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Age structure as an indicator of poaching pressure: insights from rapid assessments of elephant populations across space and time

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ABSTRACT

Detecting and monitoring illegal harvesting pressure on wild populations is challenging due to the cryptic nature of poaching activities. Although change in population age structure has been suggested as an indicator of harvesting pressure, few studies have tested its validity when based on short-term field surveys. Using data from rapid demographic assessment surveys carried out in 2009 at six sites in Tanzania, we examined whether African elephant populations experiencing contrasting levels of poaching pressure showed significant differences in their age structure, operational sex ratio (i.e. adult males to adult females), dependent individual to adult female ratio at the group level, and proportion of tuskless individuals. We also compared similar metrics between the population sampled in Ruaha National Park in 2009 and again in 2015 following a suspected increase in poaching. Elephant populations experiencing medium and high levels of poaching in 2009 were characterised by fewer calves and old individuals, a reduced number of adult males relative to adult females, and a lower ratio of calves to adult females within groups. We also found a higher proportion of tuskless individuals in poached populations (> 6 %). Changes in age structure in the Ruaha population between 2009-15 were similar to those observed across sites in 2009. Our findings are consistent with previous work documenting how the loss of older individuals – targeted for their larger tusks – decreases recruitment and survival of elephant calves. Illegal killing for ivory is a huge threat to the survival of African elephants. In this context, the present study contributes towards validating the use of age structure as an indicator of poaching pressure in elephant populations, but also in other wildlife populations where illegal offtake is targeted at specific age classes.

KEYWORDS: age structure, operational sex ratio, rapid demographic assessment, Ruaha National Park, Tanzania, tusklessness.

1. INTRODUCTION

Illegal harvesting activities affecting wildlife populations can be hard to detect and monitor, especially in populations that are not under close observation (Gavin et al. 2010, Liberg et al. 2012). Although numerous indicators have been developed to help track illegal harvesting pressure on wild populations, including interview and market-based metrics (Jones et al. 2008, Harris et al. 2015), forensic observations (Manel et al. 2002, Retief et al. 2014), and behavioural responses (Caro 2005, Goldenberg et al. 2017), these often lack clear links to both harvesting and demographic processes. In general, harvesting removes a subset of individuals from a given population, such as those with the brightest colours or largest horns, which can often be defined as belonging to a specific age class (Ginsberg & Milner-Gulland 1994, Pozo et al. 2016). In the case of illegal and poorly regulated legal harvesting, it can be expected that selective over-harvesting of individuals according to age will result in changes to a population’s structure, and most notably decreases in the frequency of individuals in the targeted age class.

Age structure has been put forward as an indicator with which to monitor populations of large herbivores (Noss 1990, Rughetti 2016). Indeed, age structural changes in wild populations are often investigated as part of long-term, individual-based studies, which typically examine demographic processes such as the survival, recruitment and mortality of study individuals (Langvatn & Loison 1999; Milner, Nilsen & Andreassen 2007; Moss et al. 2011; Wittemyer et al. 2013). Although hugely valuable, such studies are scarce and rarely carried out on populations experiencing varying levels of legal and/or illegal harvesting, thus hindering the assessment of age structure as an indicator of harvesting pressure. When long-term datasets are not available, comparative studies may still be derived from rapid population surveys carried out over short periods of time and across multiple sites, yet indicators based on this approach have rarely been developed and tested (Tella et al. 2013).

In this study, we compare the age structure and level of tusklessness between African elephant (*Loxodonta africana*) populations experiencing contrasting levels of past and present poaching pressure in Tanzania. The illegal killing of elephants for ivory is leading to population declines across the African continent (Wittemyer et al. 2011; Wittemyer et al. 2014; Chase et al. 2016), however, recent censuses have highlighted alarming population declines in Tanzania (Chase et al. 2016), a country shown to be one of the main poaching hotspots in Africa (Wasser et al. 2015; Thouless et al. 2016). In this context, we use a rapid demographic assessment (RDA) method developed by Poole (1989) to quantify the population structure of poached populations. The RDA approach attempts to sex and age as many individuals as possible within a given population, with the overall aim of providing a snapshot of the population structure at a given point in time (Kioko et al. 2013). Despite being logistically more feasible than recently proposed methods based on aerial monitoring (Ferreira & van Aarde 2008), few studies since Poole (1989) have promoted the RDA as a tool to evaluate changes in elephant population structure, and use these as indicators of poaching pressure.

Using RDA data on 2,631 elephants, we examine whether elephant populations experiencing low, medium, and high levels of poaching prior to 2009 show significant differences in their age structure, operational sex ratio (i.e. adult males to adult females), dependent individual to adult female ratio at the group level, and proportion of tuskless individuals. We then compare similar metrics between the population sampled in Ruaha National Park (hereafter, Ruaha) in 2009 and in 2015 following a suspected increase in the level of poaching. Although Ruaha holds one of the largest populations of elephants in Tanzania – estimated at 15,836 in 2015 (TAWIRI 2015) – it has been highlighted as a centre for poaching post-2011 (Wasser et al. 2015). Given that poaching targets older bulls and matriarchs for their larger tusks (Poole 1989; Mondol et al. 2014), we expected increased poaching pressure to lead to reductions in the proportion of older individuals, but also to an increase in the proportion of individuals lacking tusks (Chiyo et al. 2015, Raubenheimer & Miniggio 2016). Based on previous studies, we also hypothesised that the loss of old individuals – and matriarchs in particular – would lead to reduced calf recruitment and survival (Gobush et al. 2008, Wittemyer et al. 2013, Turkalo et al. 2016), and consequently a reduction in the proportion of young individuals. Based on our findings, we discuss the value of age structure as an indicator with which to monitor poaching pressure across both space and time.

2. MATERIALS AND METHODS

2.1 Study sites

Demographic data were collected on elephant populations in six study sites across Tanzania (Fig. 1). Four out of the six populations were surveyed within national parks (NPs; Tarangire, Serengeti, Ruaha, and Katavi) that permit photographic tourism only, whilst two populations were surveyed within game reserves (GRs) designated for both photographic tourism and trophy hunting (Selous and Ugalla). All study sites are characterised by distinct wet and dry seasons, which generally occur between

November-April and May-October, respectively. Annual rainfall across the study sites in 2009 ranged from 439.6 mm in Ugalla GR to 707.6 mm in Selous GR (Fig. 1).

