

Differential influence of human impacts on age-specific demography underpins trends in an African elephant population

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Abstract. Diagnosing age-specific influences on demographic trends and their drivers in at-risk wildlife species can support the development of targeted conservation interventions. Such information also underpins understanding of life history. Here, we assess age-specific demography in wild African elephants, a species whose life history is marked by long life and extreme parental investment. During the 20-yr study, survival and its variation were similar between adults and juveniles in contrast to relationships found among many large-bodied mammals. Prospective analysis on age-specific Leslie matrices for females demonstrated survival is more influential than fecundity on λ , with sensitivity of both decreasing with age. Results aggregated by stage classes indicate young adults (9–18 yr) demonstrated the highest elasticity, followed by preparous juveniles (3–8 yr). Mature adults (36+ yr) had the lowest aggregate elasticity value. Retrospective analysis parameterized by data from the early and latter periods of the study, characterized by low then high human impact (faster and slower growth, respectively), demonstrated fecundity (particularly for adults; 19–35 yr) explained the greatest variation in λ observed during the period of low human impact, while survival (particularly juvenile and adult) was more influential during the high human impact period. The oldest females (mature adult stage) weakly influenced population growth despite demonstrating the highest fecundity and their behavioral importance in elephant society. Multiple regression models on survival showed the negative effects of human impacts and population size were the strongest correlates across sexes and ages. Annual rainfall, our metric for environmental conditions, was weakly informative. The presence of dependent young was positively correlated with survival for breeding females, suggesting condition-based mortality filtering during pregnancy. Notwithstanding the stabilizing effect of high juvenile survival on elephant population growth, demographic processes in elephants were similar to those shaping life history in other large herbivores. Implications of the study results with respect to the conservation of elephants and analysis of demographic impact of poaching are discussed, along with the study's relevance to theories regarding the evolution of life history and parental care.

Key words: age structure; demographic modeling; density dependence; fecundity; illegal wildlife use; life history; poaching; population growth; survival.

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INTRODUCTION

Survival and its ecological correlates are often challenging to determine but critical for

understanding life-history evolution and addressing applied objectives such as predicting population change and viability (Horswill et al. 2019). Differential survival across age classes

strongly influences population demographic processes and shapes the slow-fast continuum of life histories (Roff 1992, Stearns 1992). Such information is invaluable to diagnose drivers of population decline and develop targeted conservation interventions (Beissinger and Westphal 1998, Staerk et al. 2019). For species on the slow side of the life-history continuum, juvenile survival tends to be lower and more variable relative to that of other age classes, prime adult survival high, followed by decreasing survival for old adults (Caughley 1977). In relation, demographic trends of large, longer lived species are thought to be most sensitive to the high and relatively invariable adult survival (Eberhardt 1977, Gaillard et al. 2000, Eberhardt 2002). Despite this sensitivity, population fluctuations among such species typically stem from variable juvenile survival (Gaillard et al. 2000) though this is context dependent (Coulson et al. 2005). Due to this pattern, it has been proposed that ubiquitously high adult survival among large-bodied mammals is a function of evolutionary canalization, where the same phenotype is manifested regardless of underlying variation in the system (Gaillard and Yoccoz 2003). However, the applicability of this paradigm to monotocous, tropical species with greater predation pressures has been questioned (Owen-Smith and Mason 2005). Further, high parental investment in offspring that modulates their survival may drive different dynamics in species where such behaviors are prevalent (CluttonBrock 1991). As such, deeper examination of the consequences of parental care on demography can enhance understanding of life-history and population dynamics (Cubaynes et al. 2020).

Individual-based monitoring over long periods provides detailed age-specific demographic data allowing identification of the vital rates that most influence population change and how each rate responds to variation in density and the ecology of a system (Tuljapurkar and Caswell 1997, Coulson et al. 2001). Unfortunately, such data are available and analyzed for few large ungulate species, typically being those of high economic value or conservation concern from temperate climatic zones (Gaillard et al. 1998). Increasing the sample of species for which detailed demographic analyses are available, particularly those that represent different ecological niches or

life-history strategies, is valuable to expand life-history understanding as well as to increase accuracy of inference drawn across species or populations (Horswill et al. 2019). Recently, attention has been drawn to the importance of testing demographic paradigms derived primarily from temperate species on a broader suite of species and relating results to life-history or ecological differences of the systems (Owen-Smith et al. 2005). The importance of collating information on life history, survival, reproduction, and growth for monitoring of vulnerable species is increasing in the face of accelerating human impacts and climate disruption (Pearson et al. 2014).

As the largest terrestrial mammals with the longest mammalian gestation period, a long reproductive life and extended parental care of young, elephants (*Loxodonta africana*, *L. cyclotis* and *Elphas maximus*) provide an extreme for assessment of animal biological traits and understanding of the spectrum of life-history strategies. Concurrently, African elephants are at risk from myriad pressures, and demographic modeling has been critical in assessing their status and the development of conservation policy (Wittemyer et al. 2014, Thouless et al. 2016). Elephants are monotocous, typically breeding once every four years with an extended, multi-year-dependent juvenile period (Moss 2001, Wittemyer et al. 2013). While high and less variable adult relative to juvenile survival is common among temperate ungulates (Gaillard et al. 2000) and to a lesser degree tropical ungulates (Owen-Smith et al. 2005), the degree of investment in offspring by elephants potentially drives different sensitivities and demographic processes as found in polar bears (Cubaynes et al. 2020). In particular, being the extreme on the slow-fast continuum of life-history traits may drive different trade-offs and evolutionary pressures. For example, cohort effects may stabilize over years due to an extended adult phase (Hamel et al. 2016), which could dampen the effect of parameter variability on population growth. It is important to assess the application of a paradigm developed largely through inferences on polytocous or annually monotocous species to a species with a notably different life history (long lived, relatively slow reproduction, and extended offspring investment). Understanding its applicability

to such a species can elucidate the relative constraints on life-history traits in large mammals and the selective pressures shaping their reproductive tactics, as well as provide fundamental information for targeted conservation and management actions (Caswell 2001).

