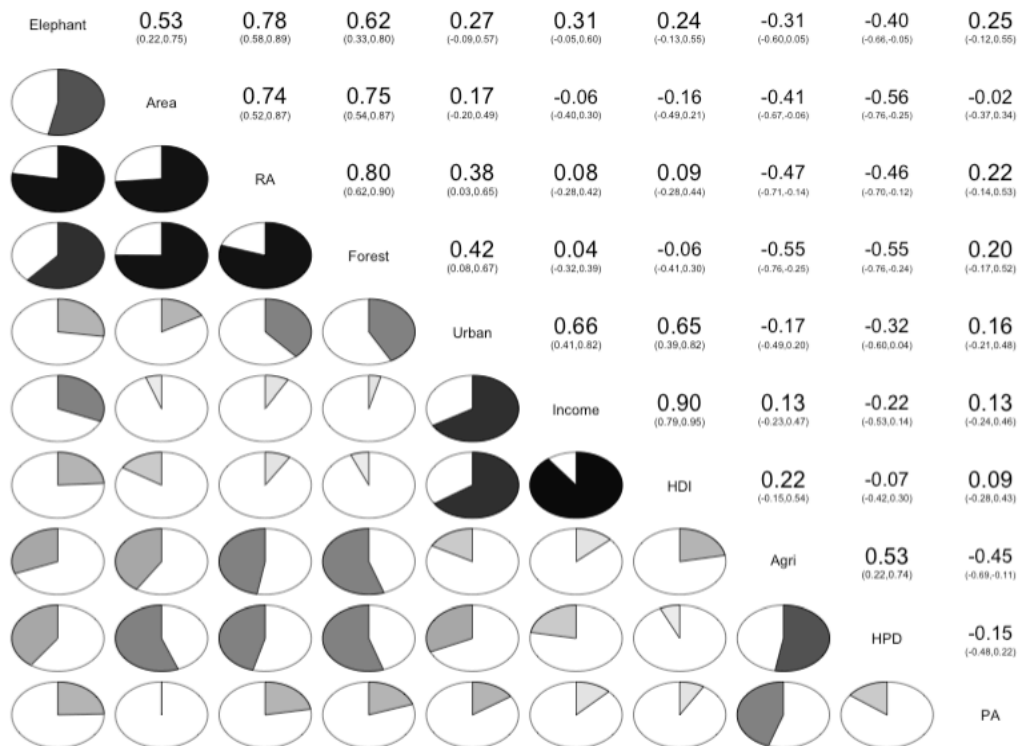


Figure 2 Correlation-matrix of the response variable (Elephant) and the explanatory variables; results from the 2006 data. Underneath the variable-name diagonal is a visual representation of the correlation coefficients (above diagonal).

3 Results

Although the elephant population data from the IUCN AESR cannot be used to observe trends over years because there is a lot of data uncertainty and the protocol used to obtain the continental results does not allow for trends over time to be made (Blanc, et al., 2007) (see *Methods*), the continental sum of elephants seems to rise steadily until 2006 (from ca. 370 000 in 1998 to ca. 555 000 elephants in 2006) but drops slightly in 2012 (ca. 517 000 elephants). The GDP *per capita*, on the other hand, increased steadily over the years for most countries, from a *per capita* average income of 734 US\$ in 1998 to an average of 891 US\$ in 2012.

Correlations were high and positive between all spatial variables: total country Area, Range Area and Forest Area ($r > 0.70$, $p < 0.001$). Other highly positively correlated variables were Income, HDI and Urbanization ($r > 0.65$) (*Figure 2*). Another relevant yet not statistically significant correlation is seen between Income and total African elephant numbers, which are slightly positively correlated ($r = 0.31$, $p = 0.09$). Similarly, a higher percentage of protected area and a larger range area influence population numbers positively (resp. $r = 0.25$, $p = 0.18$ and $r = 0.77$, $p < 0.001$). An increase in human population density is correlated with a decrease in total African elephant numbers ($r = -0.40$, $p = 0.03$) (*Figure 2*).

The 9 different models for each the 4 years of data were submitted to an AICc based model selection protocol (see *Methods*). The best model out of the 9 initial models differed significantly from the second best model in each year ($\Delta\text{AICc} > 3.00$) (see *Appendix Table A*). The selected models were subsequently submitted to a *dredge* function in R to select only the most significant parameters (up to 4 parameters per model). The ΔAICc between the different models in the *dredge* function was most often lower than 3, however, as explained in *Methods*, the power of the models would be too low if 5 parameters were used.

Table 1 Linear regression models controlling for data quality (IQI) for each of the four data points. Variables were checked for normality and some were *log*-transformed to achieve normal distribution of data.

	β	SE	Z	P
Elephant population data 2012				
(Intercept)	-10,284	2,765	-3,72	< 0,001
<i>log</i> (RA)	0,988	0,126	7,84	< 0,001
<i>log</i> (HPD)	0,378	0,275	1,37	0,181
<i>log</i> (Income)	1,088	0,259	4,20	< 0,001
Elephant population data 2006				
(Intercept)	-10,211	2,537	-4,03	< 0,001
<i>log</i> (RA)	1,081	0,115	9,41	< 0,001
<i>log</i> (HPD)	0,317	0,248	1,28	0,213
<i>log</i> (Income)	0,996	0,235	4,23	< 0,001
Elephant population data 2002				
(Intercept)	-7,140	2,293	-3,11	0,005
<i>log</i> (RA)	0,949	0,151	6,30	< 0,001
PA	0,064	0,051	1,25	0,223
Agriculture	0,006	0,019	0,33	0,748
<i>log</i> (Income)	0,692	0,282	2,45	0,022
Elephant population data 1998				
(Intercept)	-6,801	2,559	-2,66	0,014
<i>log</i> (RA)	0,809	0,169	4,78	< 0,001
PA	0,191	0,091	2,10	0,046
Agriculture	-0,012	0,022	-0,54	0,594
<i>log</i> (Income)	0,843	0,335	2,52	0,019