2.2 Poaching levels

Historical patterns of poaching intensity across Tanzania are unreliably documented and primarily anecdotal (Mduma et al. 2010). Although all of the elephant populations considered in this study experienced poaching in the 1970s and 80s (Poole & Thomsen 1989), recent and current poaching levels vary considerably from one site to another (Thouless et al. 2016). We classified study populations as experiencing low, medium, and high levels of poaching based on population trends in the three years prior to the 2009 surveys (Fig. 2). Populations in Tarangire and Serengeti were categorised as undergoing low levels of poaching as they demonstrated rapid growth between 2006 and 2009 (Hilborn et al. 2006; Foley & Faust 2010; Fig. 2). In contrast, populations in Ruaha and Katavi were found to be stable between 2006 and 2009, with suspected but unreliably documented poaching occurring at both sites (Martin & Caro 2012; Fig. 2). These populations were thus classified as experiencing a medium level of poaching. Lastly, elephant populations in Selous and Ugalla underwent dramatic declines between 2006 and 2009 (Mduma et al. 2010; Thouless et al. 2016; Fig. 2), due to high levels of illegal killing (Wasser et al. 2009; Wilfred & MacColl 2014).

2.3 Data collection

An RDA survey was carried out at each of the six study sites during 2009-10 (Fig. 1) following the method described by Poole (1989). Observers were trained in ageing and sexing elephants on the northern sub-population of Tarangire NP, which has been the focus of a continuous study since 1993 (Foley & Faust 2010). Observer accuracy and inter-observer consistency were tested until they had reached a satisfactory level (>95% accuracy on known individuals). The observers then surveyed each study site for two to four weeks, with the exception of Tarangire NP, where all sub-populations of elephants were surveyed over three days.

The primary aim of RDA surveys is to record the age, sex and unique physical attributes of as many different elephants as possible in a given population, as well as record the size of the group they are in (Poole 1989). Selection of survey areas within study sites followed local advice on where elephants were most likely to be encountered. Search area was shifted by at least 10 km each survey day. Surveys were carried out in a motorised vehicle and followed road networks. All recorded individuals were geo-referenced using a Global Positioning System and, whenever possible, portrait photos and/or identification notes were taken. Together these data were used to ensure no double counting of individuals had occurred. In all study sites, a minimum sample size of 300 individuals was sought.

Elephants spotted from the road were approached to within 20-50 m so as to maximise viewing quality whist minimising disturbance. Individuals were sexed and assigned to one of seven age classes (0-4, 5-9, 10-14, 15-19, 20-24, 25-39 and 40+; inclusive of the last age shown) based on shoulder height, back length, head and body shape, and size of tusks (Poole 1989; Moss 1996). Age-assignments were made relative to other individuals in the same population, thereby minimising bias associated with differing height across populations. Individuals under 10 years of age were sometimes difficult to sex, and their gender was recorded as "unknown" when this was the case.

Demographic data pertaining to the Ruaha population in 2015 were collated from monthly road transect surveys and opportunistic monitoring carried out between May and October 2015 (Fig. 1). Observers followed the same protocol for approaching and ageing elephants as that used in the 2009 surveys. Data were collected as part of an ongoing elephant monitoring study implemented by the Southern Tanzania Elephant Program, which operates an elephant ID database for Ruaha containing >1 200 individually identified elephants. Each individual is identified from a unique ID code, and its sex, age, and identifying features are known from direct visual observation and portrait photographs. The Ruaha 2015 dataset comprises all unique elephants sighted between May and October 2015 in the same geographic area as surveyed in 2009 (Fig. 1).

The analyses described below only consider groups in which every member was assigned to an age class, and all individuals older than 10 years of age were accurately sexed, in order to minimise bias associated with the non-detection of calves, which are more likely to be concealed by vegetation. Furthermore, we wanted to ensure use of a consistent dataset when assessing group and population level patterns. Owing to the uncertainty associated with the sexing of individuals younger than 10 years (especially females), we split all individuals falling into the 0-4 and 5-9 age classes according to a 1:1 ratio (Moss 2001; see also Gough & Kerley 2006).

2.4 Data analysis

2.4.1 Sensitivity of age structure to sampling effort

To assess the degree to which the observed age structure of a given population was sensitive to the number of individuals sampled, we performed a subsampling exercise whereby a reduced number of observations – ranging from 1 to the observed sample size – was randomly selected to estimate a “pseudo” age structure. The latter was then compared to the observed age structure using a Pearson’s chi-square test. Resampling was carried out without replacement to simulate the avoidance of double counting. For each level of effort, we produced N = 1000 subsamples, and derived a probability of obtaining an age structure that was significantly different to the observed by dividing the number of iterations resulting in $P < 0.05$ by N. In doing this, we were interested in assessing whether a small reduction in the number of individuals sampled rapidly increased the probability of deriving a different age structure for a given population.

2.4.2 Multi-site comparison

For the purpose of this study, we consider the Tarangire NP population in 2009 as relatively undisturbed by poaching, and use it as a reference sample against which to compare the age-class structure of other sampled populations. Following a ban on international ivory trade in 1990, poaching in Tarangire was reduced to a very low level, and the elephant population has since shown a rapid recovery (Foley & Faust 2010). We thus compared age class frequencies obtained for the Serengeti, Ruaha, Selous, Katavi and Ugalla populations (hereafter, test populations) to those observed for the reference Tarangire population. For each test population, we performed separate chi-square tests on age-class frequencies derived from all sampled individuals, males only, and females only, and used the proportion of individuals obtained in each age class for the Tarangire population as expected probabilities. For each comparison and age class, we calculated the standardised residual (SR) between the observed (O) and expected (E) frequencies as $SR = (O - E)/\sqrt{E}$. Negative and positive SR values denoted observed frequencies that were less or more than expected, respectively, and we used these to assess age-class specific patterns across sampled populations.

