RESEARCH

The Gorongosa elephants through war and recovery: tusklessness, population size, structure and reproductive parameters

Joyce Poole[1] and Petter Granli[1]*

[1]ElephantVoices, Buskhellinga 3, 3236 Sandefjord, Norway
*corresponding author: jpoole@elephantvoices.org

Abstract

How does an elephant population recover after being pushed to the brink of extinction? In this and a separate paper on behaviour we present an account of war-induced collapse and post-war recovery of an elephant population. Mozambique's 15-year civil war from 1977–1992 had a profound impact on the elephants of Gorongosa National Park. Elephant numbers plummeted from ~2,200 pre-war to <200 post-war impacting the structure of the population and its families, the physical appearance of the elephants, their genetic make-up and behaviour (companion study). Using individual registration, this study aimed to collect baseline data to estimate the population size, reproductive parameters and growth and to document its composition, including age and sex structure, tusk configuration, family and clan membership. A quarter of a century after the war, rapid reproductive rate and growth in numbers are indications of recovery, but the skewed sex ratio among older age classes and the prevalence of tusklessness in post-war generations are evidence of long-lasting scars.

Additional Keywords: Age at first birth, inter-calf interval, growth rate

Résumé

Comment les populations d'éléphants parviennent-elles à se rétablir après avoir été poussées à la limite de l'extinction ? Dans ce document — et dans une seconde publication traitant du comportement — nous présentons un compte-rendu de la chute du nombre d'individus provoquée par le conflit au Mozambique, puis de son rétablissement au lendemain de la guerre. Les quinze ans de guerre civile de 1977 à 1992 ont eu de profondes répercussions sur les éléphants du parc national de Gorongosa. Près de 2200 avant la guerre, leur nombre a chuté en deçà de 200, affectant la structure de la population et les familles qui la composent, l'apparence physique des éléphants, leur constitution génétique et leur comportement (étude parallèle). À l'aide de la reconnaissance individuelle, la présente étude a pour objectif de collecter des données de référence afin d'estimer la densité de cette population, ses paramètres de reproduction et sa croissance. Il s'agit également d'en documenter la composition, notamment la répartition des âges et des sexes, la configuration des défenses, la famille et l'appartenance au clan. Un quart de siècle après la guerre, le taux de reproduction rapide et le nombre croissant d'individus sont des indicateurs de rétablissement, mais un rapport des sexes déséquilibré parmi les classes d'âges les plus avancées et l'absence de défenses dans les générations nées après la guerre sont les preuves de séquelles durables.

Mot-clés supplémentaires: âge de la première naissance, intervalle entre les naissances, taux de croissance

Introduction

War and other forms of human conflict can disturb ecosystems and cause severe biodiversity loss (Dashkin and Pringle 2018). African elephants (*Loxodonta africana, L. cyclotis*) are particularly vulnerable due to their dependence on large areas of suitable habitat, relatively small population sizes, and long generation times and because of the value of their tusks (Beyers et al. 2011). Killing for ivory, often during civil conflict, has caused catastrophic declines in many savannah and forest elephant populations (Blanc et al. 2007).

Demographic data based on long-term studies of known individuals are critical for evaluating what conservation interventions might be effective in these cases and for estimating time to recovery. While highly valuable, few such studies exist due to the logistical difficulties and lengthy commitment required. Given the number of elephant populations affected by poaching, these studies (e.g. Foley and Faust 2010, Moss and Lee 2011, Wittemyer et al. 2013, 2021, Turkalo et al. 2017, 2018) provide invaluable data on the reproductive responses of elephants to environmental perturbances, such as poaching for ivory. Savannah elephants (*L. africana*) in Tarangire NP (Foley and Faust 2010) and Samburu NR (Wittemyer et al. 2013), for example, showed greater reproductive effort following periods of heavy poaching, while the 31-year generation time documented by Turkalo et al. (2018) in forest elephants (*L. cyclotis*) predicts very slow recovery of populations of this savannah species.

Tusk growth is sexually dimorphic and continues through most of an elephant's life (Laws 1966). Thus, the selective removal of elephants with larger tusks means that heavily poached populations are characterized by relatively few individuals in older age classes and the sex ratio of these individuals skewed toward females (Poole 1989, Wittemyer et al. 2013, 2021, Jones et al. 2018). One consequence is that during recovery, such female bias can drive faster population growth (Slotow et al. 2005).

Another characteristic of populations heavily hunted over time for ivory, is the prevalence of elephants without tusks. Tusklessness occurs naturally; however, high frequencies of tuskless and one-tusked elephants can represent markers of historical loss (Poole 1989, Jones et al. 2018, Campbell-Staton et al. 2021). Due to tusk inheritance patterns consistent with an X chromosome-linked dominant male-lethal trait (i.e. males who are homozygous for the tuskless gene are presumed to die in utero), tuskless individuals are almost entirely female (Campbell-Staton et al. 2021; Poole 1989). For example, Campbell-Staton et al. (2021) illustrated that killing for ivory during Mozambique's civil war resulted in strong selection that favoured tusklessness in females amid rapid population decline. Assessment of historical footage showed that prior to the war 18.5% of adult females were tuskless (n=54), while among survivors of the war the percentage of tuskless females had increased to 50.9%.

In 1972 Gorongosa National Park (GNP), in central Mozambique, held ~2,200 elephants ranging across 3,674 km^2 of protected habitat (Tinley 1977). Together with the surrounding area and the Marromeu area of Zambezi River delta there were an estimated 6,000 elephants (Tinley 1977). In 1977 Mozambique was plunged into a 15-year civil war during which hostilities raged in and around GNP and >90% of the elephant population was extirpated. An aerial survey of the Gorongosa–Marromeu Complex in 1994 estimated only 108 elephants remained, these all within GNP (Cumming et al. 1994).

In 2004 a public–private partnership between the Mozambiquan government and the Greg Carr Foundation was established to restore GNP and began to provide Gorongosa's elephants and other wildlife with protection and stability. Almost three decades after the war elephant numbers are beginning to recover, but the enduring consequences of the violence perpetrated is still visible in the elephants' markedly changed distribution (Stalmans and Peel 2020), degree of tusklessness and underlying genetic make-up (Campbell-Staton et al. 2021), diel activity patterns (Gaynor et al. 2018) and individual and group behaviour (Poole and Granli. In press).

From 2011–2019 we carried out nine month-long field trips to GNP. We used individual registration to document the status of Gorongosa's elephants, to better understand the war's impact on the population and to provide scientific data to help guide strategic conservation measures towards recovery. Almost three decades post war Gorongosa's female elephants were unusually fearful of and aggressive towards vehicles, as we describe in a separate manuscript. (Poole and Granli. In press). In this paper we examine tusk configuration and the prevalence of the tuskless trait across families, age cohorts and generations; population age structure and reproductive parameters; estimated population size and growth. The dense habitat of Gorongosa makes counting elephants challenging and, at different intervals, aerial surveys have indicated both very slow and very explosive growth. We compare our estimates of population size based on individual registration with those achieved through aerial total counts. Based on previously published research and our studies of other populations we predicted: i) older ages classes (survivors of the war) to be skewed toward females; ii) tuskless and one-tusked individuals would be limited almost entirely to females; iii) be more prevalent in some families than in others; iv) be more prevalent among survivors who were adults during the war than among those who were born during the war; v) decline in frequency from the first to second post-war generations; vi) population growth rate to be high; and vii) our estimates of population size to be greater than the those derived from aerial total counts.

Methodology

Study site

GNP covers 3,674 km^2 of Sofala Province, Mozambique. Elephants historically ranged throughout GNP and in the Marromeu area (includes hunting blocks and the Buffalo Reserve) of the Zambezi River delta to the east. After the war (which ended in 1992), the range of the surviving elephants in GNP contracted to the area south of Lake Urema (Fig. 1) in the vicinity of the Urema River and Pungue River with some venturing into human settlement south of the Pungue. In recent years there is evidence (dung, footprints, collared elephants) that the Gorongosa elephants are expanding their range again. Separately, there are an estimated 350 elephants in the Marromeu area (Beilfuss et al. 2010). While there is little evidence of regular movement between the two areas, ongoing efforts to restore the greater ecosystem could change that.

