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REVIEW

A systematic map of demographic data from elephant populations throughout Africa: implications for poaching and population analyses

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ABSTRACT

1. The crisis facing Africa's elephant populations is a notorious example of ongoing wildlife declines caused by illegal harvesting. Targeted conservation interventions require detailed knowledge about changes in population sizes and the effect of illegal activities. However, accurately quantifying poaching intensity is a difficult task: commonly calculated from ranger-based carcass-encounter data, the proportion of illegally killed elephants (PIKE) is a function of poaching and background mortality. Hence, at constant poaching intensity, PIKE decreases with increasing natural mortality and also with hunting, management interventions, and other anthropogenically induced deaths. Natural mortality is often more difficult to quantify with accuracy than mortality due to illegal killing, as elephants that die naturally are more likely to be missed than those taken by poachers. In recent analyses, constant background mortality rates were assumed. Yet, for example climate-driven fluctuations in natural mortality, if not quantified and accounted for, may lead to biased estimates of poaching intensity.
2. Varying background mortality rates can be accounted for in the analysis of PIKE, but this requires near-complete counts of natural and management-related deaths and hunting records. Carefully developed population models, which simulate population dynamics and demographic changes while accounting for variation in environmental conditions and management strategies, are alternatives. However, successful calibration of such models requires integrating comprehensive demographic data.

3. We systematically review the scientific and 'grey' literature on African elephant demography with the objective of facilitating poaching and population analysis possibilities through an inventory of information relevant to demography.
4. Our screening of 10900 publications resulted in the review of relevant information provided by 431 studies from 420 study sites throughout Africa. From these, we extracted demographic data collected between 1900 and 2017, and collated them in the newly created African Elephant Demographic Database (AEDD; 10.6084/m9.figshare.19387085). We found 37 natural mortality estimates from five different study sites. Other mortality data, demographic rates, and age- and sex-structured population data were substantially more abundant, both temporally and spatially.
5. This new collection of demographic rates, age- and sex-structured population data, and cause-partitioned mortality estimates identifies spatial and temporal data gaps and provides prior information needed for African elephant population models. Closing these data gaps and subsequent analyses of realistic population models may aid elephant conservation via improved policies, legislation, and protection.

INTRODUCTION

The African elephants *Loxodonta africana* and *Loxodonta cyclotis* (see Roca et al. 2001) are iconic. Not only are the large pachyderms important ecosystem engineers that contribute to maintaining savanna and forest biodiversity (Haynes 2012), but their charisma also helps to boost the local tourism economy and attract funding for conservation (Naidoo et al. 2016). And yet, anthropogenic influences such as poaching, habitat fragmentation, and urban encroachment make the protection of African elephants a real concern. Specifically, increasing poaching in the early 2000s hit many subpopulations hard, driving a continental population decline (Wittemyer et al. 2014). Recently, this trend seems to have reversed: estimated poaching rates have decreased since 2011 (Hauenstein et al. 2019), but the effect on population numbers and structure is still unclear.

Sustainable conservation of African elephants requires accurate quantification of poaching to serve as a basis for international conservation policy and decision-making. With the aim of providing reliable and impartial data to obtain such information, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Secretariat, together with African elephant range-states and supported by the European Union, implemented the Monitoring the Illegal Killing of Elephants (MIKE) programme in 2001. Since then, MIKE has been consolidating and analysing annual site-specific data to determine the subregional and continental trends in poaching based on the Proportion of Illegally Killed Elephants (PIKE). PIKE is calculated as the number of illegally killed elephants found, divided by the total number of elephant carcasses encountered by law-enforcement patrols or other means (CITES 2017).

Proportion of illegally killed elephants is a function of both illegally killed elephants and so-called background mortality, comprising natural mortality, legal trophy hunting, management interventions and other anthropogenically induced deaths (e.g. train collisions or accidental electrocution). For example, if the number of natural deaths in a given year and site is relatively high – as perhaps in a drought year – the total number of elephant carcasses encountered will be large, relative to the number of carcasses resulting from illegal activities, and thus, PIKE will be low, as long as patrolling effort stays approximately constant. Natural mortality is often more difficult to quantify with accuracy than mortality due to illegal killing, as elephants that die naturally are more likely to be missed than those taken by poachers. Therefore, unquantified variation in background mortality rates might substantially bias PIKE and estimated poaching rates (Burn et al. 2011, Hauenstein et al. 2019). To resolve this issue, systematic observations of natural and management-related deaths and hunting records would ideally be used to account for variation in background mortality. While African elephants have been studied extensively, such data are probably only available for the handful of sites in which detailed demographic studies have been conducted (e.g. Amboseli National Park, Kenya: Moss et al. 2011; Tarangire National Park, Tanzania: Foley & Faust 2010; Samburu and Buffalo Springs National Reserves, Kenya: Wittemyer et al. 2013; Dzanga Bai, Central African Republic: Turkalo et al. 2018).

Mechanistic and process-based models (Connolly et al. 2017) can provide alternatives to correlative, regression-type analyses commonly used to estimate poaching intensity

(Burn et al. 2011, Wittemyer et al. 2014, Hauenstein et al. 2019). Models have advantages for integrating structural realism (Grimm & Berger 2016), identifying causal relationships (Cuddington et al. 2013), interpreting parameters, and forecasting and predicting (Kearney & Porter 2009, Hefley et al. 2017, Getz et al. 2018). In the case of African elephants, dynamic process-based models of population dynamics could be built and calibrated explicitly to estimate variation in population sizes and poaching, while accounting for demographic changes, environmental conditions, and management strategies. Integrating physiology, demography, and environmental fluctuation can help to separate natural dynamics from human-induced mortality, and thus create more realistic PIKE estimates from statistical models (Connolly et al. 2017). A major challenge for such an approach is meaningful model parameterisation with an accurate representation of uncertainty (Hartig et al. 2011), which requires process-specific data on age- and sex-structured mortality and reproduction numbers. Model scaling, validation, and balancing complexity are additional challenges (Cabral et al. 2017). Another prerequisite is reliable prior information on relevant model parameters, such as the duration of the calving interval and life span, and on model structure, such as sex-specific functions of poaching mortality and the shape of age-specific functions of fecundity.