While demographic assessments of wild African elephants demonstrated differential fecundity and survival across age classes in line with those predicted from life-history theory (Moss 2001, Gough and Kerley 2006, Wittemyer et al. 2013), age-specific influences on population dynamics have not been assessed. We have limited understanding of what drives population processes (Wittemyer 2011) and how this species responds to ecological variation and changes in population density or age structure (Gough and Kerley 2006). Given the multiple threats to elephants, such information is invaluable to directing conservation actions (Thouless et al. 2016). In particular, demographic modeling of the impacts of illegal killing of elephants for ivory relies directly on resolving the interplay between human impacts, environmental conditions, and intrinsic demographic processes (Wittemyer et al. 2014). Further, diagnosing demographic processes in elephants provides broader understanding of the evolution of life-history traits in megaherbivores. Here, we present detailed demographic data compiled over 20 yr from a wild, individually identified African savanna elephant population inhabiting the Samburu ecosystem of northern Kenya. In addition, we leverage temporal differences in population growth during the study to assess how shifts in survival affect demographic processes and their sensitivities, looking independently at the relatively consistent period of increase during the first half of the study and a period of little change in population size the latter half of the study marked by substantial differences in illegal killing by humans (Wittemyer et al. 2013).

The specific objectives of this study were to identify the critical life-history stages that govern population growth and determine the relative drivers of variation in these stages in a free-ranging elephant population across periods of low and high human impact. Specifically, we addressed the following questions: (1) How do survival probabilities and their variability differ between juveniles and adults? (2) Which

life-history stages are most influential to population growth and how do their contributions through survival and reproduction differ? (3) Did the degree of influence shift across periods of lower and higher human impact (corresponding to high and lower growth)? (4) How do correlates of survival differ between sexes and ages across the study (particularly the age classes to which growth is most sensitive)? Identifying the role of different factors on age-specific demography can provide detailed insight to the proximate drivers of population trends. We employed prospective and retrospective population matrix analyses and multiple regression models on sex and age classes to address these questions. The implications of our results are discussed in the context of the diverse management issues facing this species across Africa (Cumming et al. 1997, Wittemyer et al. 2014, Thouless et al. 2016), including excessive poaching pressure (Wittemyer et al. 2014). In addition, the implications of the results are discussed relative to the life history of this species and other large mammals.

MATERIALS AND METHODS

Study system

Beginning in 1997, all individual elephants regularly using the semiarid savanna of the 220 km² Samburu and Buffalo Springs national reserves in northern Kenya (0.3–0.8° N, 37–38° E) were identified and the focus of intensive monitoring that allows accurate records of population trends (Fig. 1A, C; Wittemyer 2001). These elephants are part of the wider Laikipia/Samburu elephant population, which is the second largest population in Kenya and resides primarily outside protected areas (Thouless et al. 1995; see additional details in Appendix S1). The population has been subject to repeated episodes of illegal harvest, resulting in densities today thought to be lower than historic highs (Okello et al. 2008). The reserves are centered on the Ewaso N'giro River, which is the only permanent water source in this semiarid region and, as such, a focal area for wildlife particularly during the dry season. Rainfall in the region is highly variable; it averages approximately 350 mm/yr and occurs during biannual rainy seasons generally taking place in April/May and November/December (Fig. 1B, D). Due to the rainfall pattern in the