Within GNP fifteen landscape types are recognized with floodplain grasslands and Acacia-Combretum savannah predominating in the Rift Valley and miombo woodlands occurring at higher elevations to the east and west (Stalmans and Beilfuss 2008). Mean annual rainfall is 700–900 mm, with peak rain falling from December to February during which the floodplains around Lake Urema are inundated (Stalmans et al. 2019). By May the roads are usually dry enough to use, although tall grass makes observations difficult. As the dry season progresses elephants begin to concentrate near two primary permanent water sources: a) around Lake Urema and along the upper Urema River; and b) along the lower Urema River and the Pungue River (Fig. 1). We undertook two field trips in May (5/2015 and 5/2016), but due to better visibility, most of our visits to GNP were in the late dry season (08/2011, 10/2012, 10/2013, 10/2015, 10,11/2016, 10/2017, 10/2019).

Area covered

Due to the thick vegetation our search for elephants was largely limited to the extensive network of roads in the south-central section of GNP (Fig. 1). We used an iPhone app, GPS-Trk2, to record the routes we drove.

Sightings

We collected sightings data via the Gorongosa *EleApp* and uploaded the information to the Gorongosa Elephants Who's Who & Whereabouts Database (see Granli and Poole 2022). Sightings consisted of: date, time, location, group type (*family group, family group with associating adult males, all-male group or unknown*), number of individuals, count accuracy (*exact, good estimate or guess*), name of individuals and families present when they could be identified (see below), the presence of musth males and oestrous females, and the occurrence of wounded individuals and mortalities (Granli and Poole 2022). Recording an individual as present depended on it being seen or photographed, which was influenced by the elephant's physical appearance, age and behaviour,

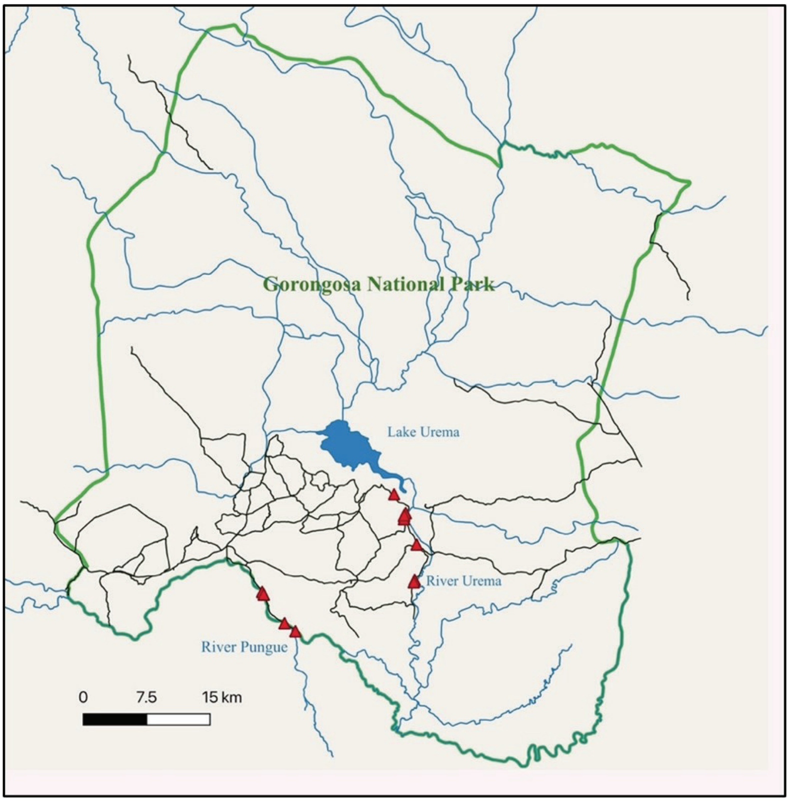

Figure 1. Map of Gorongosa National Park. Blue: Lake Urema, permanent rivers (Urema and Pungue) and seasonal waterways; black: dirt roads; red triangles: positions of trail cameras. (*Map drawn by author JP using QGIS*).

and the observer's skill. Large, demonstrative individuals with characteristic features were more likely to be documented. Groups could represent any number of individuals of either or both sexes in which individuals were coordinated in activity and movement direction, and where no member of the group was located further than the diameter of the aggregation. Detailed field notes on the age, sex and behaviour of individuals were recorded into an iPhone and later transcribed into the uploaded sightings record. The database contains 879 sightings records collected by the authors (n=375), other scientists (n=108), park management officers (n=183), experienced guides (n=207) and tourists (n=6). We specify when we have relied on subsets of these data.

Trail cameras

The Pungue River forms the southern boundary of GNP. A single track runs along the river through dense habitat. Across the river communities are engaged in subsistence agriculture. To monitor the frequency, approximate number, group type and identity of individual elephants using this inaccessible part of the Park, crossing the river and entering farms, we set up a series of Bushnell HD trophy cameras along the Pungue River (May–October 2015: DD01, DD02, DD03; May–October 2016: DD01, DD03, DD04, DD05; October 2017: DD01, DD05) and along the Urema River (October 2016: UR01, UR02, UR03; May 2017 UR04, October 2017 UR05, UR06, UR07, UR08). Fig. 1 shows the locations that we placed cameras.

We entered information collected via cameras into the *Gorongosa Elephants Who's Who & Whereabouts Database* as trail camera sightings in the same manner as sightings (Granli and Poole 2022). We took the date and time of each group from the timestamp of the first elephant photographed. We attempted to mirror how we might score a group in a sightings context, defining individuals as belonging to a group if they were photographed within 15 minutes of one another (Gaynor et al. 2018). We noted the group type, counted individuals, and entered a count accuracy. Since we were not able to know whether we had photographed every elephant *exact count* was never used. We identified as many elephants as possible and registered new individuals (see below).

Since almost all Pungue trail camera images were infrared photographs taken at night, identifying elephants was time consuming. We have yet to analyse trail camera data after 2016, but photographs from 2017 reveal new individuals and an unregistered family. The database contains 550 trail camera sightings.

Registration and reidentification of elephants

We photographed elephants for individual identification and behaviour with a Canon 6D and a 200-400mm lens with a built-in 1.4 extender (279 groups; ~30,700 photographs) or Bushnell HD Trophy Cameras (550 groups; ~98,000 images). Not all elephants in a group were photographed nor could all be identified. Among adults, young females were less likely to be photographed and registered due to their smaller size and less prominent role in group defence and, therefore, we underestimated them relative to older females and males of the same age.

Each clearly visible adult was checked against already registered elephants by searching a selection of features (e.g. sex, age, tusk configuration, ear notches, tears and holes) in the *Gorongosa Elephants Who's Who* (Granli and Poole 2022). Known individuals were added to the already uploaded sighting. New elephants were registered (Granli and Poole 2022) and added to the sighting. All photographs containing known individuals were key worded with their ID codes.

Elephants were aged according to methods developed in Amboseli (Moss 1996) and analysed within five-year categories. We counted as adults those estimated to be 15+ years. Ageing males is easier than ageing females due to the greater variability in their body size and changes in face contour as tusks become thicker. Ageing GNP females was especially difficult because so many lacked tusks. We included a level of accuracy ranging from +1 month – +10 years, with ages of younger elephants more accurate than older elephants.

Tusk configuration

Tusk configuration (two tusks, one left, one right or no tusks) was coded into our database as part of the registration of each adult elephant. We also noted tusk configuration for the putative offspring of registered adult females. These data were available only for offspring whose tusks had erupted (males:>1.5 yrs; females > 2 yrs) and who were less than five years old when first recorded.