Often motivated to aid conservation, ecologists have monitored and studied African elephants extensively (*Loxodonta africana* more than *Loxodonta cyclotis*). So, in principle, age- and sex-structured demographic data should be available, but it is unclear for how many subpopulations and for which time periods. We review the existing literature on African elephant population dynamics and demography with the objectives to provide a systematic map (see James et al. 2016) of African elephant demographic data and to explore the feasibility of mechanistic and process-based analysis approaches. We extract demographic data after review of scientific and 'grey' literature, and collate the estimates in the African Elephant Demographic Database (AEDD). This newly created open database is further explored to summarise the availability and spatial distribution of the extracted data, broken down into the categories 'mortality', 'reproduction' and 'demographic population structure'. In a section on future research, we discuss spatial and temporal data gaps and how the extracted demographic data can be used in conservation management and in future analyses of poaching intensity and population dynamics.

METHODS

The existing African Elephant Database (AED; Thouless et al. 2016) provides abundance data from many African elephant populations and several monitoring programmes, but does not include any other demographic information. To make these data readily available, we aimed to review all relevant studies on African elephant population dynamics and demography published as both scientific and 'grey' literature. To do so, we first carried out a systematic search based on Web of Science to cover primarily scientific literature. In a second round, we reviewed all entries of the African Elephant Library, which comprises scientific and 'grey' literature studies on the biology, ecology, and management of African elephants.

Web of science

To evaluate relevant search terms for studies on African elephant population dynamics and demography, we first conducted a scoping search according to the guidelines given by Collaboration for Environmental Evidence (2018). On 26 February 2019, we carried out a comprehensive search of Web of Science literature in eleven bibliographic databases (Web of Science Core Collection, BIOSIS Citation Index, BIOSIS Previews, Current Contents Connect, Data Citation Index, Derwent Innovations Index, KCI Korean Journal Database, MEDLINE, Russian Science Citation Index, SciELO Citation Index, and Zoological Record) using the following topic search terms: [(Africa* AND Elephant* OR "L* africana" OR "L* cyclotis") AND (population* OR demograph* OR mortality* OR "vital rate*" OR reproduct* OR fecundity OR fertil*) NOT elephantiasis]. This search resulted in 4248 studies, of which 33 were duplicate (i.e. duplicates in the database or supplementary material for other included studies) and 60 were redundant (i.e. results/data presented in other studies); these records were removed (see Fig. 1).

African elephant library

The African Elephant Library (https://www.iucn.org/ssc-groups/mammals/african-elephant-specialist-group/african-elephant-library) is an online literature database comprising references on the biology, ecology, and management of African elephants for registered users. The database is maintained by the conservation organisation Save The Elephants in collaboration with the African Elephant Specialist Group of the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC), and its records are updated manually by active African elephant researchers. On 9 January 2020, the library comprised 8076 studies, of which 1331 were duplicates of studies derived through our Web of Science literature search and were hence removed.

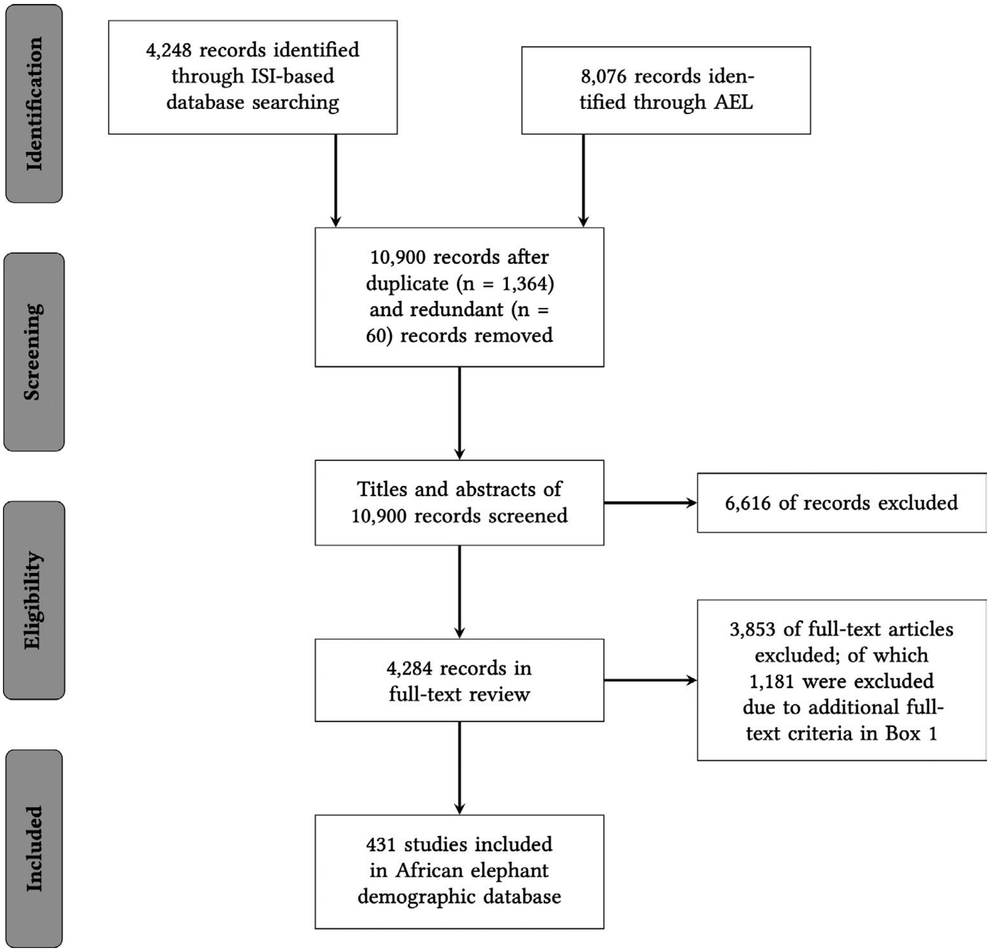

Fig. 1. PRISMA flow diagram illustrating the review process of Web of Science (ISI) and African Elephant Library (AEL) literature. Exclusion criteria are presented in Box 1; parameters for which estimates were extracted from the studies included in the review are listed in Box 2.