The selected linear regression models (based on AICc) revealed that, although with different model structure between years, both a spatial explanatory variable (Range Area) and Income were associated with the Elephant population data (Table 1). Larger (range) areas and higher averaged *per capita* income inferred higher populations of African elephant; for the 2006 model, resp. $\beta = 1.081$, $SE = 0.115$ and $\beta = 0.996$, $SE = 0.235$. Standard errors on the estimates are small enough to deduct that there is a significant effect on the elephant data. Similar results were found in the 2012 and 2006 data. Although the best model from the AICc selection included other explanatory variables, these were not significant except for the percentage of Protected Area in the 1998 data ($\beta = 0.191$, $SE=0.091$, $p = 0.046$). Human population density was, even if included in the selected model, not significant in the best models, and the Agriculture variable was also non-significant ($p > 0.15$).

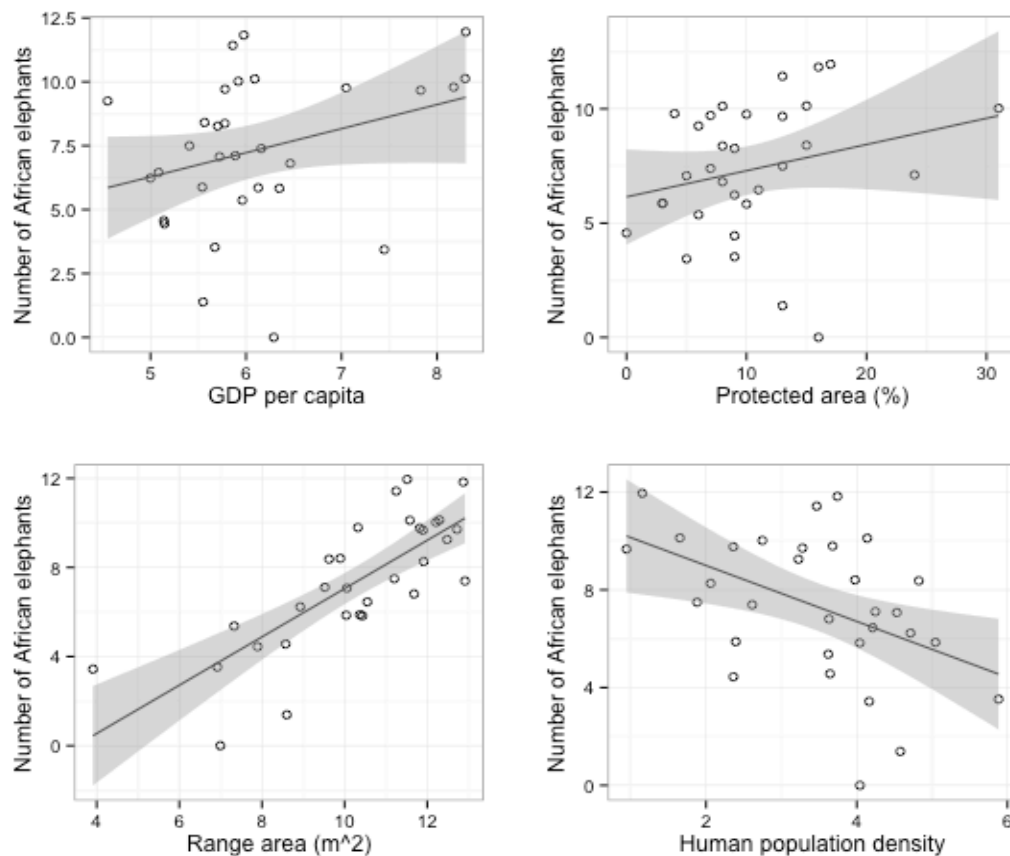


Figure 3 Scatterplots showing the relation between the number of African elephants and several explanatory variables. The linear regression line with in grey the 95% confidence region is plotted as well.

The hierarchical partitioning (*Figure 4 and Appendix Table B*) revealed a trend over the years in importance of the variables to the elephant population data. Percentage Protected Area had initially the most effect on the population of African elephants (67.7% in 1998) but this gave way to the importance of Income, which became the most important predictor variable in the last 2 years of data collection (resp. 36.8% in 2006 and 57.2% in 2012). Range Area, although not as big an influence on the population data as Income or PA, was the third most influential explanatory variables of the selected 6 variables (30.2% in 2006). These results are analogous with the regression model output, where PA was only significant in 1998 and RA and Income where the only significant variables in later years.

Percentage of illegally killed elephants (PIKE) decreased with an increased *per capita* Income ($r = -0.74$, $p = 0.003$). The linear regression model concerning PIKE numbers in 2006 revealed that HDI, which is very strongly correlated with Income ($r = 0.92$, $p < 0.001$), and PA were both significant explanatory variables (resp. $\beta = -1.835$, $SE = 0.212$ and $\beta = 0.018$, $SE = 0.003$). However, unlike HDI and Income, PA had a positive influence on the PIKE index: the more protected area the higher the PIKE index appeared to be (2012 data) (*Table 2*). Poaching was also positively influenced by the total Area ($\beta = 0.246$, $SE = 0.729$).