For each population, we also calculated the ratio of adult males (individuals > 25 years) to adult females (individuals > 10 years) following Poole (1989), which we hereafter refer to as the operational sex ratio. We interpret the latter as the number of adult males available to adult females for mating. We expected the operational sex ratio to decrease with the level of poaching, a pattern that has been highlighted in previous studies (Poole 1989; Poole & Thomsen 1989; Dobson & Poole 1998; Mondol et al. 2014). We also investigated whether the ratio of dependent individuals (individuals < 10 years) to adult females measured at the group-level was affected by the level of poaching experienced by the population. We modelled the number of dependent individuals within a group as a function of study site using a Poisson generalised linear model with the number of adult females as an offset term. We interpret the dependent to adult female ratio as the number of dependents an adult female is able to recruit, and expect a decrease in this ratio with increased poaching. Lastly, we estimated the proportion of all sampled individuals older than 5 years of age that were observed to be tuskless.

2.4.3 Temporal comparison in Ruaha

We compared the age class frequencies of the Ruaha elephant population sampled in the dry season of 2009 to that sampled in dry season of 2015 following a suspected increase in the level of poaching (see Wasser et al. 2015 and Table A.1). We used the proportion of individuals obtained in each age class in 2009 as expected probabilities for 2015. We also compared the operational sex ratio, the dependent to adult female ratio, and the level of tusklessness between the two years using the same tests as for the multi-site comparison. All analyses were carried out in R version 3.2.1 (R Core Team 2016), with statistical significance based on an alpha level of 0.05.

3. RESULTS

A total of 2,361 elephants were sampled across the six sites for the purpose of this study. Details pertaining to populations sampled in 2009-10, as well as in Ruaha in 2015, are summarized in Table 1 and Fig. A1. Only the age structure of the Ugalla population was sensitive to small changes in sample size (Fig. A2). The probability of obtaining a significantly different age structure for this population occurred after removal of only one individual from the observed sample size (n=153; Table 1). In contrast, this probability fell to zero for simulated sample sizes that were much smaller than the observed for all the other study populations (range of observed sample sizes from 329 for Ruaha to 443 individuals for Tarangire) (Table 1, Fig. A2). We view this result as an indication that estimated age structures for all but one of the study populations were not sensitive to the number of individuals sampled.

3.1 Multi-site comparison

Comparison of age class frequencies revealed no significant differences between the age structures of the Tarangire and Serengeti populations in 2009-10, regardless of whether all individuals, males or females were considered (Table 2). In contrast, populations experiencing medium and high levels of poaching showed consistent differences in age structure relative to the Tarangire population (Table 2, Fig. 3). These populations showed a lower proportion of calves (aged 0-4) and adults above 40 years of age, and a higher proportion of individuals in the 15-19 and 20-24 age classes (Fig. 3a). Other age classes (5-9, 10-14 and 25-39) showed both positive and negative SR values depending on the sampled population. The proportion of males in age classes 15-19 and 20-24 was greater in all sampled populations experiencing medium to high poaching than those with low levels of poaching, with the exception of the Ugalla population, which showed no difference in the proportion of males aged 20 to 24 (Fig. 3b). It must be noted that the latter population was also characterized by a small sample size for males (n = 46, Table 1). There were also fewer males aged 25 to 39 in populations with medium to high poaching. This was not the case for females, which showed higher proportions of individuals in the 20-24 and 25-39 age classes in the same populations (Fig. 3c).

The ratio of adult males to adult females was highest in populations experiencing low levels of poaching and lowest in those under high levels of poaching (Fig. 4a). A similar trend was found for the dependent to adult female ratio, with a significant decrease for populations in Katavi, Selous and Ugalla, relative to the population in Tarangire (Fig. 4b, Table 3). Sampled populations in Tarangire, Serengeti and Ruaha did not differ in their dependent to adult female ratio (all were above 1), although the Serengeti population did show a higher ratio than that sampled in Tarangire. Lastly, the proportion of tuskless individuals was higher in populations classified as experiencing medium to high poaching (Ruaha: 7.0 %; Katavi: 6.3 %; Selous: 6.3 %; Ugalla: 9.7 %) relative to those experiencing comparatively low levels of poaching (Fig. 4c).

3.2 Temporal comparison in Ruaha

Elephant density in Ruaha-Rungwa ecosystem more than halved between 2009 and 2015, decreasing from 0.79 to 0.32 elephants per km^2 (Fig. 2). Comparison of age class frequencies between the two years revealed significantly different age structures

(χ^2 = 30.7, P < 0.001, Fig. 5a), with the population sampled in 2015 presenting a lower proportion of calves (0-4 years of age). Overall, there was a loss of individuals in older age classes, with lower proportions of females aged 25 and above (χ^2 = 15.7, P < 0.05; Fig. 5c) and males aged 40 and above. With the exception of the 10-14 age class, age categories between 5 and 24 years showed increased proportions relative to the population sampled in 2009.

The operational sex ratio of the Ruaha population showed a very slight increase between 2009 and 2015 from 0.120 to 0.133. This was the result of a decrease in the number of adult females (from 100 to 90), with the number of adult males encountered remaining the same at 12 individuals. Average dependent to adult female ratio at the group-level did not differ significantly between the two years (1.177 ±0.093 for 2009 and 1.155 ±0.125 in 2015, P = 0.860), whilst the proportion of tuskless individuals showed a small increase from 7.0 % in 2009 to 7.5 % in 2015.

4. DISCUSSION

The present work builds on and corroborates that of Poole (1989) by highlighting clear and consistent differences in the age structure of elephant populations experiencing contrasting levels of poaching pressure in Tanzania. In doing so, we validate the use of the RDA – and the resulting indicators based on age and group structure – to monitor poaching pressure in elephant populations. Our approach is flexible and cost-effective, and has the potential to be used more widely across elephant range states. Importantly, it is also applicable to other wildlife populations where illegal offtake is targeted at specific age classes. Our assessment of age structural changes is reliant on a clear reference, which could be either a different control population, such as those in Tarangire and Serengeti in our case, or previous surveys on the same population carried out in the past (such as in Ruaha). It thus provides a mean to track changes in wildlife population structure across both space and time, while at the same time offering key insights into cryptic poaching pressure.