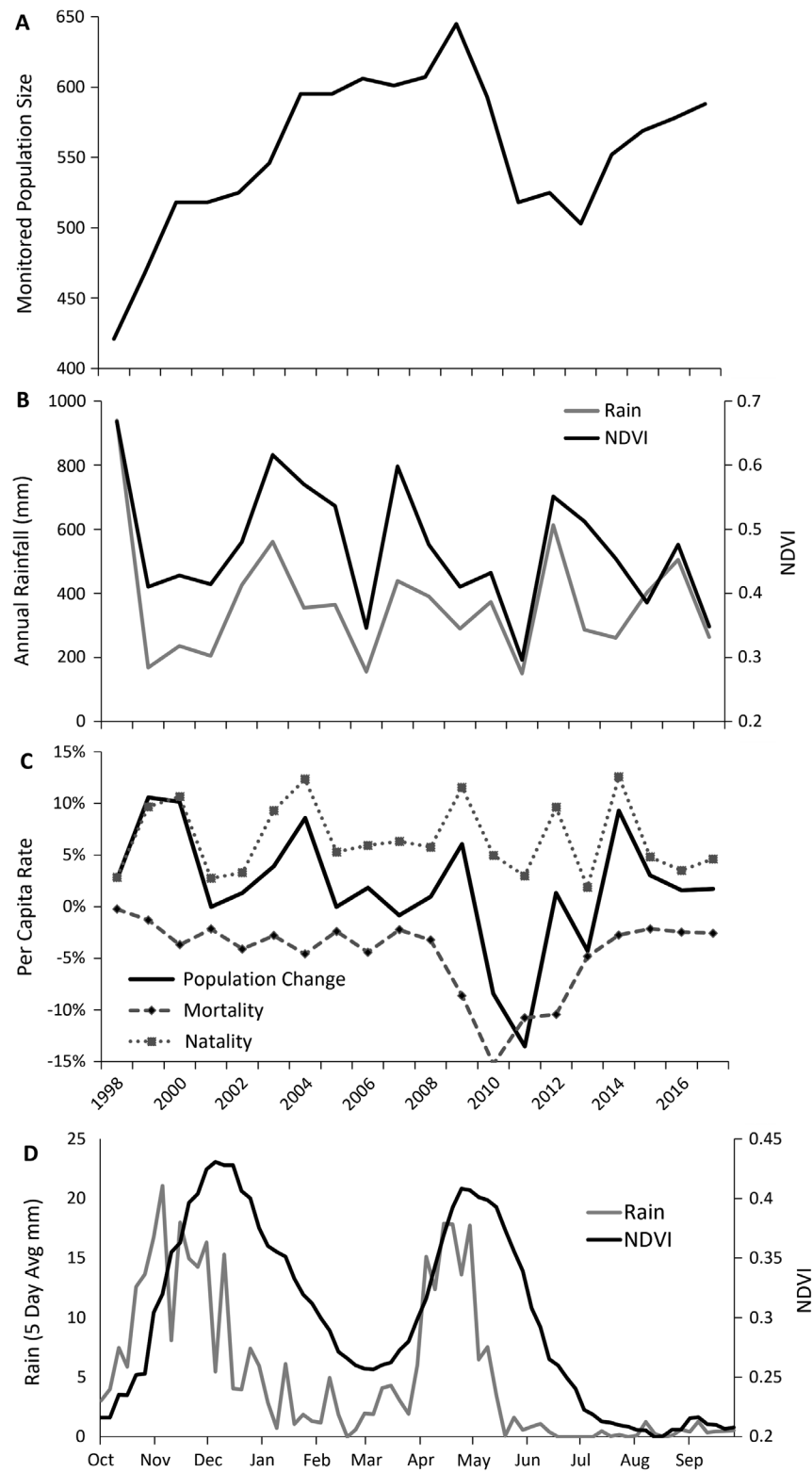


Fig. 1. Population trends and ecological conditions during the 20-yr study. (A) The study period was marked

(Fig. 1. *Continued*)

by robust growth during the initial decade, followed by moderate decline. (B) Metrics of ecological conditions of rain and normalized difference vegetation index (NDVI) indicate strong inter-annual variation. (C) Annual rate of population growth (r), natality, and mortality. (D) Intra-annual rainfall (5-d average in mm) and NDVI values (10-d composite values) used to identify the start of the ecological year which served as the basis of all analyses.

system, data on survival and fecundity were collated annually for the period between 1 October and 30 September in relation to the date of consistent separation between wet and dry periods in the ecosystem (Fig. 1D).

Demographic data

The data presented in this study were collected from November 1997 through September 2017 from the most resident elephants of the national reserves, with the total live population numbering between 421 and 645 individuals during the 20-yr study (Fig. 1A). In total, analysis is conducted on 642 females (accounting for 6725 live female years) and 570 males (accounting for 4346 live male years); see Appendix S1 for annual sample size breakdown. The presence or absence of individual elephants, location, and time was recorded during weekly travel along five established transects (approximately 20 km long) in the protected areas (Wittemyer et al. 2005b), from which mortalities and births were inferred (Fig. 1C; further details on mortality assignment are provided in the Appendix S1). Because the study elephants are not always present in the national reserves (Wittemyer et al. 2005a), sampling was opportunistic along these transects. During the 20-yr study, 715 births (389 of which were female calves used in Leslie matrix analyses) and 499 deaths (285 of which were females used in Leslie matrix analyses) were recorded among these resident, focal elephants (Fig. 1C). The median estimated age at the first observation of newborn elephants was 7 d (I.Q.R. = 2–19). Because calves are dependent on their mothers for survival during their first 2 yr in the ecosystem (Wittemyer et al. 2013), females were assigned as having a dependent calf the year of and following birth (unless the calf died, for which the female was not assigned a dependent calf) in analyses.

Of the 1212 elephants in this study, the age of 952 individuals (79%) were known (i.e., they were observed within 2 yr of the estimated date

of birth) with the rest estimated. Elephants with unknown ages tended to be over 30 yr old. Visual characteristics established from elephants of known age (Moss 2001) were used to estimate the age of individuals, and these age estimates were validated in the study population by comparing visual estimates of age with ages of dead or anesthetized individuals determined from dentition (Rasmussen et al. 2005). Age estimates of mature individuals based on physical appearance were within ± 3 yr of the age based on molar progression for 80% of the assessed individuals (Rasmussen et al. 2005). We summarize analytical results by age classes that subsume this degree of error.

Data analysis

Age-specific survival was calculated for male and females annually as $S_a = 1 - d_{a,i}/Y_{a,i}$, where $d_{a,i}$ is the number of individuals that died of age a during year i and $Y_{a,i}$ is the number of individuals of age a at risk at time i (Ebert 1999). Similarly, age-specific fecundity was calculated annually for females (reproductive success data were lacking for males). This allowed age-specific survival or fecundity to be amalgamated for different periods during the study.