Selection criteria, data extraction, and data availability

We randomised the order of the 10900 studies (4155 from the Web of Science search, plus 6745 from the African Elephant Library) to avoid observation biases throughout the selection process. During a first screening, only titles and abstracts were considered and studies were dropped if they met our exclusion criteria (see Box 1). The 4284 studies that were not excluded went into full-text review, in which we excluded studies that reported only numbers of live and dead elephants aggregated by study site without providing any information of the population structure (Box 1); these studies were excluded by us but are likely to be included in the AED. We included in the review only studies in which population sizes and densities were structured by age or sex, or those in which carcass numbers were structured by age or sex or if the cause of death was provided.

From the 431 papers that were included in the review, data were extracted for the parameters presented in Box 2. In many studies we reviewed, data were presented in graphical Figures, which we manually digitised using the R Core Team (2018) package metaDigitise (Pick et al. 2018). All extracted estimates of parameters were stored in the newly created African Elephant Demographic Database (AEDD) with one row per estimate. For example, if a study provided annual mortality rates for x time periods and y subpopulations, the extracted estimates from that study would require $x \times y$ rows in the AEDD.

In addition to the extracted demographic data, relevant general information was extracted from each study and entered in separate columns of the AEDD, as detailed in Box 3.

The current AEDD accompanying metadata, raw and processed Web of Science exports, and R code to reproduce data extraction are available at Figshare: https://doi.org/10.6084/m9.figshare.19387085. The CITES Secretariat

Box 1. Literature review exclusion criteria

All studies meeting one or more of the exclusion criteria listed were dropped during initial screening or full-text review. In order to exclude studies of zoo and captive elephants, we reviewed 50 random hits resulting from the following topic search terms: (((Africa* AND Elephant*) OR ("L* africana") OR ("L* cyclotis")) AND (population* OR demograph* OR mortality* OR ("vital rate*") OR reproduct* OR fecundity OR fertil*) AND zoo*). As six of the 50 studies contained potentially valuable information, we excluded this restriction from the search term, but studies of zoo and captive elephants were excluded during the screening or full-text review. More details are provided as part of the African Elephant Demographic Database's metadata.

Exclusion criteria

- Study of elephants kept in captivity (e.g. zoos or orphanages)
- Study of species other than the African elephants Loxodonta africana and Loxodonta cyclotis
- Study without demographic data (see Box 2)
- Study of low quality; data presented are not reliable (e.g. survey or sampling method unknown or invalid or sample size <10)
- Population size studied < 50 elephants
- Study presents theoretical results only; simulation study
- Study provides data from before 1900
- Study inaccessible through the subscriptions held by the University of Freiburg or personal communication with the authors

Additional exclusion criterion for full-text review

- Study exclusively provides population size or number of carcass estimates without further details of age- or sex-structure or cause of death

maintains the AEDD through the MIKE Programme. The maintained database can be found at: https://citesmike.org/resources/.

RESULTS

Availability and distribution of demographic data

The review included 431 studies that provided demographic data (i.e. any of the estimates listed in Box 2). For most elephant range-states, there is at least one study that contributed data (see Fig. 2). The countries showing highest study abundance are Kenya (85), Tanzania (58), South Africa (39), Zimbabwe (34), and Uganda (32).

As expected, the literature review found far fewer studies providing demographic data for forest elephants *Loxodonta cyclotis* than for savanna elephants *Loxodonta africana*. Individuals of *Loxodonta cyclotis* are generally difficult to observe. Moving through thicker vegetation, they are more difficult to locate, count, and identify than their savanna-inhabiting relatives. In all, 60 studies provided 679 estimates (*c.* 6% of all extracted estimates) for forest elephants, in, among other places: Dzanga Bai, Central African Republic (Turkalo et al. 2013, 2017, 2018); Gamba Complex, Gabon (Eggert et al. 2014); Kakum National Park, Ghana (Eggert et al. 2003); Loango National Park, Gabon (Head et al. 2013); Lobéké National Park, Cameroon (Ekobo 1995); and Odzala National Park, Congo (Marechal et al. 1998, Querouil et al. 1999). The data extracted from these studies comprise age- and sex-structured population proportions, fecundity and survival estimates, number of births and carcasses, and age at first calf and inter-calf interval estimates.

For both species, 58 reviewed studies provided data from individual recognition surveys in 31 ecosystems. In total, 2914 estimates were extracted, primarily from populations in:

- Addo Elephant National Park, South Africa (Whitehouse & Hall-Martin 2000, Whitehouse & Kerley 2002, Gough & Kerley 2006),
- Hluhluwe–Imfolozi Park, South Africa (Kuiper et al. 2018),
- Pilanesberg National Park, South Africa (Woolley et al. 2008),
- Amboseli National Park and surrounding area, Kenya (Western et al. 1983, Lee & Moss 1986, Moss 1988, 2001, Poole & Thomsen 1989, Poole 1989, Hollister-Smith et al. 2007, Lee et al. 2011, 2013, 2016),
- Meru National Park, Kenya (Njumbi 1995, Onyango & Lesowapir 2016),
- Samburu and Buffalo Springs National Reserves, Kenya (Wittemyer 2001, Wittemyer et al. 2005, 2013, Rasmussen et al. 2008),
- Sweetwaters Game Reserve, Kenya (Ogola & Omondi 2005),
- Tsavo National Park, Kenya (Poole 1989, McKnight 2000),
- Dzanga Bai, Central African Republic (Turkalo et al. 2013, 2017, 2018),
- Kasungu National Park, Malawi (Jachmann 1980, 1986),
- Kidepo Valley National Park, Uganda (Aleper & Moe 2006),
- Queen Elizabeth National Park, Uganda (Poole 1989),
- Mikumi National Park, Tanzania (Poole 1989),
- Tarangire National Park, Tanzania (Foley et al. 2008, Foley & Faust 2010), and
- Odzala National Park, Congo (Querouil et al. 1999).