We found that elephant populations classified as experiencing medium and high levels of poaching between 2006 and 2009 were characterised by fewer calves and old individuals, a reduced number of adult males (defined as > 25 years of age) for the number of adult females (> 10 years), and a lower ratio of calves (< 5 years) to adult females within groups. These patterns likely reflect the demographic impacts of poaching highlighted by previous studies, whereby loss of older individuals, particularly males over 25 years, suppresses recruitment into the population (Dobson & Poole 1998; Mondol et al. 2014). The latter may be the result of fewer breeding opportunities for females (Ishengoma et al. 2008) and/or reduced survival of calves owing to disrupted groups with a loss of leadership from older matriarchs and increased stress levels (Dublin 1983; Gobush et al. 2008; Archie & Chiyo 2012). The loss of old and young individuals – and the consequently higher proportions attributed to adolescents and young adults – was also characteristic of the Ruaha population in 2015. This pattern mirrors that described by Barnes & Kapela (1991), who noted that intense poaching in the late 1970s and early 1980s had “affected both ends of the age distribution” of the Ruaha population. Furthermore, the reduction in the proportion of individuals younger than five years of age observed in medium and highly poached populations resembles the pattern found in Mikumi NP by Poole (1989), where the elephant population experienced high levels of poaching in the 1980s.

The higher proportion of tuskless individuals was another consistent feature of poached populations sampled in 2009. This finding is in agreement with previous studies that have highlighted increased tusklessness in local elephant populations subject to heavy illegal harvesting (Poole 1989; Jachmann, Berry & Imae 1995; Whitehouse 2002), and also concurs with a recent study showing a decline in tusk size in recovering populations (Chiyo et al. 2015). In comparison to the relatively undisturbed elephant population of Amboseli NP, which shows a proportion of tuskless adults of less than 1 % (Poole 1989; Moss, Croze & Lee 2011), a proportion of 6-8 %, as found in populations experiencing medium to high poaching in 2009 and in the Ruaha population in 2015, is unusually high (Poole & Thomsen 1989). Increases in tusklessness and decreases in the size of tusks may well mirror phenotypic and evolutionary changes observed in the size of trophies in harvested ungulate species (Douhard et al. 2016), and as such represent important areas for future research and monitoring.

Although poaching levels were based on population trends measured between 2006 and 2009, we feel confident they provided a reasonably accurate description of recent illegal harvesting activities. Firstly, such sustained and dramatic population declines as those observed in Selous and Ugalla GRs are unlikely to have been caused by climatic factors (e.g. drought; see Foley et al. 2008) or repeated methodological biases, and likely reflect true population declines as a result of documented poaching (Wasser 2009). Secondly, increases in the proportion of illegally killed elephants (PIKE) among carcasses collected in Ruaha and Katavi NPs between 2006 and 2009 highlight significant levels of poaching activity at both sites (Wasser et al. 2015; Martin & Caro 2013). Lastly, our assumption that poaching was less intense in both Serengeti and Tarangire NPs is supported by a prolonged increase in the density of elephants at both sites (Hilborn et al. 2006, Foley & Faust 2010), although it must be noted that the rapid rate of increase in Serengeti is likely also due to migration into the area (Morrison et al. 2017).

Like behavioural indicators of anthropogenic pressure (Goldenberg et al. 2017), inferences on population structure must be interpreted with the RDA sampling methodology in mind. Age structure indicators are unlikely to be reliable when population density is too low or population size too small to achieve meaningful sample sizes (Rughetti 2016). Although this might have been the case for the Ugalla population in the present study, we view the combined patterns observed for age and group structure, as well as tusklessness, to be reflective of poaching pressure. Other considerations might include if the vegetation is too dense to allow sightings of all individuals in observed groups (for operational sex ratio and dependent to adult female measures especially), or if shyness and flight behaviour in response to observers does not enable good age records to be taken (Graham et al. 2009; Goldenberg et al. 2017). Importantly, RDAs rely on accurate sexing and aging of surveyed individuals, which can only be achieved by suitably trained observers. In our study, the sex-specific frequencies for individuals younger than 10 years of age were dependent on the chosen 1:1 ratio. Moreover, we only considered data from groups for which all individuals were aged and sexed to avoid under-representing individuals that are less likely to be detected (e.g. calves). However, we acknowledge that this might have led to other biases, such as the over-representation of bull herds, for instance. Nevertheless, our approach was applied in the same way to all populations and thus relative comparisons were judged to be reasonable.

Surprisingly, the 5-9 age class observed in Ruaha in 2015 showed higher proportions than expected relative to the population sampled in 2009, while the 10-14 age class showed lower proportions. This could be due to undocumented historical mortality events (e.g. drought) ten years previously, which would have affected the survivorship of individuals in the 0-4 age class (Foley, Pettorelli & Foley 2008), thereby leading to a lower representation of 10-14 year olds in 2015. In addition, all of the populations considered underwent a period of heavy poaching from the late 1970s to the early 80s, the effects of which might still be reflected in age structures observed in 2009 (Shannon et al. 2013). More generally, knowledge of poaching history is important to the interpretation of RDA data, and we recommend that comparisons between populations be assessed with due regards to potential differences in historical poaching levels.

5. **CONCLUSIONS**

The present study contributes towards validating the use of age structure as an indicator of poaching pressure in elephant populations, but also, by extension, in other wildlife populations where illegal offtake is targeted at specific age classes. We further validate the use of RDAs, which could be extended to a wide range of species for which ageing and sexing is feasible in the field. If repeated over time, such surveys could provide valuable insights into demographic processes influencing population growth rates. Not only would such an approach represent a cost-effective alternative to individual-based monitoring programs when funding is limited or uncertain, but also facilitate the monitoring of poorly known populations and provide insights into possible factors that might affect future recovery.

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8. TABLES

Table 1. Number of individuals sampled in each of the six elephant populations considered. Numbers in parentheses denote the number of individuals as a proportion of population abundance estimated during the corresponding year.

Dry season	Population	# individuals sampled	# males	# females	# gender unknown
2009	Tarangire NP	443 (0.17)	85	163	195
	Serengeti NP	364 (0.12)	151	213	130
	Ruaha NP	329 (0.01)	145	184	114
	Katavi NP	413 (0.06)	170	243	105
	Selous GR	347 (0.01)	123	224	124
	Ugalla GR	153 (0.15)	46	107	39
2015	Ruaha NP	312 (0.02)	145	167	33

Table 2. Age class frequencies for six elephant populations experiencing different levels of poaching pressure. $\chi2$ and P values relate to Pearson's chi-square tests between age class frequencies of the corresponding population and those of the Tarangire population. Note that the Ruaha population was surveyed in both 2009 and 2015. Numbers of male and female individuals for age classes 0-4 and 5-9 were derived from the number of individuals with unknown gender using a sex ratio of 1:1 (Moss 2001).