Table 2 Linear regression models controlling for data quality (total amount of carcasses found) for each of the two data points. Variables were checked for normality and some were *log*-transformed to achieve normal distribution of data.

	β	SE	Z	P
PIKE 2012				
(Intercept)	0,773	0,060	12,83	< 0,001
<i>log</i> (Income)	< 0,001	< 0,001	2,28	0,0418
PIKE 2006				
(Intercept)	-2,369	0,729	-3,25	0,009
<i>log</i> (Area)	0,246	0,050	4,92	< 0,001
PA	0,018	0,003	5,28	< 0,001
HDI	-1,835	0,212	-8,66	< 0,001

4 Discussion

In search of statistical evidence for the ultimate factors influencing African elephant populations, we investigated several Sub-Saharan countries containing elephant populations. Country specific traits such as agricultural activity and human population density are supposed to have significant impacts on the elephant populations (Murcia, 1995). We analyzed several (6) of these country specific, human related factors in order to find statistical evidence for their importance to the African elephant populations.

The elephant populations in Africa have known a turbulent past but were slowly recovering again in several countries between 1998 and 2007 (Blanc, et al., 2007). In 2012 we see again a drop, likely because of illegal poaching activities (Wittemyer, Northrupa, Blanc, Douglas-Hamilton, Omondif, & Burnhama, 2014). The data on poaching used in this research was too incomplete (data was available for only 14 countries in both 2006 and 2012, (CoP16 Doc. 53.1, 2013)) to be used in the models yet could have proven very interesting as seen in Lemieux & Clarke (2009).

Due to the online data collection method, there was often no detailed information available on how the data was collected; the lack of the collection methods, initial sources and data management makes it not easy to reflect on possible data artifacts or confounders present in this dataset. Poor data quality restrains the outcome of a study and missing data points (e.g. Protected Area data of 2012 was missing) can have important effects on the results and conclusions. The 1998 elephant population data was far from perfect: several countries had no data and others had only speculations. The latest data period, 2012, missed data in PA and there was unfortunate mismatch with other parameters such as

Urbanization (2011), Agriculture (2009) and HDI (2011). Data for HDI was only available for the years 2000, 2006 and 2011.

A high correlation between all spatial variables was to be expected ($r > 0.70$, $p < 0.001$) and all three spatial variables explain a great amount of variation in the elephant population data. African elephants need extensive areas to sustain a viable population (Armbruster & Lande, 1993) and prefer forested areas to savannas (Barnes, Blom, & Alers, 1995); elephant range area will always include mostly forested area. Our models revealed that the preserving elephant range area is vital in order for elephant populations to grow. Although forest area was also important, it explained less variation in the population data and was thus discarded through the AICc selection.

From our models, the most intriguing and significant factor appeared to be 'Income', which is the average GPD *per capita*, corrected for inflation over the years (The World Bank, 2014). This parameter not only represents a measurement of poverty of the human population but also gives an idea on the welfare and economical stability of the respective country. Income was of course very strongly correlated with the Human Development Index (HDI) ($r = 0.86$, $p < 0.001$), which apart from an income *per capita* parameter, includes a quality of education index and average lifespan as well. From the AICc selection, Income appeared to be the variable explaining most variance in elephant populations, suggesting that the economical welfare of a country and its inhabitants is an important factor to be considered while discussing elephant conservation management plans.

Oddly enough, factors which were initially thought to be most important like the Human Population Density (HPD) and agricultural activity, were not significant in any models and were often even discarded by the AICc selection, meaning they did not explain enough variation in the elephant population data. This contradicts findings from other papers that show the impacts these factor can do to natural populations (Leimgruber, Gagnon, Wemmer, Kelly, Songer, & Selig, 2003 ; Hoare & du Toit, 1999). The results from this study suggest that the HPD and the agricultural activities in a country aren't that important to the elephant's survival. They did however correlate negatively with the elephant population data (*Figure 3*). Additionally, this is in direct conflict with the supposedly important effect of the forest area on the elephant populations. One of the main consequences of expanding agricultural activities is deforestation (Angelsen, 1999), which we know has a devastating effect on elephant range sizes (Leimgruber P. , 2003). This

mismatch might be due to a data artifact and/or some confounding factors not included in these analyses. The parameter for agricultural activity is measured as the percentage of total land area that is used for agricultural purposes. Data artifacts are present due to a mismatch in year of data collection between Agricultural (last data from 2009) data and elephant population data (last data from 2012) and due to errors in data collection, be it from misinterpreting satellite images or inaccurate area measurements.

Another variable deemed important for the conservation of elephants are protected areas. In this analysis a measurement of protected areas in countries was included to have a basic and initial view on how important protected areas were in explaining elephant population data because this is far from an easy topic. Numerous confounding factor and indirect effect reduce the effectiveness of a protected area (Metzger, Sinclair, Hilborn, Hopcraft, & Mduma, 2010), such as edge effects (Woodroffe & Ginsberg, 1998). From the linear regression models the amount of protected areas, calculated as percentage of the countries that was