Using a post-breeding Leslie matrix analysis for females (Caswell 2001) parameterized using annual age-specific data (i.e., 1-yr age classes), we calculated the λ , stable age distribution and age-specific reproductive values (Caswell 2001). We employed prospective analysis (i.e., exploration of functional dependence of lambda on vital rates) to estimate sensitivities and elasticities for age-specific survival and fecundity. To simplify interpretation given the 50+ yr of life span of elephants, 1-yr age class metrics from the elasticity analysis were aggregated and summarized by biologically relevant life stages (multiple year stage categories described below). In addition, retrospective variance decomposition analysis (Horvitz et al. 1997) was implemented to

assess the relative contribution of age-specific demographic parameters to observed variation in λ over the study, where the contribution of a given parameter was calculated by multiplying the trait's squared elasticity to its squared coefficient of variation (CV) and divided by the total variance in λ . The total variance in λ was calculated as the sum of these products across all rates (Caswell 2001). Again, this was calculated using annual age-specific rates that were then aggregated in stage classes to simplify presentation of results. Analyses were conducted on all data and data collated for the periods of higher (1998–2008) and lower (2009–2017) growth in the population (Fig. 1A) to identify changes in drivers of these demographic periods in the population. Finally, a life table response experiment was used to evaluate the degree to which variation in population growth rate across the earlier and latter periods of the study was driven by observed variation in age-specific fecundity and survival (Caswell 2000). Covariances were ignored in this analysis.

Given elephant fecundity and survival were expected to change in relation to developmental stages in elephant life history, we simplified presentation of metrics (survival, fecundity, elasticity, stable age structure/reproductive value) by aggregating metrics processed for each age/year into age-based stages: (1) dependent calves—defined as individuals 2 yr and under (ages of lactational dependence for survival); (2) juveniles—defined as those individuals between the ages of 3 and 8 yr old (the lower bound for primiparity in the population); (3) young adults—defined as individuals between the ages of 9 and 18 yr (the span of age during which females produce their first calf and males disperse from their natal groups); (4) adults—between the ages of 19 and 35 yr; and (5) mature adults over the age of 36 yr, being the stage class during which females often become grandmothers and take over leadership of family units (Wittemyer et al. 2005b) and males are in their prime reproductive ages (Rasmussen et al. 2008).

Modeling drivers of survival

To further understand processes underpinning the results from the Leslie matrix analyses, we assessed correlates of annual survival using generalized estimating equations (GEE) with a

logistic link function. We controlled for the non-independence of repeated measures of the annual survival status of individuals (both males and females) using an exchangeable (compound symmetry) covariance specification, assuming consistent correlation between measurements. Specifically, we explored the effects of individual age, monitored population size, ecological conditions (annual rainfall measured at a point source in the protected areas), human impacts, and interactions between ecological conditions and population size and human impacts and age on the probability of survival in a given year. Our human impact metric was the annual number of individuals killed (i.e., carcasses found) and wounded by humans observed within the protected reserves during routine, route-based monitoring patrols conducted on a daily basis (Wittemyer et al. 2005a, b, 2013). We conducted analyses on males and females separately.

Information theoretic approaches were used to compare the performance of models on the basis of quasi-likelihood information criteria (QICu) as implemented in the R package GEE (Pan 2001, Carey et al. 2012). Similar to Akaike's information criterion (AIC; Burnham and Andersen 1998), we computed ΔQICu values and ranked models by QICu weights. Models with ΔQICu values ≤ 2 were assumed to be equivalent, and we selected the model with the fewest parameters as the top model based on parsimony.

Prior to running models, we selected among several, highly correlated metrics characterizing the ecological conditions, human impacts, or individual reproductive state (see Appendix S1 for more details). We ran equivalent GEE models of survival for females and males using each metric for these three categories with other covariates, using model selection to identify the variable in each category with the greatest explanatory power (Appendix S1: Tables S1–S3). Subsequent models were run using only annual rainfall, the annual count of individuals wounded or killed by humans, and dependent calf and calf sex (in female models) as these covariates came out in the top model relative to their peers.

Differences in covariate influence across study period (1998–2008 or 2009–2017) or age class (calves, juveniles, young adults, adults, or mature adults) were explored by incorporating period and age class-specific dummy variables in

the top model for each sex (selected as described above). To aid in interpretation, period and age-specific variables and interactions were assessed independently on the top model for each sex. Model selection was employed to identify meaningful interactions. Finally, we ran sex-specific models that included all age-specific dummy variables, but no covariates, to assess differences in survival between stage classes. Model results for covariate selection and equivalent models are summarized in Appendix S1. All continuous covariates were standardized $(x - \bar{x})/\sigma$ prior to analysis, and all models were computed using R v.3.2 (R Development Core Team 2013; Appendix S2).

RESULTS

Among the mortalities recorded during the study, 147 carcasses (~30% of the total mortalities) of known elephants were located and 40% of these located carcasses attributed to illegal killing by humans, with nearly all age and sex classes being impacted by humans (Table 1). Elephants over 8 yr old were illegally killed more frequently than juveniles and calves regardless of sex. Notably, half of identified natural mortalities in the primiparous stage class of females were caused by birth complications.