Population	Individuals	Age class							$\chi2$	P-value
		0-4	5-9	10-14	15-19	20-24	25-39	40+		
Tarangire NP	All	181	74	53	20	17	75	23	-	-
	Males	90	37	21	3	4	23	4	-	-
	Females	91	37	32	17	13	52	19	-	-
Serengeti NP	All	143	60	42	19	22	60	19	5.3	0.502
	Males	71	30	18	6	7	17	2	10.0	0.125
	Females	72	30	24	12	15	43	17	2.5	0.872
Ruaha NP (2009)	All	120	47	48	22	30	56	6	39.1	< 0.001
	Males	60	23	23	13	14	10	2	93.5	< 0.001
	Females	60	24	25	9	16	46	4	15.6	< 0.05
Ruaha NP (2015)	All	94	60	34	36	40	46	2	123.3	< 0.001
	Males	47	30	16	22	18	12	0	244.6	< 0.001
	Females	47	30	18	14	22	34	2	35.9	< 0.001
Katavi NP	All	116	81	67	24	50	69	6	111.1	< 0.001
	Males	58	40	23	10	25	14	0	155.8	< 0.001
	Females	58	41	44	14	25	55	6	38.6	< 0.001
Selous GR	All	125	28	35	25	70	60	4	276.3	< 0.001
	Males	62	14	14	13	13	6	1	110.3	< 0.001
	Females	63	14	21	12	57	54	3	216.1	< 0.001
Ugalla GR	All	38	15	27	23	23	26	1	111.6	< 0.001
	Males	19	7	10	8	1	1	0	79.0	< 0.001
	Females	19	8	17	15	22	25	1	82.0	< 0.001

Table 3. Differences in the ratio of dependent individuals (< 10 years) to adult females (individuals > 10 years) across the six elephant populations sampled in 2009. Estimates were obtained from a generalized linear model (GLM) with Poisson error structure, the number of dependent individuals as response, and the number of adult females as offset.

Population	# Groups sampled	Mean dependent to female ratio	GLM coefficients		
			Estimate	SE	P
Tarangire NP	43	1.917	-	-	-
Serengeti NP	24	1.981	0.032	0.095	0.733
Ruaha NP	30	1.650	-0.150	0.100	0.133
Katavi NP	34	1.361	-0.343	0.095	<0.001
Selous GR	46	1.048	-0.604	0.102	<0.001
Ugalla GR	7	0.667	-1.056	0.152	<0.001

9. FIGURES

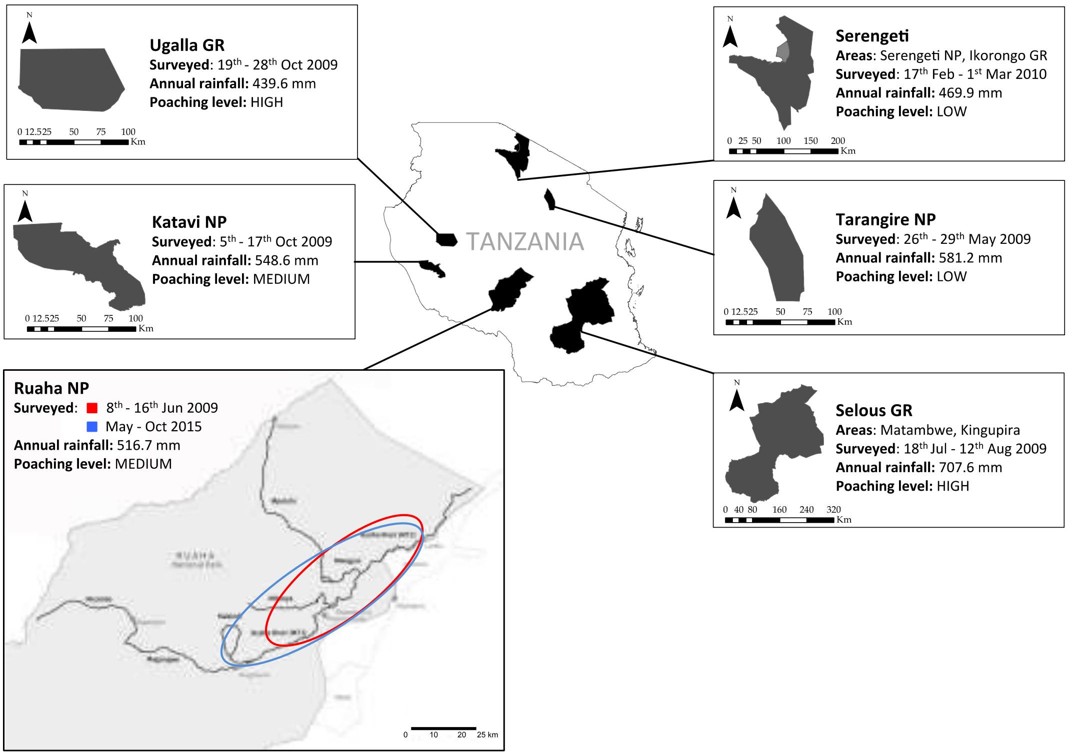

Figure 1. Description of the six study sites showing the areas sampled, survey dates, the annual rainfall estimate for the year 2009, and the level of poaching. For Ruaha, areas surveyed within the National Park in 2009 (red) and 2015 (blue) are shown together with the road network (black lines).