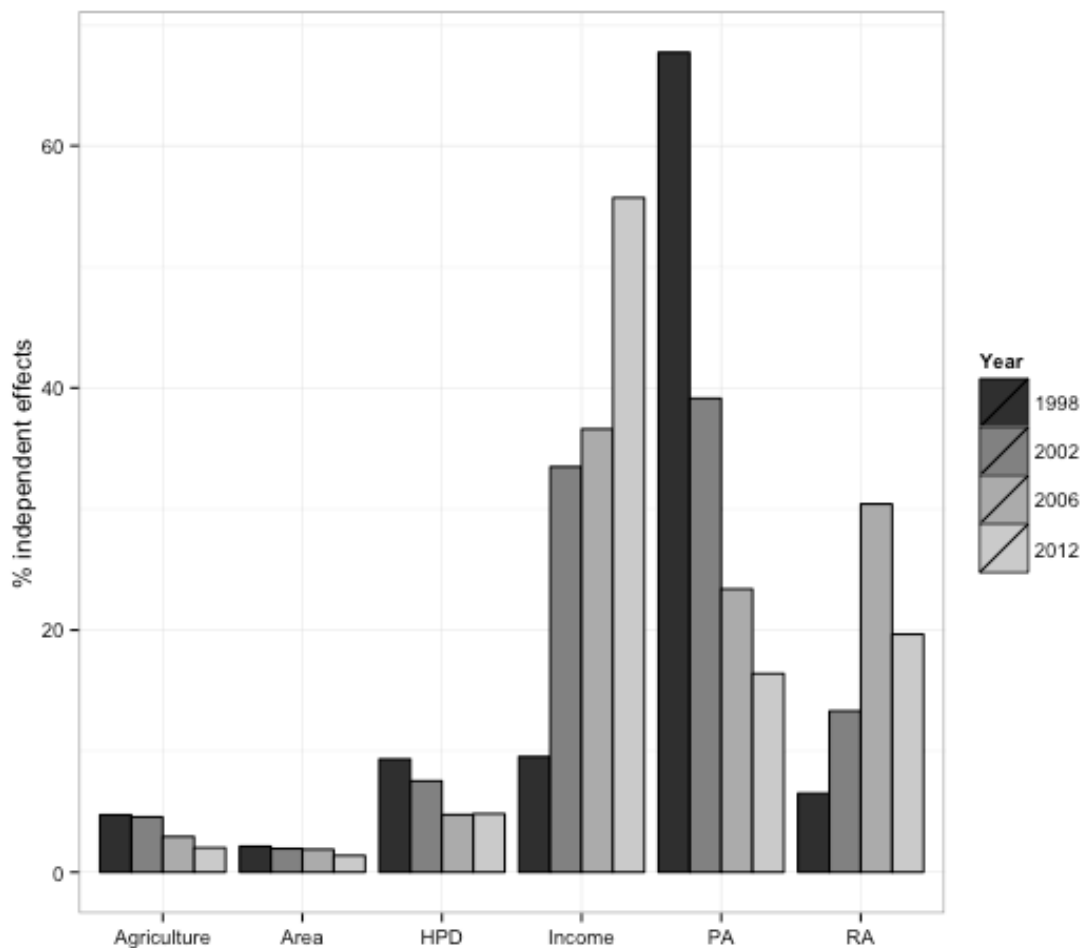


Figure 4 Hierarchical partitioning of variance showing the independent effects of each predictor variable for the four years of data analysed in this study.

created as National Park or Game Reserve (IUCN Category II or higher) (Blanc, et al., 2007), it was expected that countries with higher income and higher tourism rates would invest more in these protected areas; this was not enforced by this study (corr. between Income and PA: $r = 0.07$, $p = 0.72$).

Including the amount of areas under protection and how big each of them are could change the outcome of this result (Armbruster & Lande, 1993), since elephants need huge areas or several connected protected areas to flourish. Moreover, including a more detailed model of protected areas used by elephants would also benefit the Human Elephant Conflict (Douglas-Hamilton, Krink, & Vollrath, 2005).

The hierarchical partitioning analyses performed in this study, give an interesting view on the trend in importance of several variables over the years. Only a few variables have any impact at all and they change drastically over the years. As the model approach already revealed, the Income variable is of very high importance in this dataset. The relative importance of the economical welfare to the elephant populations appears to increase severely from only 15% in 1998 to over 50% in 2012. This in sharp contrast to the relative importance of the amount of protected areas, which was the most important factor in 1998 (over 65%) but dropped down to less than 20% in 2012. This could suggest that even if countries have relatively large protected, without sufficient funds or economical grow, those countries cannot protect their elephant populations. Interestingly, although the range area was one of the most significant variables in the linear regression models, it's of only marginal importance in the hierarchical partitioning analyses.

Data on poaching was analyzed separately due too few and incomplete data and the purpose of this was solely to see if similar factors were important in explaining the variance in poaching data compared to the elephant population data. The 2012 model lacked fit and power and shows only the variable income to be marginally significant ($p = 0.0418$). Interestingly, the 2006 model does not include Income but the highly correlated HDI as most influential explanatory variable. The model, which included Income as variable, was discarded after AICc selection. Apart from a big influence of HDI on the poaching data, the model also reveals that the spatial variable Area and the amount of Protected Area explain a significant amount of variation. However, although the effect of Area and HDI is as expected (a negative and positive effect, respectively), it seems that the total size of protected areas has a negative effect on poaching: the higher the amount of Protected Area, the more elephants get illegally killed. This is most likely due to the underlying factor that there is much more surveillance in the national parks which logically amounts in a better and more substantial detection corpses and

thus of illegally killed elephants. This confirms findings in other papers that poverty is one of the main drivers behind poaching (Wasser, et al., 2008; Blanc, et al., 2007; CoP16 Doc. 53.1, 2013).

That the HDI, which includes an income *per capita* parameter, explains much variation in the poaching data is similar to what we found with the elephant population data, where Income was the most influential factor.