Among the five stage classes (dependent calves: 0–2 yr, juveniles: 3–8 yr, young adults: 9–

18 yr, adults: 19–35 yr, mature adults: 36+ yr) for which survival probabilities were calculated, survival was similar between females and males until the adult stages (Fig. 2, Table 2). Sex differences were notable in the adult stage class (19–35 yr; female = 0.957 [SE = 0.010]; male = 0.915 [SE = 0.016]), but 95% confidence intervals overlapped in all other stage classes (Table 2). The highest survival was found among subadult adolescent (9–18 yr) males and females, which averaged 0.983 and 0.974 annually, respectively (Table 2). Dependent and juvenile survival was relatively high, similar to that of adults among females and greater than that of the mature adult (36+ yr) stage class for both sexes. The lowest annual survival was recorded among the mature adult stage class at 0.883 and 0.920 for males and females, respectively (Table 2), indicating that juvenile survival was equal or greater to that of adults (Question 1). For females, regression models demonstrated that calves and mature adults had significantly lower survival than juvenile females, but juvenile, young adult and adult stage classes did not differ significantly. Among males, survival among calves did not differ significantly from juveniles, but juvenile survival was significantly lower than that of young adults and higher than that of adults and mature adults (Appendix S1: Table S4).

Table 1. Causes of death among found carcasses presented by sex and stage classes.

Stage class	Total carcasses	Natural	Illegally killed	Unknown
Females				
Prewean 0–2	22	21	1	0
Juvenile 3–8	7	6	1	0
Young adult 9–18	14	6	8	0
Adult 19–35	19	3	12	4
Mature adult 36+	24	9	15	0
Males				
Prewean 0–2	7	7	0	0
Juvenile 3–8	14	11	2	1
Young adult 9–18	12	4	7	1
Adult 19–35	19	7	9	2
Mature adult 36+	9	2	6	1

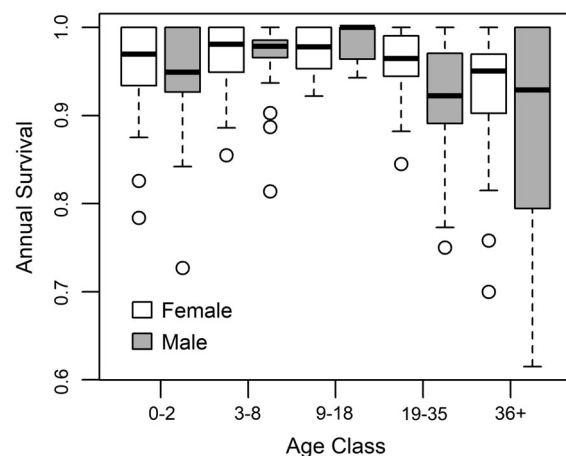


Fig. 2. Boxplot of annual age-specific survival median and interquartile ranges. Survival was high across stage classes, particularly for dependent young. Male (gray) survival tended to be lower and more variable than female (white) survival.

Table 2. Age- and sex-specific annual survival rates and coefficient of variation over the 20-yr study.

Stage class	Sex	Average	SD	SE	CV
Prewean 0–2	F	0.950	0.059	0.013	0.063
	M	0.946	0.068	0.015	0.072
Juvenile 3–8	F	0.966	0.042	0.009	0.044
	M	0.963	0.046	0.010	0.048
Young adult 9–18	F	0.974	0.025	0.006	0.025
	M	0.983	0.022	0.005	0.022
Adult 19–35	F	0.957	0.044	0.010	0.046
	M	0.915	0.073	0.016	0.080
Mature adult 36+	F	0.920	0.082	0.018	0.090
	M	0.883	0.131	0.029	0.148

Survival of the mature adult stage classes demonstrated the greatest annual variability, with the highest variation found among mature males (CV = 0.148) followed by mature females (CV = 0.09). Survival of young adult males and females demonstrated the least variation (CV = 0.02; Table 2). Survival during the period of low human impact and population growth (1998–2008) was greater across all sex and stage classes relative to the period of high impact and stability (2009–2017; Table 3; Appendix S1: Table S5). Generally, variability in survival tended to be greater in mature adults relative to all other stages (Question 1).

Table 3. Summary of population growth rate, age structure, and indices of population conditions over the 20-yr study and the early and latter periods used in analyses.

Data characteristics	1998–2017	1998–2008	2009–2017
No. years	20	11	9
Lambda	1.020	1.042	0.992
Human impact (avg annual)	7.8	3.4	13.2
Average annual rain (mm)	369	385	349
Low population size (year)	421 (1998)	421 (1998)	503 (2013)
High population size (year)	645 (2009)	607 (2008)	645 (2009)
Percentage of calves	11.2	11.3	10.9
Percentage of juvenile	27.2	28.4	25.8
Percentage of young adult	31.4	29.7	33.4
Percentage of adult	19.9	18.5	22.0
Percentage of mature adult	10.3	12.1	7.9

Female fecundity increased from the primiparous stage through mature adults. Dissection of the mature adults demonstrated a sharp decline in fecundity among females over 50 yr (not shown), which also demonstrated the greatest annual variability (Fig. 3). Male reproductive success was not possible to ascertain for the studied individuals.