Assigning family membership

We assigned registered adult females to a family with a qualifying level of accuracy (*unknown* if no family could be assigned or *guess, good idea* or *known*). We typically assigned an individual to a family at the level of guess. As our knowledge of that individual grew, we increased the level of accuracy. We considered as belonging to a family those individuals who maintained consistent friendly association with each other, and whose movements were influenced by the oldest female or matriarch. Typically, families contained males prior to dispersal age (<12), as well as immature and other reproductively active females. We used *known* for the matriarch who defined the family, for adult females who were consistently seen with her and for the immature offspring of these individuals. Each Gorongosa family was referred to by a one- or two-letter code. We tended to "lump" regularly associating individuals into families and then "split" them if subsequent observations indicated that they belonged in separate families.

Assigning clan membership

The preferred dry season distribution of elephants can be roughly delineated by areas within ~6 km of permanent water (Kuloba et al. 2010). Within the southern portion of the park used by elephants, suitable dry season habitat lay a) around Lake Urema and either side of the upper Urema River; and b) along the northern side of the River Pungue and either side of the lower Urema River (Fig. 1). For each registered female we calculated how many times she had been sighted within ~6 km of one of these two permanent water systems. We classified those elephants with 90% of their dry season sightings within 6 km of a) as belonging to the Urema clan and those with 90% of their dry season sightings (trail cameras) in the vicinity of b) as the Pungue clan.

Determining intervals between successive calves and age at first birth

Intervals between successive calves were determined in two ways: a) When elephant families were in the open and calves visible we made note of the estimated age and sex of calves suckling or closely following their presumed mothers; b) we went through ~30,700 photographs of 279 groups trail camera images (~98,000) of 550 groups, and 5 TB videos looking for any calves who appeared to belong to known individuals (i.e. a female seen caressing or helping calf, calf suckling, following closely in the video or successive photographs, or standing by her side in images from different dates). The age of each calf was estimated, and the sex was determined where possible. Since we did not have accurate mortality records, the intervals derived cannot be considered inter-birth intervals in the normal use of the term, as some calves may have died without being recorded.

We noted young females with budding breasts, indicating a first gestation. Females in the youngest adult age classes (10–20) followed by single calves were given an estimated age at the birth of their known calf, with a ~6 month–1 year error. Age at first birth represent best estimates based on many years of experience ageing elephants.

Estimating population size and growth

To calculate the minimum number of elephants in the population from January 1994 to December 2002 we used the estimated year of birth of registered individuals. For example, based on the estimated ages of registered elephants we calculated that there were at least 161 elephants alive during the first post-war aerial survey in 1994 rather than the 108 counted by Cumming et al. (1994). Since we registered very few individuals under 15 years old, the accuracy of this method declined for elephants born after 2002. Instead, for elephants born between January 2003 and December 2019, we used our findings of an age of first birth of ~14 years and an inter-calf interval of three years to calculate additions to the population by assuming that ⅓ of registered adult females gave birth each year. These estimates fit closely with those we made in 2017 and 2019 by using the number of registered adults and an estimated number of immatures (calculated from a known 2.4:1 immature to adult female ratio). The figures do not take mortalities into consideration, nor do they account for remaining unregistered individuals.

We compared our figures to counts of elephants from aerial surveys (Tinley 1977; Cummings et al. 1994; Stalmans 2012; Stalmans et al. 2014; Stalmans and Peel 2016; Stalmans et al. 2018; Stalmans and Peel 2020).

Results

Elephant groups

The Gorongosa Elephant DB holds 1,429 records of elephant groups (sightings n=879, trail camera sightings n=550), of which 574 were all-male, 790 were one or more families with (n=286) or without (n=504) associating males and 65 were of unknown type. Using only data we collected, the median size of all-male groups was 2 (IQR=1–3, range=1–17, n=300), that for groups with one or more families present was 10 (IQR=8–15, range=2–60, n=297) and that for one or more family groups with associating males was 20 (IQR=12–34, range=4–00, n=168).

Individuals registered and age/sex structure

We registered the identities and estimated the ages of 396 elephants: 194 adult females and 142 adult males. In support of our first prediction, among elephants who lived through the civil war (those estimated >30 years), the population was heavily biased toward females (Fig. 2).

Elephant families and clans

We assigned identified females and their immature offspring to 27 putative families based on their association. As expected, due to ranging strategies and observer confidence, some adult females were recorded relatively frequently, while others were not (median=4, IQR=2–10, range=1–40, N=179 females >15 years in 2017). The median number of records was > 10 for all adult female members in only five families (C, D, I, M, V).

Trail cameras were instrumental for documenting families whose range was not easily accessible by vehicle or who were only in the vicinity of roads at night (Gaynor et al. 2019). Our knowledge of the Urema clan was almost solely based on photographs of individuals from the road network, while our understanding of the Pungue Clan was primarily based on data gleaned from trail cameras set along the Pungue River (Fig. 3). Elephants documented by trail cameras along the

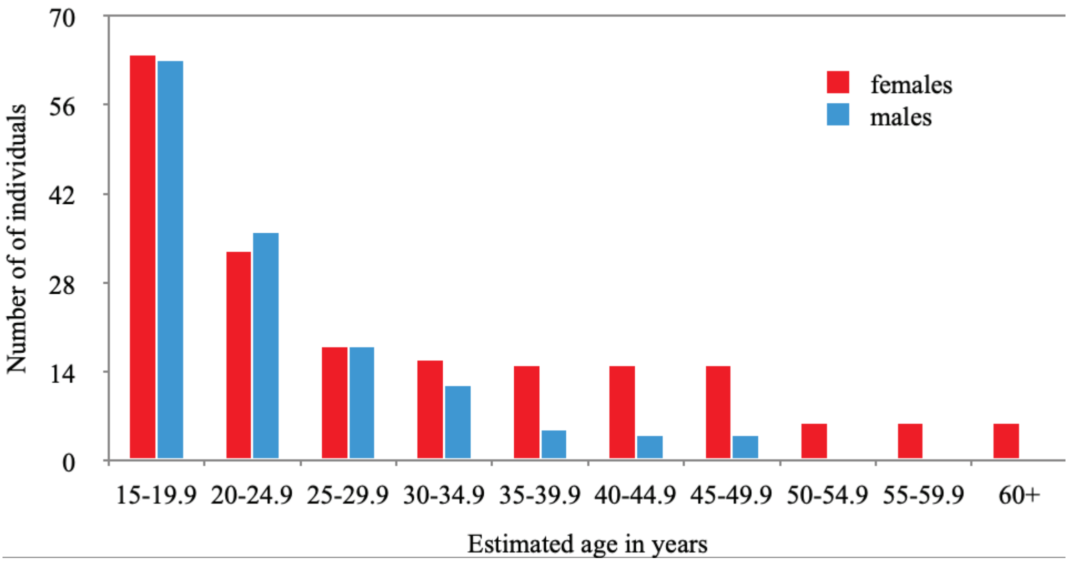

Figure 2. The age sex structure of registered adults >15 years of age in 2017.