Future work

It would be interesting to delve deeper into the importance of this income variable and what the exact influence is on the African elephant populations in Sub-Saharan Africa. Which aspects does the 'Income' variable used in this study, really cover and what could be added? The HDI was highly correlated with the Income variable; how important are the 2 other main parameter used in the HDI for the elephant populations? How important is the economic political stability compared to the political stability for the preservation of elephants? What with the black market, does it influence the prosperity of the countries involved and does it, apart from having a direct negative effect on the African elephant, have a great influence in how the economy and subsequent *per capita* welfare evolve?

The SLOSS topic is very interesting for further research as well: how do protected areas really help endangered species like the African elephant? Every species has it's own specific demands and for elephants in particular they need huge areas to survive. The SLOSS (Single Large or Several Small protected area(s)) debate will prove most valuable here. Definitely with the study species, a minimum area is necessary to sustain a viable population (Armbruster & Lande, 1993) and including the amount of protected areas and their individual sizes could give interesting insights in how to efficiently protect this particular species (Douglas-Hamilton, Krink, & Vollrath, 2005). This fell, however, beyond the scope of this thesis.

5 Conclusion

The aim of this thesis was to determine which human induced factors had a significant influence on the African elephant populations of Sub-Saharan countries. We proposed several variables that reflected parts of the Human elephant Conflict such as increasing human population density and deforestation. We hypothesized that deforestation, caused by e.g. agricultural activities (Thuppil & Coss, 2012; Angelsen, 1999), would be of major importance to the elephant populations. However, our models did not confirm this, only sporadically included in the selected models and having no significant effect. Similarly, as hypothesized, the increasing human population density does not have a significant direct effect on elephants. A rising population does translate in various other problems such as increasing poverty, which in turn increases poaching. Our data found a very strong correlation between the poverty variable ‘Income’ and the poaching levels, confirming previous findings (Wasser, et al., 2008; Bulte & van Kooten, 1999; CoP16 Doc. 53.1, 2013). Poaching was not included in our models because of poor data, but its effect has been proved times over (Blanc, et al., 2007). We hypothesized that the total amount of protected area would have a positive, but small effect on elephant populations. Our models confirm this hypothesis but also reveal that the importance of protected areas in explaining variation in elephant populations has been decreasing, being still very important in 1998 but having but little influence in 2012. Although more research needs to be done on the effect of park size and protected migration routes (Armbruster & Lande, 1993; Berger, 2003), our study suggest that total protected area is of only marginal importance to the survival of the elephant. Furthermore, our findings suggest that with increasing park area, poaching levels rise as well; this might be an artifact due to non-random sampling of elephant carcasses.

The main result for our models is that poverty drives the decline in elephant populations. Our variable, Income, which represents the average per capita GDP, was by far the most significant and constant variable in our models. This can be the result of several indirect effects to the elephant populations. First of all it can reflect on a countries welfare (reflected better in the HDI, which was very strongly correlated with Income) and economic stability. Without sufficient funds, even countries with relative large protected areas can't enforce the protection of their wildlife and poachers roam free. Income also reflects on the individual: poverty forces local people to hunt for food and be able to trade. A higher living standard would give them less incentive to illegally kill wildlife (Fischer, Muchapondwa, & Sterner, 2010). As found in many other studies, poaching has a huge effect on African elephant populations, and the economical (and political) situation of a country and its inhabitants might be the drive behind the black market and poaching in general.



Figure 5 Elephants at dusk, Okaukuejo, Etosha National Park, Namibia

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References

- Ahlering, M. A., Maldonado, J. E., Eggert, L. S., Fleischer, R. C., Western, D., & Brown, J. L. (2013). Conservation outside Protected Areas and the Effect of Human-Dominated Landscapes on Stress Hormones in Savannah Elephants. *Conservation Biology* .
- Amwata, D. A., & Mganga, K. Z. (2014). The African elephant and food security in Africa: experiences from Baringo District, Kenya . *Pachyderm* .
- Angelsen, A. (1999). Agricultural expansion and deforestation: modelling the impact of population, market forces and property rights. *Journal of development economics* (1), 185 -218.
- Armbruster, P., & Lande, R. (1993). A Population Viability Analysis for African Elephant (*Loxodonta africana*): How Big Should Reserves Be? . *Conservation Biology* .
- Barnes, R. F., Blom, A., & Alers, M. P. (1995). A Review of the Status of the Forest Elephants *Loxodonta africana* in Central Africa. *Biological Conservation* (71), 125-132.
- Barton, K. (2015). MuMIn: multi-model inference. R package, version 1.13.4. .
- Barua, M. (2011). Mobilizing metaphors: the popular use of keystone, flagship and umbrella species concepts . *Biodivers Conserv* .
- Berger, J. (2003). The Last Mile: How to Sustain Long-Distance Migration in Mammals. *Conservation Biology* .
- Best, D. J., & Roberts, D. E. (1975). Algorithm AS 89: The Upper Tail Probabilities of Spearman's rho. *Applied Statistics* (24), 377-379.
- Blanc, J., Barnes, R., Craig, G. C., Dublin, H., Thouless, C., Douglas-Hamilton, I., et al. (2007). African Elephant Status Report 2007 An update from the African Elephant Database . *Occasional Paper series of the IUCN Species Survival Commission* .