Influence of age classes on female population growth

Over the course of the study, lambda calculated using a post-breeding Leslie matrix on females was 1.020, but growth was not consistent among years (Fig. 1C). The population demonstrated a sustained period of increase from 1998 to 2008, during which lambda was 1.042, but the later years of the study experienced several years of excessive poaching causing survival to vary from 2009 to 2017 with a lambda of 0.992. The number of human impacted elephants was substantially higher and average annual rainfall slightly lower during the latter period (Table 3).

Prospective analysis demonstrated the sensitivity of population growth to both age-specific survival and fecundity declined with age, and fecundity had lower sensitivity than survival (Appendix S1: Fig. S1). Similarly, elasticity of population growth was greater to survival than fecundity (Question 2; Appendix S1: Fig. S2). In line with the demographic buffering hypothesis, age-specific elasticity and variability were negatively correlated, where variation increased with age as

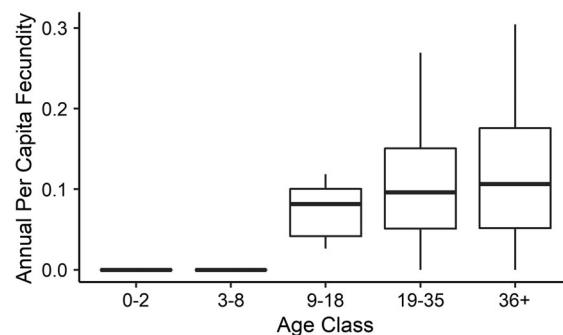


Fig. 3. Female stage class-specific fecundity highlights the parabolic relationship between age and fecundity, where peak fecundity among the study elephants was found among mature adults (36+ yr) followed by adults (19–35 yr).

elasticity declined (Appendix S1: Fig. S3). To simplify interpretation, we aggregated age-specific elasticity values by stage class, finding that young adult (9–18 yr) survival had the largest proportional impact on population growth, followed by survival of juveniles (3–8 yr; Appendix S1: Fig. S2). In contrast, population growth was least affected by fecundity across all stage classes and survival of mature adults (Appendix S1: Fig. S2). Elasticity values aggregated by stage class were similar across the low and high impact periods of the study. The stable age distribution indicated around half of the population is prepubertal, with young adults (9–18 yr) containing the greatest proportion of individuals. Age-specific reproductive value indicated mature females (19–35) had the highest value, with young and mature adults having similar values. Both stable age distribution and the age-specific reproductive value were robust to changes in survival, demonstrating stability despite differences across the two periods (Appendix S1: Fig. S4).

Retrospective variance decomposition analysis (age-specific metrics were aggregated by stage classes) indicated strong shifts in the demographic parameters driving variation in population growth during the first and second half of the study (Question 3; Fig. 4). Despite lower elasticity, fecundity explained 68% of the variation in population growth between 1998 and 2008, with fecundity in adults explaining over 40% of the variation in population growth (followed by fecundity in young adults) largely due to the high variation in annual fecundity (related to elephants 3- to 4-yr inter-calf interval). The relative influence of fecundity and survival flipped in the latter half of the study when survival was lower and illegal killing more common, with survival explaining 74% of the variation in population growth. Survival of adult and juvenile stages was most influential, accounting for 27% and 26% of observed variation in λ , respectively. Mature adult survival and fecundity were the least influential to observed variation during both the period of higher growth and the period of lower growth. The proportion of observed variation explained by calf and juvenile survival increased markedly in the high impact period, from a combined 12% to 33% (Fig. 4). A life table response experiment contrasting matrices parameterized for the two periods demonstrated

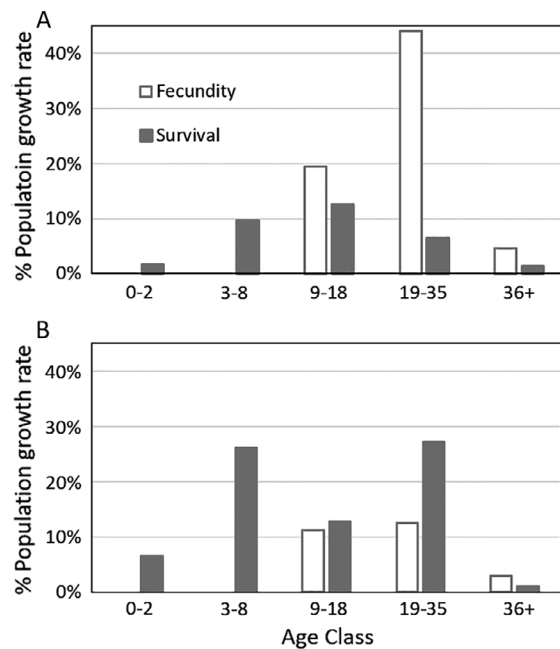


Fig. 4. The proportion of the variation in the observed population growth rate (where percent sum to 100% across all parameters) accounted for by life history relevant stage classes during the period of (A) higher (1998–2008) and (B) lower (2009–2017) growth.

declines in fecundity and survival across most stages contributed to the observed difference in population growth rate. Notably, survival in adult, juvenile, and young adult stage classes (ordered by effect size) was the primary matrix elements contributing negatively to differences in λ between the time periods (Appendix S1: Fig. S5). Only fecundity in mature adults had a positive contribution.

Sex and age differences in correlates of survival

The top model for male elephant survival indicated age, monitored population size, annual rainfall, human impacts, and year of study were influential to male survival (Table 4, Fig. 5). The covariates with the largest effect sizes were human impacts followed by monitored population size (Question 4), both of which were negatively correlated with survival. Age demonstrated a quadratic function whereby survival decreased with age, with a rapid decline for the oldest ages. Annual rainfall was the least influential covariate, but generally was positively

Table 4. Covariate coefficient values with standard errors from the top performing generalized estimating equation models for male and female survival.