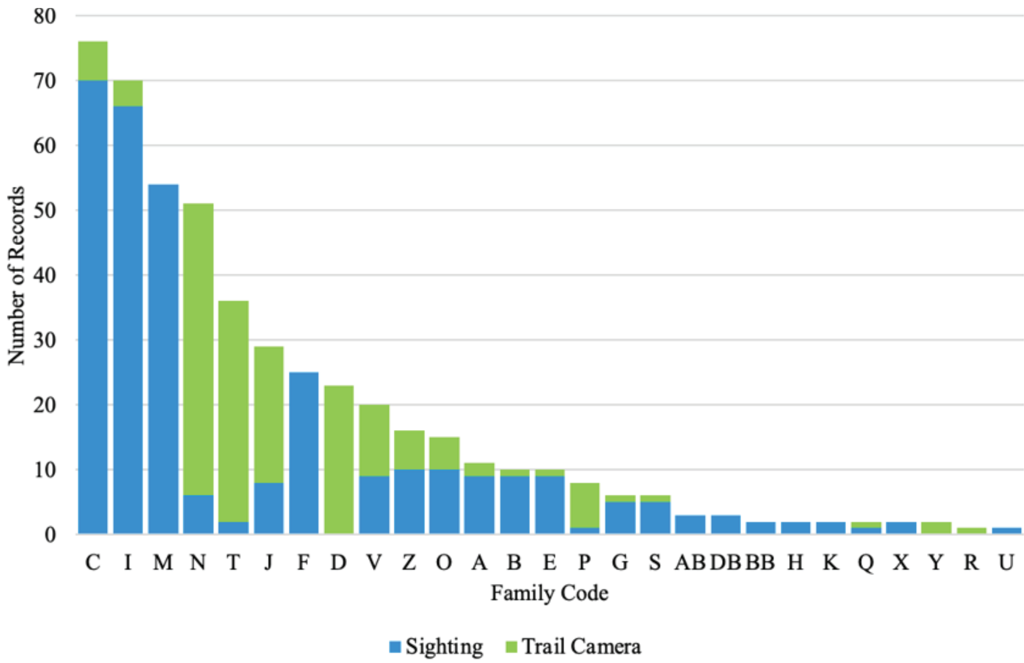

Figure 3. Frequency distribution illustrating the number of times families were recorded by regular sightings or via trail camera photographs (data up to end 2017).

Pungue River were unlikely to be sighted in the vicinity of Lake Urema and vice versa.

Tusk configuration by sex and across families, female age cohorts and generations

We examined tusk configuration and the pervasiveness of the tuskless trait across families, age cohorts and generations, since tuskless and one-tusked individuals can represent markers of historical loss and fragmentation of families and can, therefore, indicate population disruption and possible recovery.

In support of our second prediction, all tuskless individuals were female and one-tusked individuals were more common among females than among males. Across adult females 43% were tuskless and 8.7% were one-tusked (N=194), while among adult males none were tuskless and only three (2%) were one-tusked, although a fourth was documented to lose a misshapen right tusk (N=142).

The majority of families contained tuskless females. Among the 27 putative families only six did not contain tuskless or one-tusked females and only one of these (D) was known well enough to be sure that all were two-tusked (Fig. 4). The tuskless and one-tusked trait was more prevalent in some families than in others. In seven families over 70% of adult females were either tuskless or one-tusked.

Prior to the war 68.5% of adult females were two-tusked (n=54; (Campbell-Staton et al. 2021). In support of our fourth prediction, only 31% (n=39) of female survivors who were born prior to the war had two tusks, while among the cohort of females born during the war 42% (n=24) were two-tusked.

Among the first generation born after the war (daughters of survivors) 58% (n=120) were two-tusked (Fig. 5). Since tuskless females produce equal numbers of tusked and tuskless female offspring and tusked females produce predominantly tusked female offspring (see below), we expected to observe an increase in the proportion of two-tusked female offspring among the second generation. However, contrary to our expectations, we found the proportion of two-tusked females remained the same (57%; n=23).

For daughters whose mother accuracy was categorized as *known* or *highly likely* we examined tusk configuration of 81 mother-daughter pairs (mothers: 21 two-tusked, 7 one-tusked, 32 tuskless). Two-tusked mothers produced almost entirely two-tusked daughters and only rarely one-tusked or tuskless daughters. Tuskless mothers produced 42% two-tusked, 14% one-tusked and 44% tuskless daughters (Fig 6). The sample of one-tusked mother-daughter pairs was small (n=8), but 75% of daughters were two-tusked.

Intervals between successive calves

The interval between successive surviving calves ranged from 2 to16 years. We truncated the intervals at eight years as it is highly likely that those longer (n=5) represent mortalities (i.e., calves that were not recorded). The median interval between calves was three years (IQR: 2–4; range: 2–8; N=124; Fig. 7). Remarkably, almost a quarter of all recorded intervals between successive calves was less than 2.5 years. Taking the inter-calf intervals of the I family for which we had the best records over time and using only those intervals recorded between 2011 and 2019 (n=18), the median inter-calf interval was 2.5 years (IQR: 2–3; range: 2–4). Between 2009 and 2018 one adult female, Iria, produced 5 calves, thus conceiving within a couple of months of giving birth.

The breasts of Gorongosa mothers appeared fuller than those we have observed elsewhere, and it was not uncommon to observe mothers double-suckling their calves of rather similar size (Fig. 8). Juveniles of six and even seven years of age were also observed to suckle. In 2017 we observed Iria suckling her three different aged offspring and, on one occasion, we observed three calves alternatively suckling from two different mothers. Shared suckling of different calves by lactating mothers has only rarely been observed elsewhere, and then typically occurring between grandmothers and grand-calves.

Age at first birth

Females observed with what we presumed were their first calves ranged from an estimated 10–17 years. The median age at first birth was 14 years (IQR: 13–14; N=45; Fig. 9). The median estimated age at first birth in the family with best records (I) was 14 years (IQR: 12.5–14; range: 11–16; N=8). It is quite possible that females with a recorded first birth at 15+ years may have had first calves at a younger age that died without being recorded.

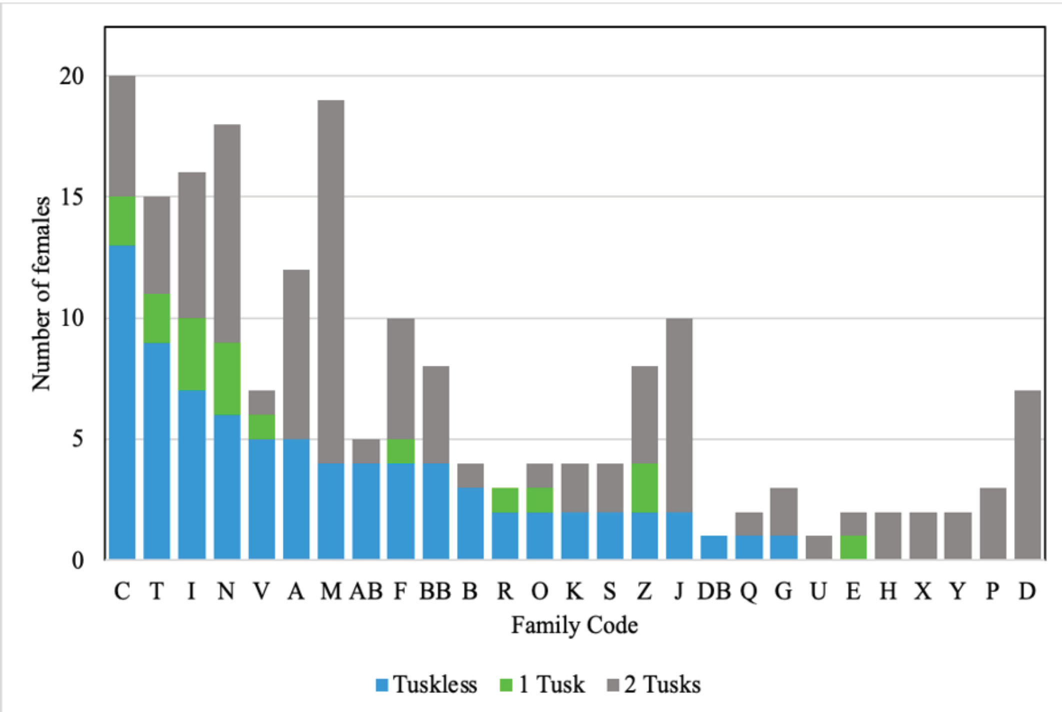

Figure 4. Frequency of two-tusked, one-tusked and tuskless females by family.