Ideally, such comprehensive – and often reliable – individual recognition data would be available from each study

Box 2. Parameters used for African elephant demographic data, sorted by process

Studies providing any of the parameters presented (or derived values) were included in the review and used for data extraction if none of the exclusion criteria (see Box 1) applied. Data were extracted for each time period and subpopulation.

Mortality

- Number of deaths
- Annual mortality rate by cause of death
- Number of carcasses by cause of death and age of carcasses
- Carcass ratio by cause of death and age of carcasses
- Proportion of the total number of carcasses that died due to a specific cause (e.g. PIKE)
- Survivorship (i.e. proportion of the population that survives up to a certain age)

Reproduction

- Number of births
- Annual birth rate
- Annual conception rate
- Reproductive value
- Inter-calf interval estimates
- fecundity (e.g. fecundity_{mx})
- Age at first calf estimates
- Age at first spermatogenesis estimates
- Age at puberty estimates

Population size and structure

- Population size or density
- Annual exponential rate of increase
- Annual population growth rate
- Number of translocated elephants (in or out)
- Number of dispersed elephants
- Foetal sex ratio
- Sex ratio
- Proportion of the total population that is of a certain sex or age
- Proportion of the female population that is of a certain age
- Proportion of the population living/observed in family groups that is of a certain sex or age
- Proportion of the mature population that is of a certain sex or age
- Proportion of the mating population that is of a certain sex or age
- Proportion of the reproductively available population that is of a certain sex or age
- Proportion of the female population that is reproductively available/active and of a certain age

population for multiple years. Yet, while most monitoring efforts run for a longer time period, only 18 of 31 individual recognition studies made data available for more than two years of survey.

The varying availability of demographic studies and data over time might be influenced by varying topics of interest in African elephant population ecology, and also by changing funding opportunities. Itemised by main study focus, Appendix S1 shows that censuses, status reports, and the characterisation of the demography of the population that is monitored have been the focus of study most frequently and consistently between 1960 and 2019. Yet, a systematic temporal pattern in study focus is not readily apparent. Making data publicly available to ensure a study's reproducibility has become increasingly relevant in scientific publishing, so it seems unsurprising that the number of studies providing data has also increased over time.

Quantitative information on density dependence in elephant populations is extremely scarce. The only estimates of how population density affects demographic rates via the processes of reproduction and mortality were reported for the population in Addo Elephant National Park, South Africa: Whitehouse and Kerley (2002) found a negative relationship of population density on conception rate based on sampling between 1955 and 1996, and Gough and Kerley (2006) obtained a positive relationship of population density on male foetal sex ratio and negative effects

Box 3. Information collected from each of the 431 studies on African elephant demography that was included in the review

- Study identification code (running index to ensure reproducibility of this literature review)
- Entry identification code (running index for all extracted estimates per study)
- Study authors
- Study title
- Year of publication
- Name of the extracted estimate (e.g. annual mortality rate; see AEDD metadata)
- Sample size
- Type (e.g. standard error)
- Variance estimate, statistical distribution (if extracted estimates are parameters of a statistical distribution)
- Reported age (of the elephants for which the estimate was observed/derived)
- Sex (of the elephants for which the estimate was observed/derived)
- Time period (for which the estimate was observed/derived)
- Time period (of all observations during the study)
- Sampling dates
- Sampling season (wet, dry)
- Annual rainfall (if readily provided, not extracted from graphical Figures)
- Study area name
- Stratum name
- Study area size
- Sampling coverage estimate
- Sampling coverage unit (unit of estimate, e.g. percentage or km^2)
- Country name (ISO 3166 standard name)
- Country code (ISO 3166-1 Alpha-3)
- Surveyed species (*Loxodonta africana* or *Loxodonta cyclotis*)
- Surveyors (if not authors)
- Survey type (aerial survey, ground survey)
- Survey method (e.g. sample count or total count, systematic or random transects)
- Combined strip width (in case of aerial transect surveys)
- Fenced (was the study area fenced during the time of observation? fully, partly, no fence)
- Qualitative poaching indication (e.g. low or heavy poaching)
- Qualitative natural mortality indication (e.g. extreme mortality events due to drought conditions)
- Qualitative management indications (e.g. culling started in year X, or area is highly protected)
- Focus of study
- Included in African Elephant database (AED; yes, no, partly)
- Contains map of study area (yes, no)
- Additional remarks

on annual birth rate and age of females at first birth from samples between 1976 and 2003. Quantitative information on compensatory mortality is missing entirely: it is not known whether, or by how much, poaching mortality is compensated for by reduced natural deaths. While there has been research on the role of density dependence in population growth rates (Van Aarde et al. 1999, Chamaillé-Jammes et al. 2008, Foley & Faust 2010), compensatory mortality was not investigated in any of the studies we reviewed.

Mortality

From 126 studies, we extracted 2369 estimates related to mortality (see Box 2). The authors of 98 studies differentiated among mortality causes, yielding 839 estimates, mostly reporting the number of culled, poached or trophy-hunted elephants. Only six studies explicitly measured natural mortality, providing in total 37 estimates of natural mortality: Laws (1974), Conybeare and Haynes (1984) and Wittemyer et al. (2013) published numbers of elephants that died naturally in Murchison Falls National Park, Uganda, in 1946, in Hwange National Park in 1982, and in the national reserves of Samburu and Buffalo Springs in Kenya between 1998 and 2011, respectively. Lee et al. (2011) provided natural mortality rates for elephant calves living in Amboseli National Park and surrounding areas in Kenya between 1974 and 2002, and Lee et al. (2013) presented survivorship estimates for elephants of the same population that experienced droughts within the first two years of their lives. Additionally, Turkalo et al. (2017) published an estimate of annual natural mortality rate for the forest elephants in Dzanga Bai, Central African Republic, averaged for the years from 2005 to 2013 (see Fig. 3). However, such an averaged value provides no information on variation in natural mortality between years, and is thus not suitable as a plug-in estimate in an annual analysis of poaching intensity.