Covariate	Estimate	SE
Male		
Intercept	3.294	0.096
Age	−0.226	0.113
Age ²	−0.119	0.053
Human impact	−0.673	0.087
Population	−0.590	0.099
Rain	0.102	0.079
Year	0.528	0.124
Female		
Intercept	3.5459	0.11005
Age	−0.09568	0.10365
Age ²	−0.1607	0.04739
Human impact	−0.96196	0.08429
Population	−0.65984	0.11707
Rain	0.03772	0.0812
Year	0.35781	0.10709
Population × Rain	−0.21334	0.10739
Dependents	0.67875	0.18984

Note: Covariates whose coefficient 95% confidence intervals do not overlap 0 in bold.

correlated with survival. The year of study also had a positive effect in the model (Table 4).

The top models for bulls which included study period or stage class-specific dummy variables indicated the covariates of greatest importance differed across study period and stage class (Appendix S1: Tables S6, S7). The coefficient for the dummy variable for study period indicated survival did not differ significantly across periods (coefficient value overlapped zero), and the only significant interaction was with age, indicating the negative correlation between survival and age was not as strong during the later study period (survival was less differentiated by age). However, interaction covariates with human impact (weaker) and population size (stronger) and year (stronger) were included in the top model, though coefficient estimates overlapped 0. Among stage classes, the interaction with human impacts was frequently the only significant interaction, indicating correlation with other variables was not distinguishable across stage classes. The effect of human impact was more negative for calves and juveniles, lower survival with higher impacts, and less negative for young adults and adults (the interaction was more

negative for mature adults but the coefficient value did not overlapped zero). The interaction with rain and stage class was only in the top model for calves (positive relationship) and young adults (negative relationship), but confidence intervals for both overlapped 0.

The top model results for female elephants indicated age, human impacts, population size, and the presence of dependent calves were influential to survival (Table 4, Fig. 5). Human impacts demonstrated the greatest effect size in the model, being negatively correlated with survival (Question 4). Population size and the presence of dependent calves also demonstrated strong effect sizes, indicating survival decreased with population size and increased when a female had a dependent calf. The coefficient for the interaction between annual rainfall and population size did not overlap zero and demonstrated a negative correlation with survival, with rain showing a positive and population size a negative effect. Finally, as with males, age demonstrated a quadratic relationship where survival decreased with age, showing a sharp decline for older ages, and year of study was positively correlated with survival (Table 4).

The top models for females which included study period or stage class-specific dummy variables highlighted minor shifts in the importance of covariates across stages but differences across study period (Appendix S1: Tables S8, S9). The coefficient of the dummy variable for study period did not overlap zero, indicating survival was significantly lower during the later (2009–2017) period of the study. The only significant interaction was with population size, indicating the negative correlation between survival and population size was not as strong during the later study period. However, the interaction with human impacts (weaker) was included in the top model, though its coefficient estimate overlapped 0. Among stage classes, only the coefficient for an interaction between juveniles and population size (negative) did not overlap zero, indicating that relationships across covariates were not strongly differentiated between stages.

DISCUSSION

Long-term studies of wild populations have provided invaluable contributions to population

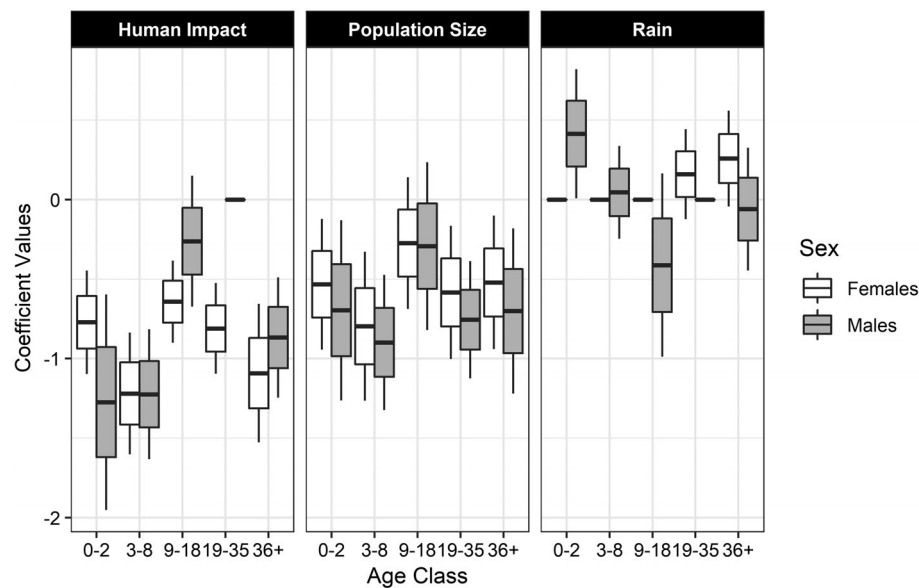


Fig. 5. Coefficient values of survival models for maminoles (gray) and females (white) demonstrate the strong negative of influence of human impacts and population size across age cohorts. Annual rainfall (mm) frequently was not included in top models of survival of females, but demonstrated a positive though relatively weak influence on survival in males.