- Bulte, E. H., & van Kooten, G. C. (1999). Economics of Antipoaching Enforcement and the Ivory Trade Ban . *American Journal of Agricultural Economics* .
- Burnham, K., & Anderson, D. (2002). Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. *Springer, New York* .
- Chambers, J. M. (1992). Linear models. . *Chapter 4 of Statistical Models in S eds J. M. Chambers and T. J. Hastie, Wadsworth & Brooks/Cole*.
- Chevan, A., & Sutherland, M. (1991). Hierarchical Partitioning. *The American Statistician* (45), 90–96.
- Comstock, K. E., Georgiadis, N., Pecon-Slattery, J., Roca, A. L., Ostrander, E. A., O'Brien, S. J., et al. (2002). Patterns of molecular genetic variation among African elephant populations. . *Molecular Ecology* .
- CoP16 Doc. 53.1. (2013). Interpretation and implementation of the Convention - Species trade and conservation - Elephants - MIKE. *CITES: Sixteenth meeting of the Conference of the Parties Bangkok (Thailand)* .
- Cumming, D. (1994). WWF/EC study of land-use trends, natural resource use and agro-ecosystem sustainability in the Zambezi Valley of Zimbabwe. *In Proceedings of a Workshop to Co-ordinate Studies of Land-use change in the Zambezi Valley of Zimbabwe* .
- Cumming, D., Fenton, M., Rautenbach, I., Taylor, R., Cumming, G., Cumming, M., et al. (1997). Elephants, woodlands and biodiversity in Southern Africa. *South African Journal of Science* .
- De Boer, W. F., & Baquete, D. (1998). Natural resource use, crop damage and attitudes of rural people in the vicinity of the Maputo Elephant Reserve, Mozambique . *Environmental Conservation* .
- Douglas-Hamilton, I., Krink, T., & Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* (92), 158–163.
- du Toit, J. T., Moe, S. R., & Skarpe, C. (2014). Elephant-Mediated Ecosystem Processes in Kalahari-Sand Woodlands . *Elephants and Savanna Woodland Ecosystems: A Study from Chobe National Park, Botswana*, .
- FAO. (2014). data retrieved from <http://data.fao.org>. *Food and Agricultural Organisation of the United Nations* .
- Fischer, C., Muchapondwa, E., & Sterner, T. (2010). A Bio-Economic Model of Community Incentives for Wildlife Management Under CAMPFIRE . *Environ Resource Econ* .
- Fossøy, F., Stokke, B. °, Ka °si, T. K., Dyrset, K., Espmark, Y., Hoset, K. S., et al. (2014). Reproductive success is strongly related to local and regional climate in the Arctic snow bunting (*Plectrophenax nivalis*) . *Polar Biology* .

- Gavin, M. C., Solomon, J. N., & Blank, S. G. (2009). Measuring and Monitoring Illegal Use of Natural Resources . *Conservation Biology* .
- Graham, M. (2003). Confronting Multicollinearity in Ecological Multiple Regression. *Ecology* (84), 2809-2815.
- Grueber, C., Nakagawa, S., Laws, R., & Jamieson, I. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* (24), 699–711.
- Hackel, J. D. (1999). Community Conservation and the Future of Africa's Wildlife. *Conservation Biology* .
- Haines-Young, R. (2009). Land use and biodiversity relationships . *Land Use Policy* .
- Harrell, F. (2001). Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis . *Springer, New York* .
- Hatt, B. E., Fletcher, T. D., Walsh, C. J., & Taylor, S. L. (2004). The influence of urban density and drainage infrastructure on the concentrations and loads of pollutants in small streams. *Environmental Management* (34), 112–124.
- Haynes, G. (2011). Elephants (and extinct relatives) as earth-movers and ecosystem engineers . *Geomorphology* .
- Hoare, R. E., & du Toit, J. T. (1999). Coexistence between People and Elephants in African Savannas. *Conservation Biology* (3), 633-639.
- Hollander, M., & Wolfe, D. A. (1973). Nonparametric Statistical Methods. *New York: John Wiley & Sons* , 185–194.
- Holmern, T. (2010). Bushmeat Hunting in Western Serengeti: Implications for Community-based Conservation. *Conservation of Natural Resources - Some African & Asian Examples* .
- Hurvich, C. M., & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika* (76), 297–307.
- Inogwabini, B.-I., Mbende, L., Bakanza, A., & Bokika, J. C. (2013). Crop damage done by elephants in Malebo Region, Democratic Republic of Congo . *Pachyderm* .
- Jones, C., Lawton, J., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* .
- Jones, C., Lawton, J., & Shachak, M. (1997a). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* .
- King, L. E., Soltis, J., Douglas-Hamilton, I., Savage, A., & Vollrath, F. (2010). Bee Threat Elicits Alarm Call in African Elephants . *PLoS ONE* .