This extreme sparsity of natural mortality data is somewhat surprising given the importance of such information and the number of individual recognition studies that must have computed estimates. However, mortality rates are more difficult to quantify than fecundity, as monitoring carcasses and emigration is extremely laborious and annual natural mortality rates are extremely low. Additionally, even when carcasses are found, assigning mortality causes in the field is difficult since many carcasses are not fresh, and in particular identifying natural mortality is subject to much more uncertainty than human-induced mortality.

In contrast, management-related interventions were better documented: we extracted 3367 carcass number estimates

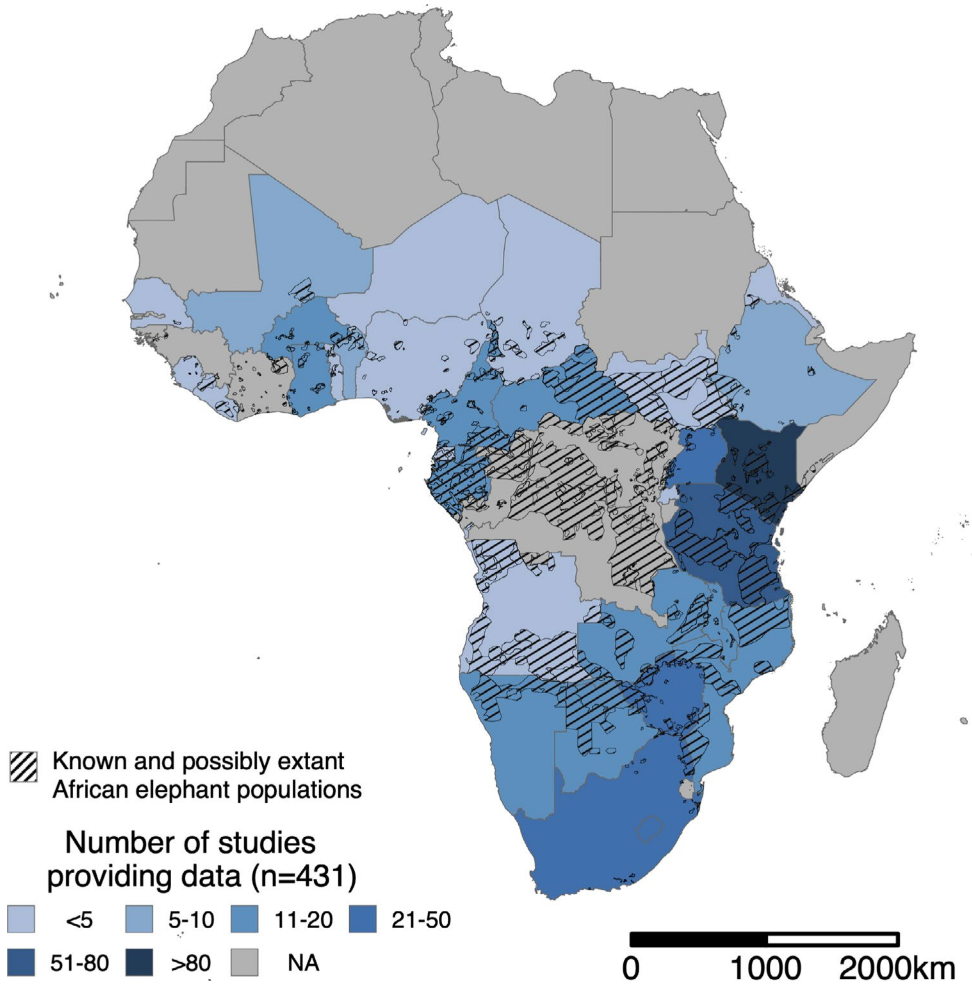

Fig. 2. Geographic representation of the abundance of studies providing demographic data broken down by country, and overlaid by the range of known and possibly extant African elephant populations (shown by crosshatching; Gobush et al. 2020). Some studies provide data for multiple countries.

from 46 comprehensive culling and management records over 69 years from elephants in Kenya, Rwanda, South Africa, Tanzania, Uganda, Zambia, and Zimbabwe, and an additional 123 carcass numbers from five hunting records from Botswana, Uganda, and Zimbabwe.

Demographically structured and mortality cause-partitioned carcass numbers, carcass ratios, survival or mortality rates, and proportions of carcasses assigned to causes of death (e.g. PIKE) were found for 21 countries (Fig. 3). Most mortality estimates were available for Kenya, Zimbabwe, and South Africa. For these countries, mortality estimates were derived for long time periods between 1961 and 2014, 1960 and 2015, and 1919 and 2015. In Kenya, most mortality estimates were provided for elephants in Amboseli National Park and its surrounding area (Moss 2001, Lee et al. 2016), the Tsavo ecosystem (Ottichilo 1987) and the Samburu and Buffalo Springs national reserves (Wittemyer et al. 2005, 2013), while the remaining estimates were derived from 44 different ecosystems. In Zimbabwe, we extracted mortality data for 16 sites; most estimates came from Hwange National Park (Conybeare & Haynes 1984, Dudley et al. 2001). In South Africa, mortality data were available for 12 sites; most estimates came from the elephants in Addo Elephant National Park (Whitehouse & Hall-Martin 2000, Gough & Kerley 2006) and Kruger National Park (De Vos et al. 1983, Whyte 2004, Ferreira et al. 2017).