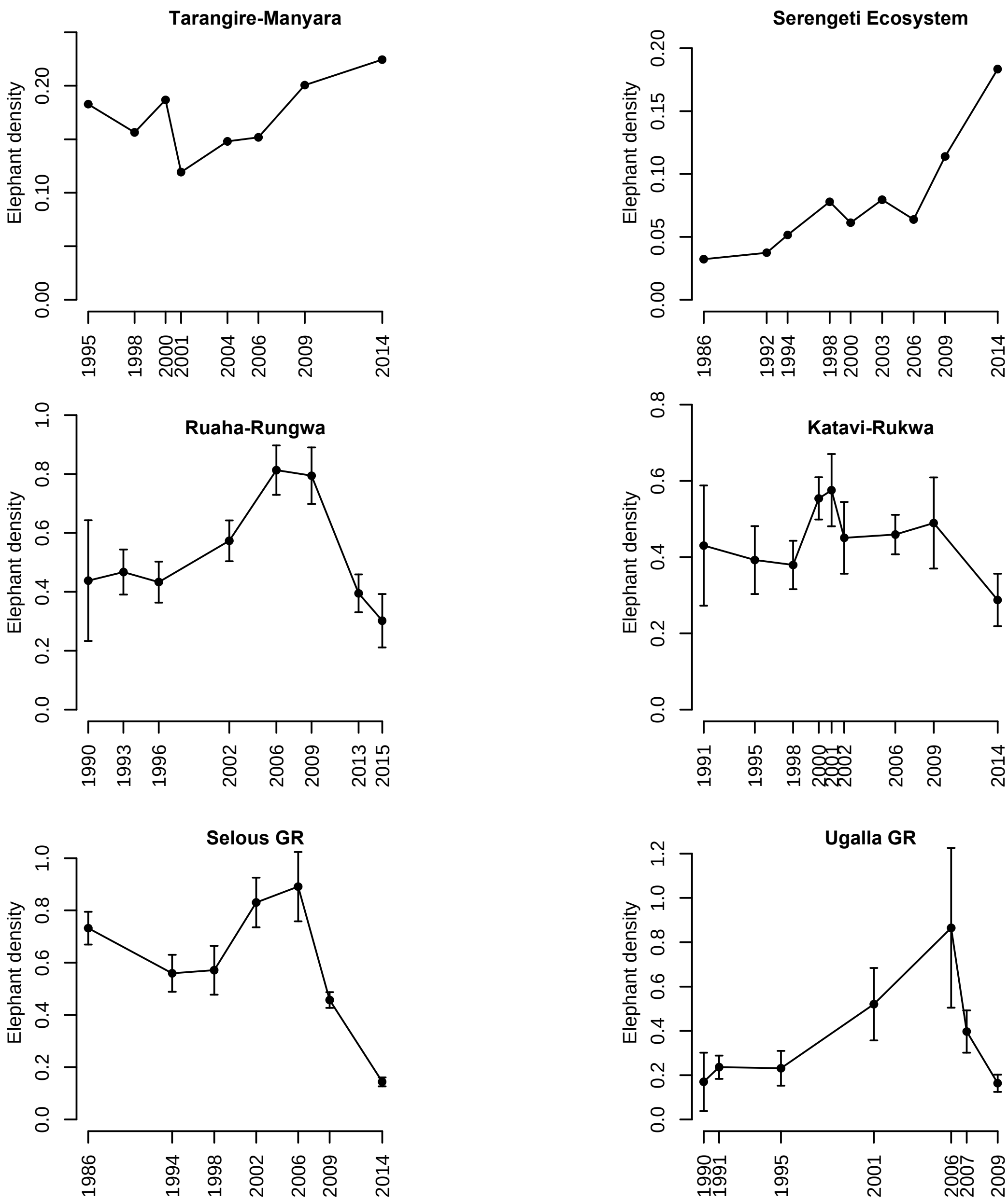

Figure 2. Elephant density trends in six ecosystems containing the sites considered in this study, over the period 1986-2015. For each ecosystem, we collated population size estimates derived from total counts (Tarangire-Manyara and Serengeti) and Systematic Reconnaissance Flight surveys (Ruaha-Rungwa, Katavi-Rukwa, Selous and Ugalla) carried out by the Tanzania Wildlife Research Institute. Density estimates (black dots) and their associated standard errors (error bars) were obtained by dividing population size estimates by the total area surveyed during corresponding flights.

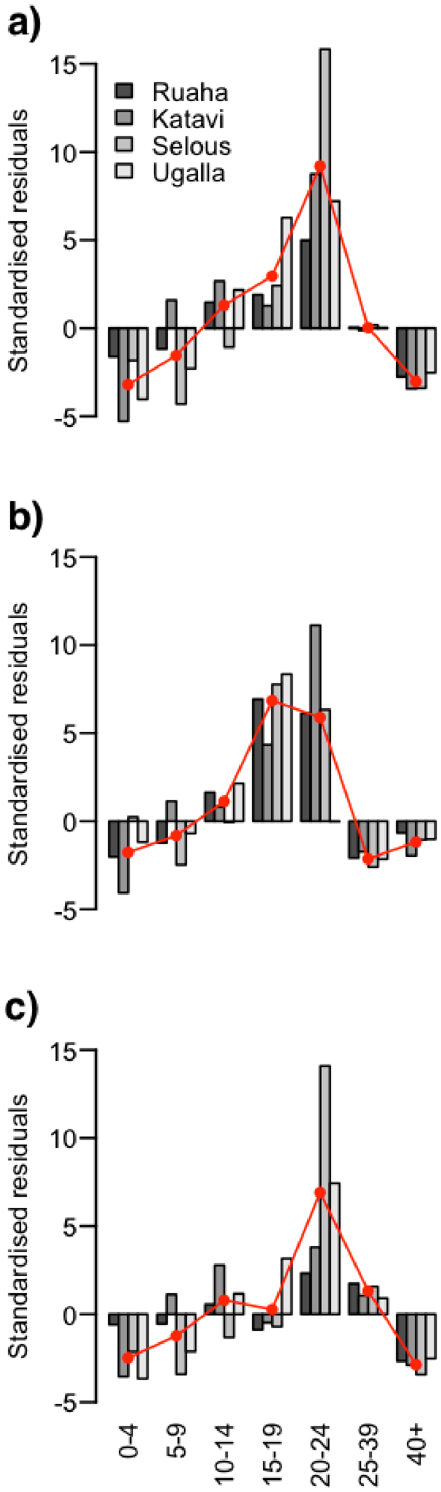

Figure 3. Standardised residuals from chi-square tests comparing the age class frequencies of four poached elephant populations to that of the population sampled in Tarangire NP. Age class frequencies were compared based on all sampled individuals (a), males only (b), and females only (c). Red dots denote mean standardised residual value across sites for a given age class.