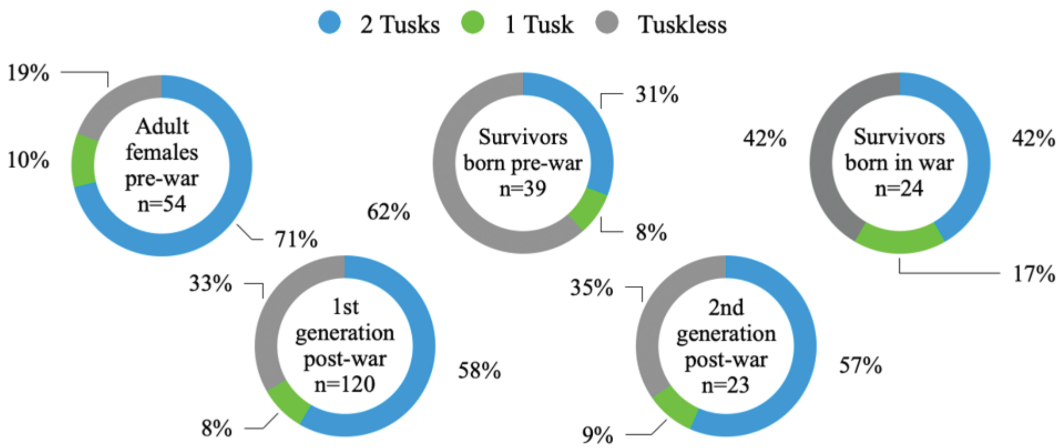

Figure 5. Generational and cohort shifts in tusk configuration.

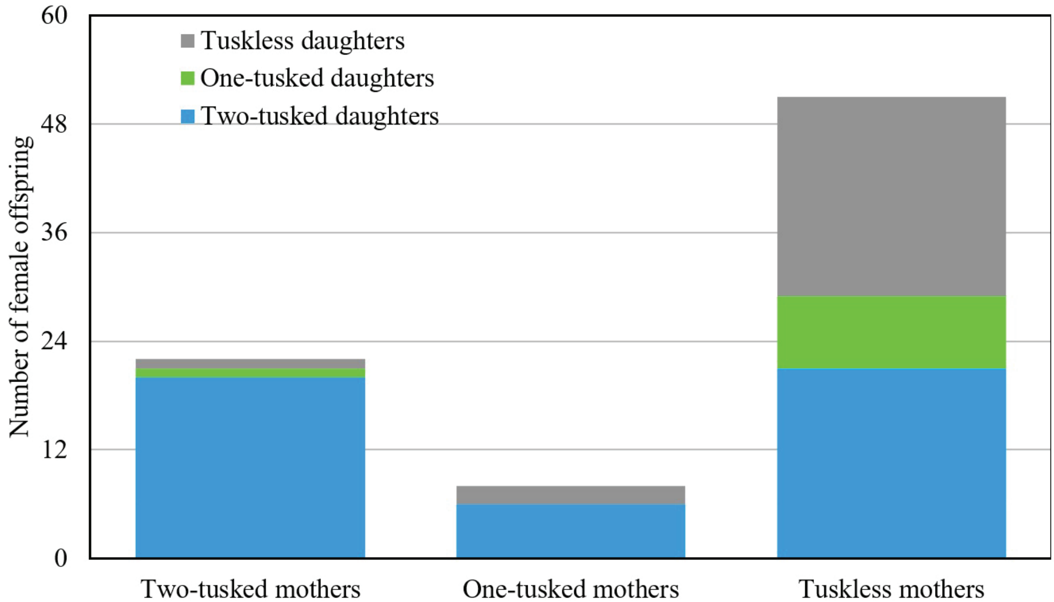

Figure 6. Tusk configuration of mother-daughter pairs.

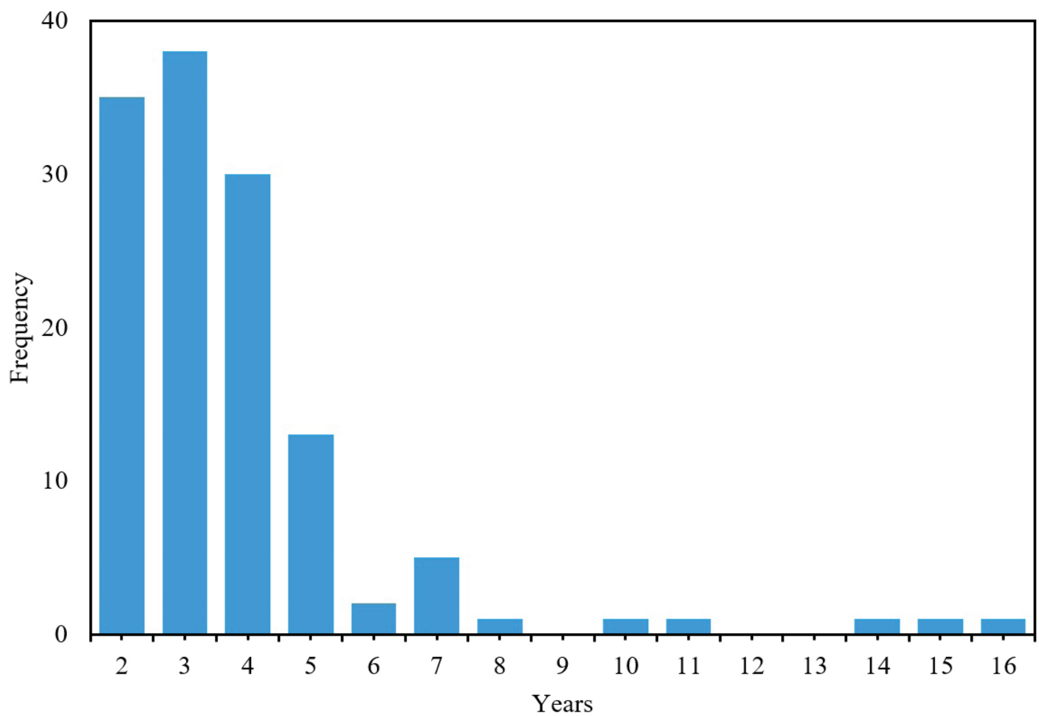

Figure 7. Inter-calf interval.

Figure 8. Isabella of the I family suckles two calves, a female age 3 and a male 5. (© *ElephantVoices*)

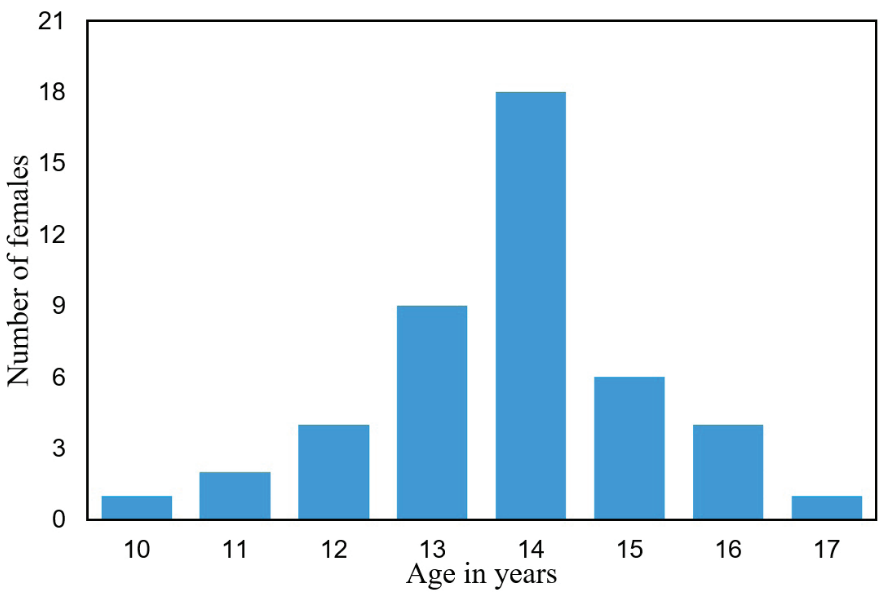

Figure 9. Age at first birth.