Reproduction

Statistics describing reproduction in elephant populations are difficult to obtain and require detailed observations. Of the 431 studies with demographic data, 61 studies provided 881 estimates of reproduction parameters for a given study population and time period. Of these, 583 estimates (obtained

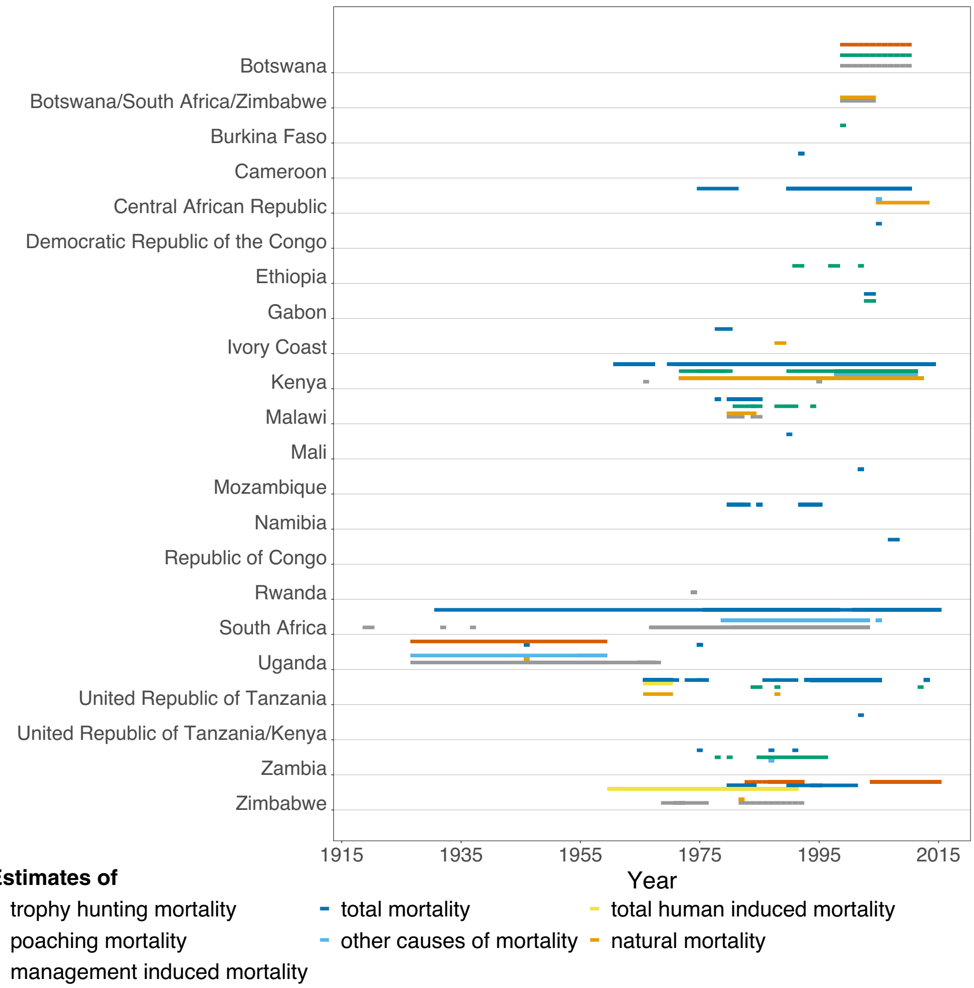

Fig. 3. Summary of African elephant mortality estimates that are available, separated by mortality cause, itemised by country over time.

from 29 studies) describe rates of reproduction (number of births, annual birth rate, fecundity, annual reproductive rate and conception rate), 62 estimates (23 studies) were available for age at first reproduction, first conception, first spermatogenesis, or puberty, and 116 estimates (40 studies) describe the duration of inter-calf intervals.

Reproduction parameters were derived for 14 countries: Botswana, Cameroon, Central African Republic, Kenya, Malawi, Mozambique, Namibia, Republic of Congo, Rwanda, South Africa, Tanzania, Uganda, Zambia, and Zimbabwe. While there are single estimates for many different populations, almost half (414) of the reproduction parameter estimates we extracted were derived from the elephants in the Kenyan Samburu and Buffalo Springs National Reserves (Wittemyer et al. 2005, 2013), Amboseli National Park and its surrounding area (Hollister-Smith et al. 2007, Lee et al. 2016), and South Africa's Addo Elephant National Park (Whitehouse & Hall-Martin 2000, Whitehouse & Kerley 2002, Gough & Kerley 2006).

Demographic population structure

The proportion of the total, female, or family group population that belongs to a certain age- or sex-class is relevant information for successful calibration of an elephant population model. With 7283 estimates derived from 198 studies, this category of demographic data is the largest. Most estimates extracted (5190 from 182 studies) are observed proportions of the total surveyed population belonging to certain age- or sex-classes for a given study site and time period. Others are proportions of the family group population excluding bull groups (778 from 10 studies), of the female population (947 from 21 studies) and of the mature population (254 from 9 studies). These estimates of the demographic structure are available for a relatively wide temporal range (1931-2017) and for 27 countries. As an example, we show continentally aggregated age-structures for each decade between 1960 and 2019 (see Fig. 4). The elephant population is generally skewed towards younger ages. Reduced relative frequency of elephants 20–30 years old, as