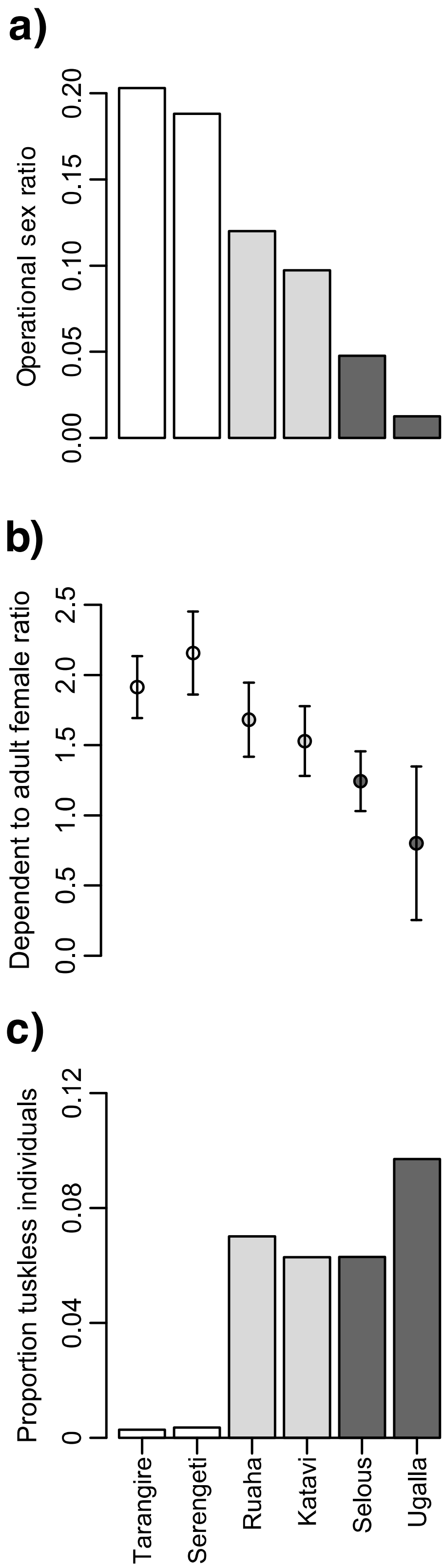

Figure 4. Comparison of the operational sex ratio (a), the ratio of dependent individuals to adult females in a group (b), and the proportion of tuskless individuals (c) across six elephant populations sampled using the rapid demographic assessment method in 2009-10. White, light grey and dark grey colours indicate low, medium and high levels of poaching (see text).

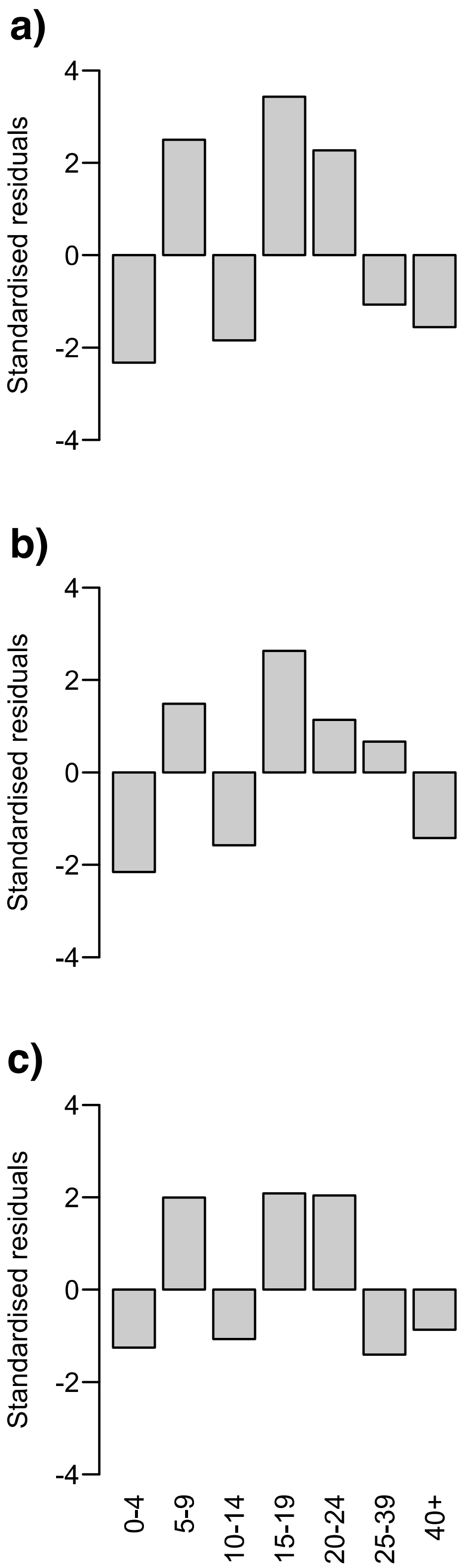

Figure 5. Comparison of the Ruaha elephant population age structure between the dry seasons of 2009 and 2015, as derived from all sampled individuals (a), males only (b) and females only (c). For each plot, bars represent the standardized residuals obtained from a chi-square test with age class frequencies of 2015 as observed values and age class frequencies of 2009 as expected.