Injuries and mortalities

We recorded 38 injuries between 2011 and 2020, 28 caused by snares. Snares were observed around the necks or legs of calves, often leading to death, whereas older elephants were observed with severed or cut trunks and survived. Two adult males with bullet wounds had to be euthanized. There was a surprising number of lame elephants (N=8). While some were likely due to old snare injuries, four were permanently lame apparently with broken or dislocated bones (Fig. 10).

Rangers recorded 24 mortalities between 2014 and 2020. We deduced a further four mortalities from missing individuals. Of these 28 deaths, 14 were illegal (seven adult males were shot, seven calves succumbed to snares), two were natural and 12 were due to unknown causes (Fig. 11). Carcasses were concentrated near the Pungue River park boundary.

Population size and growth

Our estimates of population size based on individual registration fit best with elephant numbers derived from a 9% growth rate from 1994 to 2007 declining to 7% thereafter (Fig. 12). We illustrate our population estimates against aerial surveys carried out in Gorongosa, which were a mix of sample and total counts from fixed-wing aircraft and helicopter.

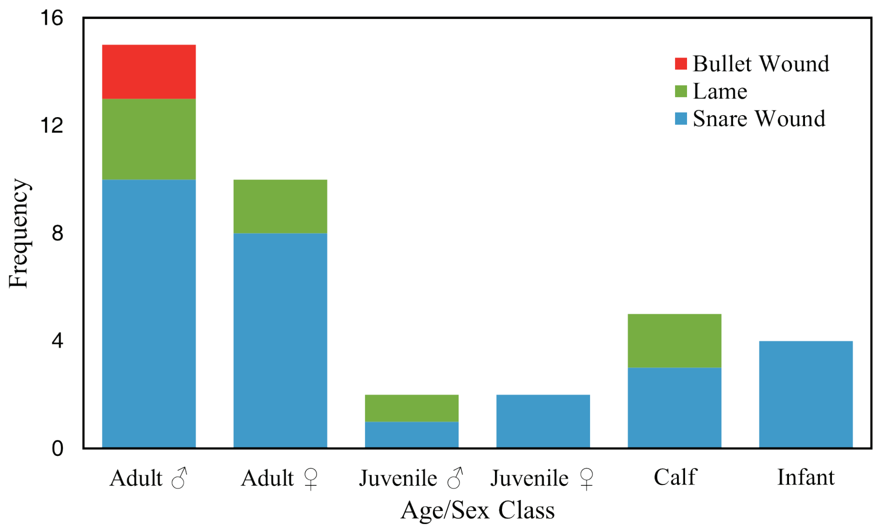

Figure 10. Types of injuries by age/sex class recorded between 2011 and 2020.

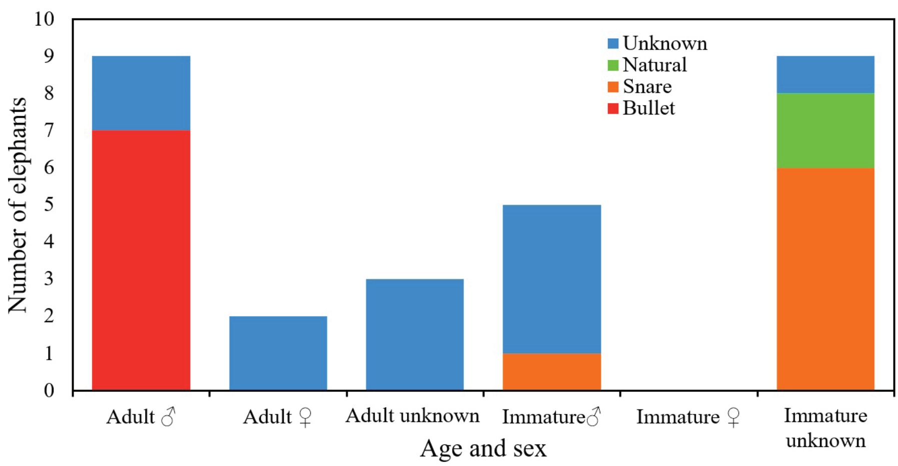

Figure 11. Number and causes of mortality recorded between 2014 and 2020.

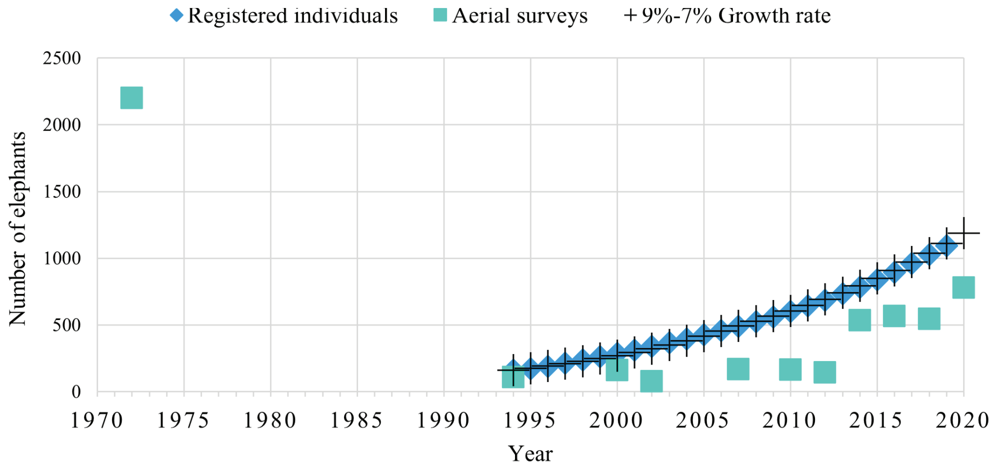

Figure 12. Population size and growth comparing numbers of elephants counted in aerial surveys with our estimates based on registered individuals. The latter fit best with elephant numbers derived from a 9% growth rate from 1994 to 2007 and a 7% growth rate thereafter.

Discussion

Armed conflict in Africa has been associated with wildlife declines of varying degree depending on its frequency and severity (Daskin and Pringle 2018). Elephants are particularly vulnerable due to human demand for ivory and meat, their large-scale habitat needs and long generation times. Mozambique's 15-year civil war had a profound and lasting impact on the Gorongosa elephant population. More than a quarter of a century after the war the population's sex ratio, age structure, and prevalence of tusklessness still bore the hallmarks of killing for ivory.

Like other heavily poached populations (Poole 1989, Wittemyer et al. 2013, Jones et al. 2018) there were relatively few elephants in the older age classes and the sex ratio among individuals over 35 years old was heavily skewed toward females. There were no males over age 50.

As has been documented in other poached populations (Poole 1989, Jones et al. 2018), the selective killing for ivory favoured tusklessness among female survivors. From analysis of historical Gorongosa footage we know that prior to the war a relatively high percentage of Gorongosa females (19%) were tuskless (Campbell-Staton et al. 2021). This was likely due to long exploitation of the population for ivory, first by Indian and Arab traders as early as 1200, followed by the Portuguese in the 1500–1600s (Tinley 1977) and then by slave traders in the 1700–1800s (Machado 2014). In the early 1900s trophy hunters commented on the poor quality of tusks and the presence of tuskless elephants (Vasse 1909). During the war, killing for ivory drove rapid population decline and strong selection favouring tusklessness in females (Campbell-Staton et al. 2021). In this study we found the prevalence of the tuskless trait among female survivors varied by age. Among older female survivors tusklessness increased to 62% (31% two-tusked, 8% one-tusked), while among the cohort of females born during the war, who would have had smaller tusks and therefore been less vulnerable to those killing for ivory, the tuskless trait was 42% (42% two-tusked, 17% one-tusked). Tusklessness among the female offspring born to these survivors remained elevated (35%), indicating a heritable genetic basis for tusklessness and an evolutionary response to poaching-induced selection in Gorongosa (Campbell-Staton et al. 2021).