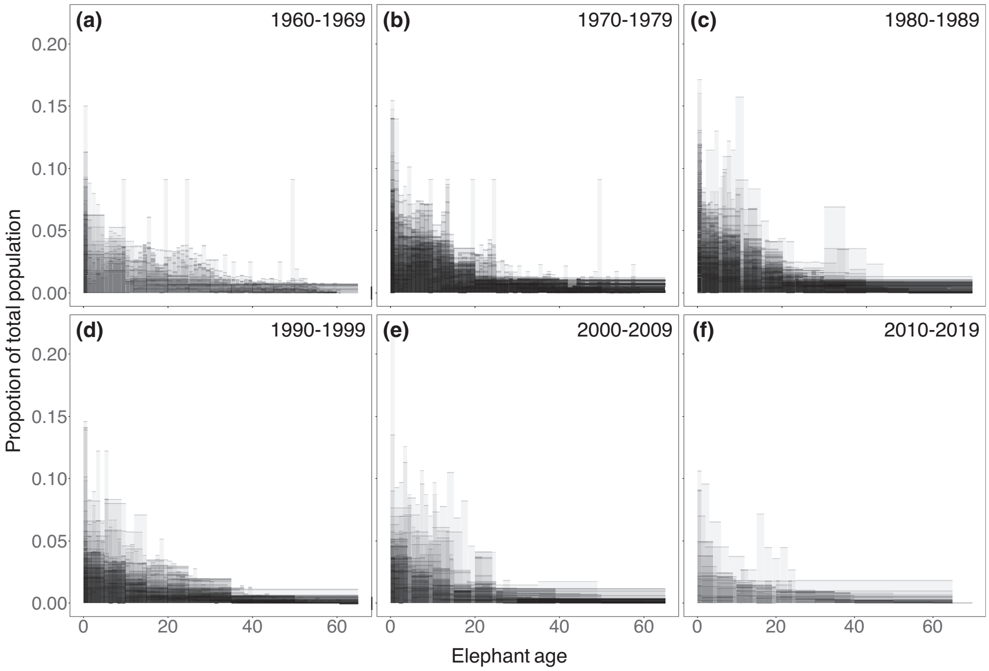

Fig. 4. Continentally aggregated African elephant age-structures for (a) 1960–1969, (b) 1970–1979, (c) 1980–1989, (d) 1990–1999, (e) 2000–2009 and (f) 2010–2019. Each bar represents the estimated proportion of the total population that belongs to an age-class. The slightly darker top of each bar highlights the heterogeneity of the proportions. We assumed a maximum age of 65 for age-classes with no upper boundary (e.g. ≥30 years). Estimates of qualitative age indications were not included.

suggested in Fig. 4d–f, might be a consequence of high-intensity poaching in former decades (Douglas-Hamilton 2009).

Reporting of age- and sex-structure among populations appears to be diverse and is not standardised. Reported ages can be exact age estimates for specific individuals or age-classes spanning one to 30 years, and even age-classes of the same length do not necessarily overlap in different studies (see Fig. 4). In several cases, elephant ages were reported as one of the following qualitative indications of age: 'calf', 'juvenile', 'young', 'half-grown', 'sexually immature', 'intermediate', 'subadult', 'sexually mature', 'full-grown', and 'adult'. The reported sex usually only discriminates between females and males, but occasionally also qualifies 'solitary male', 'dispersed male', 'male in family group', 'family individual', or 'unknown'.

As with many of the demographic data, a large proportion of demographic population age-structure estimates came from elephants living in Kenyan ecosystems (Fig. 5), such as:

- Amboseli National Park and its surrounding area (Western et al. 1983, Lee & Moss 1986, Moss 1988, 2001, Poole & Thomsen 1989, Poole, 1989, Hollister-Smith et al. 2007, Lee et al. 2011, 2013, 2016),
- Maasai Community Conservation Area (Ahlering et al. 2012),
- Meru National Park (Njumbi 1995),
- Sweetwaters Game Reserve (Onyango & Lesowapir 2016), and
- Tsavo ecosystem (Laws & Parker 1968, Ottichilo 1987, Poole 1989, McKnight 2000).

Only South Africa shows a similarly continuous stream of data over time as Kenya. Bearing in mind the difficulties, costs, and efforts necessary to conduct population studies in many elephant populations, information on population structure is available for a relatively large number of study sites and years.

DISCUSSION

Database coverage and quality

In this review, we present the first literature-based demographic database for African elephants, summarising hundreds of individual estimates from throughout the continent. This new collection of demographic rates, age- and sex-structured population data, and cause-partitioned mortality estimates provides prior information for African elephant population models and reveals spatial and temporal data gaps. Unfortunately, the data could not be mapped to subpopulation level, as exact coordinates for the areas surveyed are absent or difficult to obtain in most cases. To derive accurate coordinates for the study