10. APPENDIX

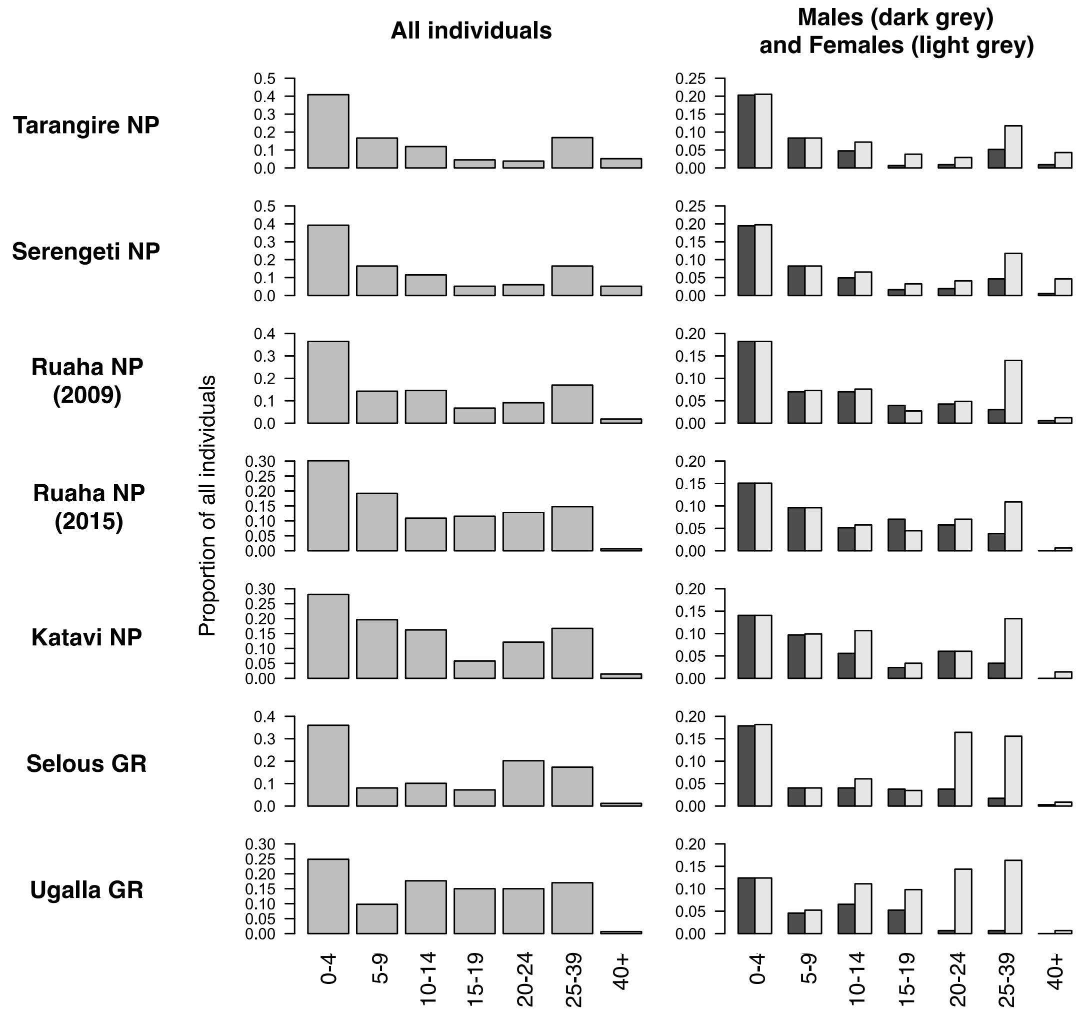

Figure A.1. Age and sex structures of study populations expressed as proportions of all surveyed individuals. Note that y-axes vary.

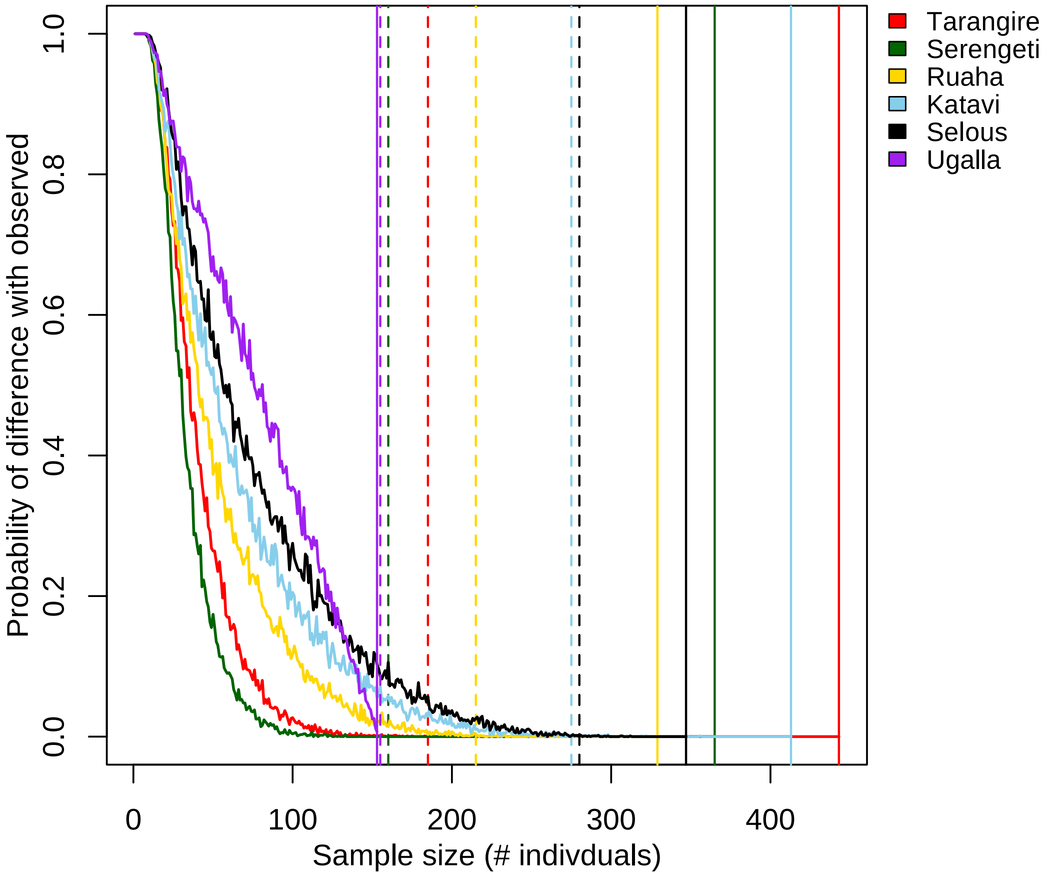

Figure A.2. Sensitivity of observed population age structure in 2009 to changes in sample size. Here, the observed age structure refers to the age structure estimated from all sampled individuals at a given site (sample size denoted by full vertical lines). For each simulated sample size (x axis) individuals in the observed sample were selected at random to create a subsample. A total of 1000 subsamples were generated for each hypothetical sample size. Each subsample is used to derive a pseudo age structure, which is then compared with the observed one. For a given hypothetical sample size, the P-value represents the proportion of subsamples for which the resulting age structure was different to that estimated from the observed sample. Dashed vertical lines mark the hypothetical sample size above which all probabilities are 0.

Table A.1. Number of carcasses reported by the Monitoring the Illegal Killing of Elephants (MIKE) program in Ruaha-Rungwa between 2007 and 2015, including total and illegal counts. MIKE records were accessed from https://cites.org/eng/prog/mike/data_and_reports.

	Number of elephant carcasses	
Year	Total	Illegal
2007	2	0
2008	3	2
2009	3	1
2010	28	16
2011	34	32
2012	110	73
2013	57	48
2014	50	29
2015	47	35