Our data revealed that tuskless mothers produced near equal numbers of two-tusked (42%) and tuskless (44%) daughters, while 14% were one-tusked. Seventy-five percent of female offspring of one-tusked mothers were two-tusked and 91% of female offspring of two-tusked mothers were two-tusked. These data indicate that the proportion of tuskless females should, theoretically, decline with each generation. We, therefore, expected fewer tuskless females in the second generation post-war. In contrast, the proportion of tuskless females in the second generation remained equally high at 37%, although our sample size was small (N=23) and tuskless (n=12) and one-tusked (n=3) mothers dominated the sample.

The estimated age of first birth of 14 years was higher than the average 11.2 years reported from Tarangire NP (Foley and Faust 2010) or 11.3 years from Samburu NR (Wittemyer et al. 2013), but not dissimilar to that recorded in Amboseli NP (Moss and Lee 2011) and the 13.4 average across 12 populations compiled by Wittemyer et al. (2013). Since younger age at primiparity has been associated with recovering populations (Wittemyer et al. 2013) and with periods of lower nutritional stress (Moss and Lee 2011), we expected to record a younger age at first birth. It is possible that we overestimated the ages of young females, but due to the high number of tuskless individuals our concern was, instead, that we underestimated their age. It is also possible that some of the females recorded with an age of first birth of between 15 and 17 years of age had had a previous calf that died unrecorded.

Gorongosa's average three-year inter-calf interval was lower than Amboseli NP's 4.2 years (Moss and Lee 2011), Samburu NR's 4.0 years or indeed any populations studied (Wittemyer et al. 2013). In Amboseli intervals of <3 years were associated with increased mortality of either younger or older calf, suggesting that mothers were rarely able to suckle two calves simultaneously. In Gorongosa, whereas, many mothers experienced inter-birth intervals of under 2.5 years and were often observed suckling two, and, on at least one occasion, three offspring.

We do not have good data on mortality, but all indications are that it was relatively low. Seven adult males were shot during a period of political unrest and two adult females died of unknown causes. Seven juveniles/calves succumbed to snares and there were likely others. No elephant carcasses were counted from the air (Stalmans pers. comm.). In Amboseli, a population that has experienced very little poaching, the highest mortality rates were among calves, 13.5% of whom died in the first year on average (Lee et al. 2022). Those who experienced a prolonged dry season were 70% more likely to die than those who experienced a moderate dry season (Lee et al. 2011). Gorongosa's adult females remained in good condition into the late dry season and large, full breasts and frequently observed double suckling suggested they had sufficient milk. In Amboseli, lions and hyenas also took calves, while there were very few lions and no hyenas in Gorongosa during our study.

Tinley (1977) estimated that there were 2,200 elephants in Gorongosa in 1972. In 1994, after the war, only 108 were counted (Cumming et al. 1994) and in 2000, Stalmans et al. (2014) estimated there were <200. The density of vegetation in Gorongosa makes accurate aerial counting difficult. A recent study using an automated "oblique-camera-count" imaging system showed fixed-wing aircraft surveys undercount elephants by 14% and 27% in sample and total counts, respectively (Lamprey et al. 2019). Aerial surveys in Gorongosa have included fixed-wing sample counts (1972, 1994, 2004), helicopter sample counts (2000, 2001, 2002, 2007, 2010, 2012) and helicopter total counts (2014, 2016, 2018, 2020).

Our population estimates based on registered individuals were consistently higher than Gorongosa's aerial sample and total counts. In 2016 and 2018 only 8 of 12 and 6 of 12 elephants with satellite collars, respectively, were detected from the air. Together with their families, at least 114 elephants were undetected. Stalmans and Peel (2020) acknowledge that the "781 elephants that were counted represent the minimum number present" and estimated the population to be between 800 and 1,000 individuals in that year, close to our 2019 estimate of 1,094 using individual registration and estimated number of immatures per adult female. Despite the potential inaccuracies, we believe our figures represent an underestimate of the population size as we have not registered new elephants from trail cameras set in 2017. While individual registration is a long-term commitment, we suggest that it can offer a more accurate method of determining elephant population size and, as our results show, simultaneously provide additional reproductive and life history data critical to elephant conservation.

Based on the estimated ages of individually known elephants, we calculated that Gorongosa contained at least 161 elephants in 1994. Twenty-five years after the war the Gorongosa population had likely experienced a six-fold increase (Stalmans and Peel 2020). Our data and the aerial counts suggest different growth patterns, however. Aerial counts after the war indicate that the population experienced very little growth (~0.01%) up until 2014 after which it appeared to be explosive (~20%). Our data suggests, instead, that the population grew at a rate of ~9% until around 2007 when it slowed to ~7%.

The average growth rate of the long-studied elephant populations in the arid landscapes of Amboseli and Samburu, Kenya was 2.7% over 46 years (Lee et al. 2022) and 2.9% over 14 years (Wittemyer et al. 2013), respectively. Elsewhere, similar to our findings, Foley and Faust (2010) documented a sustained growth of 7% over a 13-year period in Tarangire, Tanzania, and Slotow et al. (2005) in South Africa documented an average 8.3% growth rate for 58 populations composed of elephants (with a female bias) re-introduced into small, fenced reserves. Foley and Faust (2010) concluded the rapid growth observed was probably influenced by three factors that also apply to Gorongosa: favourable environmental conditions allowing for a short interbirth interval and early reproductive onset, lack of density dependence and release from the mortality of heavy poaching. Further applicable to Gorongosa and other poached populations, Slotow et al. (2005) pointed out that the female bias in their study provided huge growth potential. Fast recovery in elephant numbers after heavy poaching is not always the norm, however. In Mikumi, where 75% of the population had been killed, an unusually high proportion of adult females were observed to be neither lactating nor pregnant, as indicated by shrivelled breasts (Poole 1989). Fifteen years later 33% of the adult females were still non-reproductive (Gobush et al. 2008). Furthermore, orphaning and family fragmentation, both hallmarks of poaching, have detrimental consequences for calf and juvenile survival (Goldenberg and Wittemyer 2018, Lee et al. 2022) and, consequently, for population growth rate (Parker et al. 2021).

All considered, the rapid growth of the Gorongosa population, sustained over close to a quarter of a century, seems remarkable. Our results demonstrate that given sound protected area management, elephants have the potential for relatively rapid post-war recovery in numbers, given advantageous conditions promoting early and rapid reproduction, combined with high infant and adult survival. Nevertheless, attaining pre-war population size will likely take close to half a century, and genetic, social and behavioural recovery may take even longer.

Acknowledgements

We thank the Government of Mozambique for permission to work in Gorongosa National Park. Special thanks to Phyllis Lee and two anonymous reviewers for their very helpful comments on the draft and to our colleagues Marc Stalmans, Dominique Gonçalves, Mike Marchington and Rui Branco and the many scientists and guides who photographed and recorded elephant groups for us. We are especially grateful in this regard to the dedication of Jason Denlinger. We gratefully acknowledge support from the Elephant Crisis Fund, National Geographic, WildiZe Foundation, Crystal Springs Foundation, The Elephant Sanctuary, the Marshall Frankel Foundation, the Gorongosa Project and USAID.

References

Beilfuss RD, Bento CM, Haldane M, Ribaue M. 2010. Status and distribution of large herbivores in the Marromeu Complex of the Zambezi Delta, Mozambique. Technical Report. http://dx.doi.org/10.13140/RG.2.2.25160.32007

Beyers RL, Hart JA, Sinclair, ARE, Grossmann F, Klinkenberg B, Dino S. 2011. Resource Wars and Conflict Ivory: The Impact of Civil Conflict on Elephants in the Democratic Republic of Congo—The Case of the Okapi Reserve *PLoS One* 6 (11): e27129. https://doi.org/10.1371/journal.pone.0027129

Blanc JJ, Barnes RFW, Craig CG, Dublin HT, Thouless CR, et al. (2007) *African Elephant Status Report 2007: An update from the African elephant database*. IUCN, Gland, Switzerland.