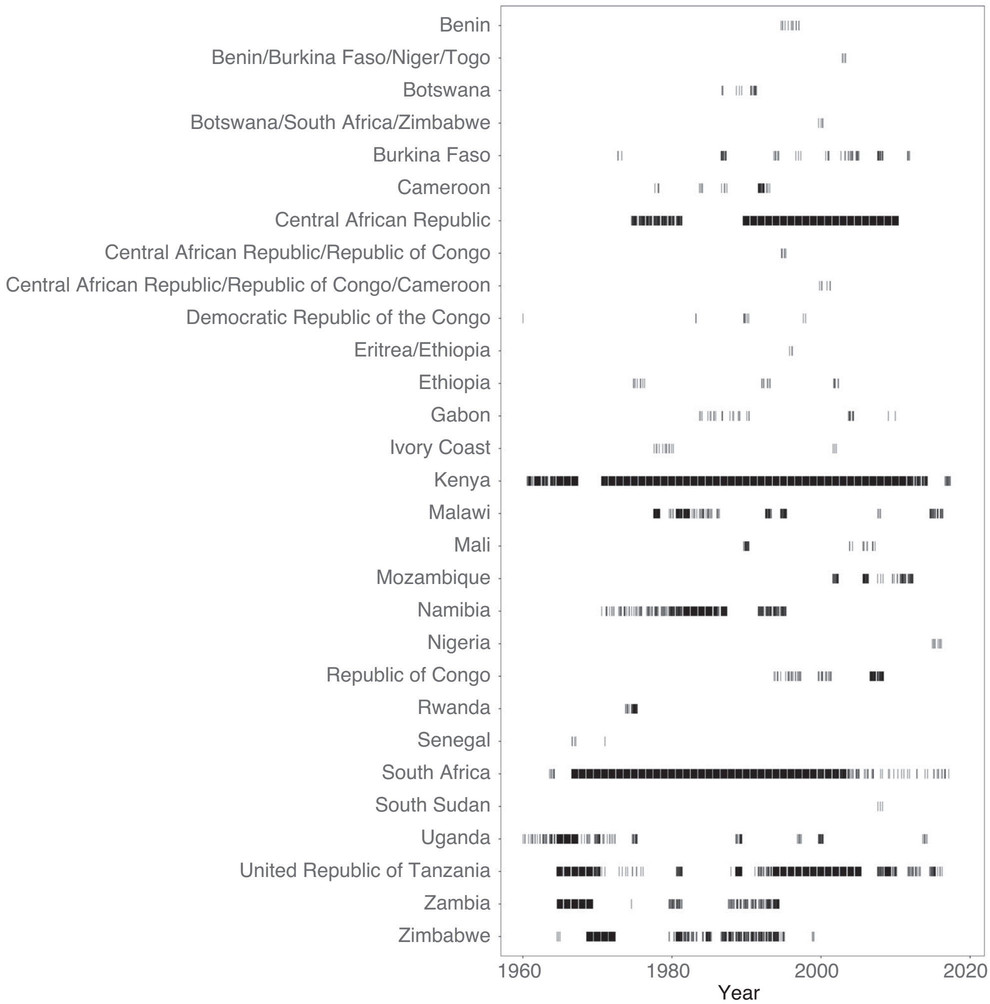

Fig. 5. Availability of African elephant demographic population structures per country and year. Each bar represents a database entry of an observed or estimated proportion of age- or sex-class for a given study country and year, calculated from all elephants surveyed, or for family group, mature, female, and reproductively active or reproductively available populations. Some ecosystems were sampled across country borders.

areas, a next step will be to digitise published maps or contact the study authors, if such information is not otherwise available. While the synthesis of this review is presented at the country level, any relevant site-specific information was extracted and is available alongside the data in the AEDD (https://doi.org/10.6084/m9.figshare.19387085).

The spatial and temporal amplitude of various demographic data extracted for this literature review seems promising. Particularly, the scope of information on demographic population structure will contribute substantially to a successful likelihood-based calibration of a complex, dynamic population model. Since most of the processes driving the dynamics of elephant populations are age- and sex-specific (Moss 2001, Wittemyer et al. 2013), accurate age- and sex-structure observations can substantially decrease the dimensionality problem when estimating model parameters (Plard et al. 2019).

For both African savanna and forest elephants, individual recognition studies such as those in Samburu and Buffalo Springs, Kenya (Turkalo et al. 2013), or Tarangire National Park, Tanzania (Foley & Faust 2010), yield the most comprehensive demographic data and are thus particularly useful, both for estimating poaching intensity and for the calibration of complex, dynamic population models. Surveyors often follow individuals closely, with the aim to observe the same individual multiple times a year, such that, in principle, no event relevant for the dynamics of a population (e.g. birth or death) passes unnoticed (Wittemyer et al. 2005). The present literature review confirms that data resulting from these monitoring efforts are scarce, patchy, and often only available as aggregated estimates, potentially caused by a focus on the publication of analyses rather than detailed descriptive studies.

Natural mortality rate estimates and use in future research

Our results show that there are few observations of natural mortality available, despite the large number of elephant population studies. In contrast, monitoring data discriminating among causes of mortality were obtained for a fairly large number of sites and years.

Attempting to account for variation in natural mortality among sites and years to correct the proportion of illegally killed elephants (PIKE) using only existing empirical natural mortality data is likely to be futile. In our screening of 10900 studies on African elephant demography ecology and management, only six studies at eight study sites explicitly measured natural mortality, providing a total of 37 highly variable (environmentally influenced) estimates describing natural mortality. Results of the present literature review also showed that qualitative indications of natural mortality, such as reporting a die-off after a drought event (McKnight 2000, Foley et al. 2008), were scarce, usually vague, and without any quantitative perspective. Since it is doubtful that this literature review captured data on natural mortality comprehensively, further communication with wildlife authorities is required to examine whether there are any unpublished carcass records. Moreover, data elicitation techniques (Sandelowski 2000) could be applied in collaboration with wildlife authorities and experts to close the natural mortality data gap further.

An alternative to using estimates of natural mortality directly was presented by Hauenstein et al. (2019): annual site-specific rainfall was used as a predictor of PIKE. This approach followed the reasoning that rainfall is the main driver of variation in natural mortality (Foley et al. 2008), but could be improved by additionally accounting for variation in other causes of mortality, such as trophy hunting or management, using the cause-partitioned mortality estimates in the new AEDD extracted from culling and trophy hunting records.

A more sophisticated option would be to build population models that simulate the demographic processes driving elephant population dynamics mechanistically (see, e.g., Boult et al. 2018). Not only is this an attractive alternative way to derive more accurate estimates of poaching intensity, it might also help us to understand demographic responses and thus to target conservation efforts more accurately (Van Aarde et al. 2008). An important precondition for this approach is an appropriate calibration of model parameters using empirical data (Hartig et al. 2011).

Using data that describe the dynamic population processes separately – for example carcass-encounter data and hunting records to partition mortality causes, age-structure data to describe age-specific responses in reproduction and mortality, and direct observations of birth events to quantify fecundity – in an integrated modelling framework leads to decreased model parameter uncertainty (Schaub & Abadi 2011). Furthermore, a triangulation with the large number of available population size estimates (Chase et al. 2016) can compensate for missing data to inform specific processes, such as natural deaths, and thus facilitate reliable population projections in the future and in the past (for the estimation of historical population trends).

CONCLUSION

Collating site-specific information on demographic rates is a prerequisite for developing a quantitative perspective on African elephant population dynamics. Future researchers should feel encouraged to provide precise definitions of their study population and location, in order to allow demographic information to be regionalised. Our new database points out gaps in our current quantitative understanding, but it also shows that many of the demographic data describing mortality, reproduction and population size are structured by age or sex, and thus present a valuable source of information for analyses of African elephant population ecology. Using these data to build and calibrate realistic African elephant population models will be a necessary next step to obtain a better understanding of African elephant ecology under the influence of poaching and to enable more targeted elephant conservation interventions through improved policies and legislation.

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DATA AVAILABILITY STATEMENT

The final database, metadata, raw and processed Web of Science exports, and R code to reproduce data extraction (in cases where figures were used to present the data) and figures are available in a Figshare data repository: https://doi.org/10.6084/m9.figshare.19387085.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Temporal distribution of studies providing data for the review, itemised by main study focus. The number of studies per study focus is shown in parentheses.