- Leimgruber, P. (2003). Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. *Animal conservation* (4), 347 -359.
- Leimgruber, P., Gagnon, J., Wemmer, C., Kelly, D., Songer, M., & Selig, E. R. (2003). Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation . *Animal Conservation* (6), 347–359 .
- Lemieux, A. M., & Clarke, R. V. (2009). The International Ban on Ivory Sales and its Effects on elephant Poaching in Africa. *BRIT. J. CRIMINOL.* , 451–471.
- Lewis, R. D. (1996). When cultures collide: Leading across Cultures.
- Lidgren, M., & Gapminder. (2013). several sources confined by M. Lidgren.
- Lindenmayer, D. B., Cunningham, R. B., & Pope, M. L. (1998). A large-scale experiment to examine the effects of landscape context and habitat fragmentation on mammals. *Biological Conservation* .
- Mac Nally, R. (2000). Regression and model building in conservation biology, biogeography and ecology: the distinction between and reconciliation of 'predictive' and 'explanatory' models. . *Biodiversity and Conservation* (9), 655–671.
- Marshall, L. (2007). Kruger Elephants head for Mozambique. *Sunday Urgus* .
- Martin, E., & Vigne, L. (2014). Luanda—the largest illegal ivory market in southern Africa . *Pachyderm* .
- Messer, K. D. (2010). Protecting endangered species: When are shoot-on-sight policies the only viable option to stop poaching? . *Ecological Economics* .
- Metzger, K. L., Sinclair, A. R., Hilborn, R., Hopcraft, J. G., & Mduma, S. A. (2010). Evaluating the protection of wildlife in parks: the case of African buffalo in Serengeti . *Biodivers Conserv* .
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *TREE* .
- Nyahongo, J. W. (2010). Community Participation in Management and Sustainable Use of Wildlife: Advantages and Disadvantages. *Conservation of Natural Resources - Some African & Asian Examples* .
- Nyahongo, J. W. (2010a). The Source-Sink Concept in the Conservation of African Ungulates. *Conservation of Natural Resources - Some African & Asian Examples* .
- Owen-Smith, R. N. (1988). Megaherbivores: the influence of very large body size on ecology. *Cambridge Studies in Ecology* .
- Parker, I., & Amin, M. (1983). Ivory Crisis.

- Pringle, R. M. (2008). Elephants as Agents for Habitat Creation for Small Vertebrates at the Patch Scale. *Ecology* .
- Pringle, R., Young, T., Rubenstein, D., & McCauley, D. (2007). Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. . *Proceedings of the National Academy of Sciences of the United States of America* .
- R - A Development Core Team, v. 3. (2015). A language and environment for statistical computing. *R Foundation for Statistical Computing* .
- Ramey, E. M., Ramey, R. R., Brown, L. M., & Kelley, S. T. (2013). Desert-dwelling African elephants (*Loxodonta africana*) in Namibia dig wells to purify drinking water . *Pachyderm* .
- Roca, A. L., & O'Brien, S. J. (2005). Genomic inferences from Afrotheria and the evolution of elephants. . *Current Opinion in Genetics & Development* , 652-658 .
- Roca, A. L., Georgiadis, N., & O'Brien, S. J. (2005). Cytonuclear genomic dissociation in African elephant species. . *Nature Genetics* , 96-100 .
- Royston, P. (1982). An extension of Shapiro and Wilk's W test for normality to large samples. *Applied Statistics* (31), 115–124.
- Royston, P. (1995). Remark AS R94: A remark on Algorithm AS 181: The W test for normality. *Applied Statistics* (44), 547–551.
- S.K., W., Clark, W., Drori, O., Kisamo, E., Mailand, C., Mutayoba, B., et al. (2008). Combating the Illegal Trade in African Elephant Ivory with DNA Forensics. *Conservation Biology* , 22 (4), 1065–1071.
- Shoshani, J. (1993). Elephants: the super keystone species . *Swara* , 25-29 .
- Skarpe, C., Aarrestad, P. A., Andreassen, H. P., Dhillion, S. S., Dimakatso, T., du Toit, J. T., et al. (2004). The Return of the Giants: Ecological Effects of an Increasing Elephant Population . *A Journal of the Human Environment* .
- Spinage, C. (1990). Botswana's problem elephants. *Pachyderm* .
- Stiles, D. (2004). The ivory trade and elephant conservation. *Environmental Conservation* , 309–321.
- The World Bank, W. D. (2014). retrieved from <http://data.worldbank.org>.
- Thuppil, V., & Coss, R. G. (2012). sing Threatening Sounds as a Conservation Tool: Evolutionary Bases for Managing Human–Elephant Conflict in India . *Journal of International Wildlife Law & Policy* .
- UNDP HDR. (2014). United Nations Development Program - Human Development Report. Retrieved from <http://hdr.undp.org/en/data> .

- Wiafe, E. D., & Sam, M. K. (2014). Evaluation of a low-tech method, pepper-grease, for combatting elephant crop-raiding activities in Kakum Conservation Area, Ghana . *Pachyderm* .
- Wilkinson, G. N., & Rogers, C. E. (1973). Symbolic descriptions of factorial models for analysis of variance. *Applied Statistics* (22), 392–9.
- Wittemyer, G. (2011). Effects of Economic Downturns on Mortality of Wild African Elephants . *Conservation Biology* .
- Wittemyer, G., Northrupa, J. M., Blanc, J., Douglas-Hamiltonb, I., Omondif, P., & Burnhama, K. P. (2014). Illegal killing for ivory drives global decline in African elephants . *PNAS* .
- Woodroffe, R., & Ginsberg, J. R. (1998). Edge Effects and the Extinction of Populations Inside Protected Areas. *SCIENCE* .
- Wright, J. P., & Jones, C. G. (2006). The Concept of Organisms as Ecosystem Engineers Ten Years On: Progress, Limitations, and Challenges. *BioScience* .