Campbell-Staton SC, Arnold BJ, Gonçalves D, Granli P, Poole J, Long RA, Pringle RM. 2021. Ivory poaching and the rapid evolution of tusklessness in African Elephants. *Science* 374: 483–487. https://doi.org/10.1126/science.abe7389

Cumming D, Mackie CS, Magane S, Taylor RD. 1994 Aerial census of large herbivores in the Gorongosa National Park and the Marromeu Area of the Zambezi Delta in Mozambique. Direcção Nacional de Florestas.

Daskin J, Pringle, R. Warfare and wildlife declines in Africa's protected areas. *Nature* 553: 328–332 (2018). https://doi.org/10.1038/nature25194

Foley CAH and Faust LJ. 2010. Rapid population growth in an elephant *Loxodonta africana* population recovering from poaching in Tarangire National Park, Tanzania. *Oryx* 44: 205–212.

Gobush KS, Mutayoba BM, Wasser SK. 2008. Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult females African elephants. *Conservation Biology* 22 (6): 1590–0. DOI: 10.1111/j.1523-1739.2008.01035.x

Gaynor GM, Branco PS, Long RA, Gonçalves DD, Granli PK, Poole JH. 2018. Effects of human settlement and road on diel activity patterns of elephants (*Loxodonta africana*). *African Journal of Ecology* 56: 872–881. https://gorongosa.org/wp-content/uploads/2020/09/aje.12552.pdf

Goldenberg SZ and Wittemyer G. 2018. Orphaning and natal group dispersal are associated with social costs in female elephants. *Animal Behaviour* 143: 1–8. https://doi.org/10.1016/j.anbehav.2018.07.002

Granli PK and Poole JH. 2022. Who's Who & Whereabouts: An integrated system for reidentifying and monitoring African elephants. *Pachyderm* 63: 72–90.

Jones T, Cusack JJ, Pozo RA, Smit J, Mkuburo L, Baran P, Lobora AL, Mduma S, Foley C. 2018. Age structure as an indicator of poaching pressure: Insights from rapid assessments of elephant populations across space and time. *Ecological Indicators* 88: 115–125. ISSN 1470-160X, https://doi.org/10.1016/j.ecolind.2018.01.030

Kuloba B, Kenana, L, Muteti D, Mwenda E. 2010. Aerial count of large herbivores in Maasai Mara National Reserve and the Surrounding Areas. Kenya Wildlife Service. Unpublished.

Lamprey R, Pope F, Ngene S, Norton-Griffiths M, Frederick H, Okita-Ouma B, Douglas-Hamilton I. 2019. Comparing an automated high-definition oblique camera system to rear-seat-observers in a wildlife survey in Tsavo, Kenya: Taking multi-species aerial counts to the next level. *Biological Conservation* 241: 108243. DOI:10.1016/j.biocon.2019.108243

Laws RM. 1966. Age criteria for the African elephant, *Loxodonta a. africana*. *East African Wildlife Journal* 4: 1–37.

Lee PC, Lindsay WK, Moss CJ. 2011. Ecological patterns of variability in demographic rates. In: Moss CJ, Croze HJ, Lee PC. Eds. *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. University of Chicago Press, Chicago. pp. 74–88.

Lee PC, Moss CJ, Njiraini N, Poole JH, Sayialel K, Fishlock VL. 2022. Cohort consequences of drought and family disruption for male and female African elephants. *Behavioral Ecology*: 33 (2): 408–418. https://doi.org/10.1093/beheco/arab148

Machado P. 2014. White gold. In: *Ocean of Trade: South Asian Merchants, Africa and the Indian Ocean, c.1750–1850*. Cambridge University Press, Cambridge. pp. 168–207 http://doi.org/10.1017/CBO9781107707375.006

Moss C. 1996. Getting to know a population. In: Kangwana K. *Studying Elephants* AWF Technical Handbook no. 7. African Wildlife Foundation, Nairobi. pp. 58–74.

Moss CJ and Lee PC. 2011. Female reproductive Strategies: Individual life histories. In: Moss CJ, Croze HJ, Lee PC. Eds. *The Amboseli Elephants: A Long-term perspective on a long-lived Mammal* University of Chicago Press, Chicago University of Chicago Press, Chicago. pp. 187–204.

Parker JM, Webb CT, Daballen D, Goldenberg SZ, Lepirei J, Letitiya D, Lolchuragi D, Leadismo C, Douglas-Hamilton I, Wittemyer G. 2021. Poaching of African elephants indirectly decreases population growth through lowered orphan survival. *Current Biology* 31 (18): 4156–4162.e5, ISSN 0960-9822, https://doi.org/10.1016/j.cub.2021.06.091

Poole JH. 1989. The effects of poaching on the age structures and social and reproductive patterns of selected East African elephant populations. In: *The Ivory Trade and the Future of the African Elephant*. Volume II Technical Reports. The Ivory Trade Review Group. Prepared for the 7th CITES Conference of the Parties.

Slotow R, Garai ME, Reilly B, Page B, Carr RD. 2005. Population dynamics of elephants re-introduced to small-fenced reserves in South Africa. *South African Journal of Wildlife Research* 35 (1): 23–32.

Stalmans M and Beilfuss R. 2008 Landscapes of the Gorongosa National Park. Unpublished report. https://www.researchgate.net/publication/314878798_Landscapes_of_the_Gorongosa_National_Park/link/58c6ebc7a6fdccde55e3dc18/download

Stalmans M. 2012. Monitoring the recovery of wildlife in the Parque Nacional da Gorongosa through aerial surveys. 2000–2012. A preliminary analysis. Unpublished. https://gorongosa.org/wp-content/uploads/2021/03/053-wildlife_count_report_2000_2012_july2012.pdf

Stalmans M, Peel M, Massad T. 2014. Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2014. Approach, results and discussion. Unpublished.

Stalmans M and Peel M. 2016. Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2016. Parque Nacional da Gorongosa. Unpublished. https://gorongosa.org/wp-content/uploads/2020/08/gorongosaaerialwildlifecount2016_report14november2016.pdf

Stalmans M, Peel M, Gonçalves D. 2018. Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, November 2018. Typescript 32pp. https://gorongosa.org/wp-content/uploads/2020/08/gorongosaaerialwildlifecount2018_report_december2018.pdf

Stalmans ME, Massad TJ, Peel MJS, Tarnita CE, Pringle RM (2019) War-induced collapse and asymmetric recovery of large mammal populations in Gorongosa National Park, Mozambique. *PLoS One* 14 (3): e0212864. https://doi.org/10.1371/journal.pone.0212864

Stalmans M and Peel M. 2020. Aerial wildlife count of the Gorongosa National Park, Mozambique, November 2020. Unpublished.

Tinley K. 1977. Framework of the Gorongosa Ecosystem. PhD Thesis, University of Pretoria, Pretoria.

Turkalo AK, Wrege PH, Wittemyer G. 2017. Slow intrinsic growth rate in forest elephants indicates recovery from poaching will require decades. *Journal of Applied Ecology*. 54 (1): 153–9. https://doi.org/10.1111/1365-2664.12764.

Turkalo AK, Wrege PH, Wittemyer G. 2018. Demography of a forest elephant population. *PLoS One* 13 (2): e0192777. https://doi.org/10.1371/journal.pone.0192777.

Vasse G. 1909. *Three Years Sport in Mozambique*. Isaac Pitman, London

Wittemyer G, Daballen D, Douglas-Hamilton I. 2013. Comparative Demography of an At-Risk African Elephant Population. *PLoS One* 8 (1): e53726 https://doi.org/10.1371/journal.pone.0053726. PMID: 23341984

Wittemyer G, Daballen D, and Douglas-Hamilton I. 2021. Differential influence of human impacts on age specific demography underpins trends in an African elephant population. *Ecosphere* 12 (8): e03720. https://doi.org/10.1002/ecs2.3720