Appendix

Table A Ranking of the linear regression models (lm()-procedure, (R - A Development Core Team, 2015)) of total elephant population data of Sub-Saharan countries. Candidate models were proposed due to high multi-collinearity between the 3 spatial variables Area, Range Area (RA) and Forest Area (Forest) and the 3 welfare variables Income, HDI and Urbanisation (Urb). The models was corrected for data quality with the command *weights* and the variables IQI and IQI1. The best model (on top) was chosen for further analyses. Df is the amount of parameters and $\Delta AICc$ is the AICc value difference between the models with lowest AICc and the other models. Agri = Agriculture; PopDens = Human population density; PA = Protected area. (*Continued on next page*)

Candidate model	df	AICc	$\Delta AICc$
Elephant data 2012			
$\log(RA2012) + PA2012 + \log(PopDens2012) + Agri2009 + \log(Income2011)$, weights=IQI1	7	129,54	0,00
$\log(RA2012) + PA2012 + \log(PopDens2012) + Agri2009 + HDI2011$, weights=IQI1	7	132,69	3,15
$\log(RA2012) + PA2012 + \log(PopDens2012) + Agri2009 + Urb2011$, weights=IQI1	7	138,18	8,64
$\log(Forest2012) + PA2012 + \log(PopDens2012) + Agri2009 + HDI2011$, weights=IQI1	7	141,49	11,95
$\log(Area) + PA2012 + \log(PopDens2012) + Agri2009 + HDI2011$, weights=IQI1	7	144,75	15,21
$\log(Forest2012) + PA2012 + \log(PopDens2012) + Agri2009 + \log(Income2011)$, weights=IQI1	7	145,11	15,57
$\log(Area) + PA2012 + \log(PopDens2012) + Agri2009 + \log(Income2011)$, weights=IQI1	7	147,26	17,72
$\log(Forest2012) + PA2012 + \log(PopDens2012) + Agri2009 + Urb2011$, weights=IQI1	7	148,81	19,27
$\log(Area) + PA2012 + \log(PopDens2012) + Agri2009 + Urb2011$, weights=IQI1	7	151,29	21,74

Table A continued from previous page

Candidate model	df	AICc	Δ AICc
Elephant data 2006			
$\log(\text{RA2006}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \log(\text{Income2006})$, weights=IQI	7	123,44	0,00
$\log(\text{RA2006}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \text{HDI2006}$, weights=IQI	7	126,90	3,46
$\log(\text{RA2006}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \text{Urb2006}$, weights=IQI	7	129,84	6,40
$\log(\text{Forest2006}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \text{HDI2006}$, weights=IQI	7	141,84	18,40
$\log(\text{Forest2006}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \log(\text{Income2006})$, weights=IQI	7	143,54	20,10
$\log(\text{Forest2006}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \text{Urb2006}$, weights=IQI	7	145,99	22,55
$\log(\text{Area}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \log(\text{Income2006})$, weights=IQI	7	146,22	22,78
$\log(\text{Area}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \text{HDI2006}$, weights=IQI	7	147,37	23,93
$\log(\text{Area}) + \text{PA2006} + \log(\text{PopDens2006}) + \text{Agri2006} + \text{Urb2006}$, weights=IQI	7	151,47	28,03
Elephant data 2002			
$\log(\text{RA2002}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \text{HDI2000}$, weights=IQI	7	126,75	0,00
$\log(\text{Forest2002}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \text{HDI2000}$, weights=IQI	7	135,41	8,66
$\log(\text{RA2002}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \log(\text{Income2002})$, weights=IQI	7	136,79	10,04
$\log(\text{Area}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \text{HDI2000}$, weights=IQI	7	137,10	10,35
$\log(\text{RA2002}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \text{Urb2002}$, weights=IQI	7	142,83	16,08
$\log(\text{Area}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \log(\text{Income2002})$, weights=IQI	7	149,71	22,96
$\log(\text{Forest2002}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \log(\text{Income2002})$, weights=IQI	7	150,23	23,47
$\log(\text{Forest2002}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \text{Urb2002}$, weights=IQI	7	153,35	26,60
$\log(\text{Area}) + \text{PA2002} + \log(\text{PopDens2002}) + \text{Agri2002} + \text{Urb2002}$, weights=IQI	7	155,04	28,29

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Table A continued from previous page

Candidate model	df	AICc	Δ AICc
Elephant data 1998			
log(RA1998) + PA1998 + log(PopDens1998) + Agri1998 + HDI2000, weights=IQI	7	120,86	0,00
log(Forest1998) + PA1998 + log(PopDens1998) + Agri1998 + HDI2000, weights=IQI	7	125,17	4,31
log(Area) + PA1998 + log(PopDens1998) + Agri1998 + HDI2000, weights=IQI	7	125,36	4,50
log(Area) + PA1998 + log(PopDens1998) + Agri1998 + log(Income1998), weights=IQI	7	135,47	14,61
log(RA1998) + PA1998 + log(PopDens1998) + Agri1998 + log(Income1998), weights=IQI	7	137,64	16,78
log(Forest1998) + PA1998 + log(PopDens1998) + Agri1998 + log(Income1998), weights=IQI	7	142,46	21,60
log(RA1998) + PA1998 + log(PopDens1998) + Agri1998 + Urb1998, weights=IQI	7	145,21	24,35
log(Area) + PA1998 + log(PopDens1998) + Agri1998 + Urb1998, weights=IQI	7	146,73	25,87
log(Forest1998) + PA1998 + log(PopDens1998) + Agri1998 + Urb1998, weights=IQI	7	148,73	27,87

Table B Hierarchical partitioning of variance showing the independent effects of each predictor variable for the four years of elephant data analysed in this study. In percentages; values relative to other parameters for a certain year. HPD = human population density, Area = total country area

	1998	2002	2006	2012
Area	2,1	2,0	1,9	1,4
Range Area	6,5	13,3	30,4	19,7
Protected Area	67,7	39,1	23,4	16,4
Income	9,5	33,5	36,6	55,7
Agriculture	4,7	4,6	2,9	2,0
HPD	9,3	7,5	4,8	4,8