ecology by quantifying key demographic rates, decomposing the drivers of these rates, and evaluating their subsequent impact on population growth (Coulson et al. 2010, Ozgul et al. 2010). Studies investigating the relative impact of human activities, density, age structure, and ecological factors (climate) on population dynamics are particularly valuable given the pressures facing natural systems (Festa-Bianchet et al. 2019) and the novel stressors driving contemporary adaptation and population change (Sih et al. 2011). However, the suite of species for which high-resolution demographic data are available remains few and it is important to increase the number and diversity of species for which such data are collected and available. This analysis of survival in wild African elephants across periods of higher and lower human impact (and conversely growth) allowed insight into several aspects of population growth in a species with prolonged parental care and among the slowest reproductive life histories found in mammals. First, population growth was most sensitive to survival, as found in other large mammals, but variation in population growth during the earlier study period when the population was

increasing and experiencing low human impact was primarily driven by fecundity. This shifted in the latter half of the study, during which survival was more influential to variation in population growth. The youngest breeding stage class, 9- to 18-yr young adults, demonstrated the highest and least variable survival. Population growth was most sensitive to survival and, to a lesser extent, fecundity in this stage class. However, retrospective analysis indicated that observed variation in population growth in the study population was influenced more strongly by other stage classes. Notably, elasticity of the mature adult stage class (over 35 yr) was the lowest found, and retrospective analysis indicated this stage class had minimal influence on population trends across the study, despite demonstrating the highest fecundity and being considered behaviorally critical to elephant populations. Finally, and most significantly given the conservation status of the species, human impacts were the dominant driver of survival particularly among adult stage classes, irrespective of sex. We present demographic parameters for two periods in the study during which human impacts were markedly different to

facilitate understanding of how demographic rates change in relation to human pressure.

Life history and population dynamics for the largest terrestrial mammal

In long-lived, iteroparous species, survival is typically the main determinant of fitness, as reproduction is limited in species with slower life history meaning lifespan explains most variation in fitness (Cluttonbrock 1988). This is particularly the case in monotocous species, of which elephants represent an extreme in terms of long life and slow reproductive rates. As such, the sensitivity to survival in elephant demographic processes was expected and fits with the broad demographic paradigm for large mammals (Eberhardt 1977, Gaillard et al. 2000). In other ungulates, population dynamics typically are most influenced by dependent offspring survival due to the high degree of volatility in their rates (Gaillard et al. 2000, Owen-Smith and Mason 2005). Here, dependent offspring annual survival and its variation were similar in magnitude to that of adults (in answer to question one), and, as a result, both prospective and retrospective analyses of female demographic parameters highlighted that the influence of dependents on population growth rate was not as strong relative to that found in other large ungulates. However, this influence of dependent calves increased when their survival was more variable in the latter half of the study. In answer to our second question, we found that population growth was most sensitive to survival in young adults (9–18 yr), which demonstrated the highest and least variability in survival. Retrospective analysis showed that this stage class was influential to observed variation in growth during this study, but less than that of adults and juveniles (in the latter half of the study), both of which showed greater variation in survival. The relatively high and stable survival in preparous elephant stage classes (Table 2) compared to that in most studied large ungulates appears to be a function of the extended parental care and long-term social support that characterizes the life history of elephants (McComb et al. 2001, Wittemyer et al. 2005b, Moss et al. 2011), which reduced variation and the influence of their survival on population growth over the study. Following the demographic buffering hypothesis, variation in

demographic parameters was negatively correlated with their elasticity, indicating selection for stability among more impactful parameters (Hilde et al. 2020). Interestingly, although the level of disturbance experienced in the study population resulted in a decline in the representation of mature adults by a third and declines in survival across all stage classes in the latter half of the study, the stable age structure, age-specific reproductive value, and elasticity derived from the Leslie matrices parameterized independently for the two periods remained relatively stable. This suggests the lack of demographic stability over the study did not strongly affect inference gleaned through the use of deterministic methods.

Variation in fecundity was expected to be greater than most ungulates given the characteristic ~4-yr inter-calf interval of elephants, and this variation was strongly influential to variation in observed population growth particularly in the earlier half of the study, when survival was generally high with low inter-annual variation. Despite similar fecundity across the study, its influence declined in the latter half of the study when survival was lower and markedly more variable. The fact that elephants forgo reproduction during poor ecological conditions ensures calves are conceived when individuals are in peak condition (Wittemyer et al. 2007a, b), a behavior that likely increases calf survival but also variation in fecundity. This contrasts with many large ungulates that attempt reproduction regardless of conditions resulting in costs of reproduction falling on offspring (Gaillard et al. 2000, Festa-Bianchet et al. 2019). Age class-specific analyses indicating a correlation between survival and dependent calf presence provide additional evidence for a fundamentally different survival filter related to reproduction (see *Discussion* below). The results from this study suggest that by reducing variation in dependent survival, enhanced parental care can drive better alignment between the parameters population growth is most sensitive to and those it is most influenced by, which may underpin evolutionary drivers of extended parental care. As with adult survival, parental care may drive evolutionary canalization of high, stable juvenile survival.

The relatively low sensitivity of population growth to survival and reproduction of mature

(older) adults, which demonstrated the highest fecundity, contrasts with results for other large ungulates (Hamel et al. 2016). In elephant populations, mature adults are thought to have disproportionate influence on the success of their family groups through behavioral mechanisms (McComb et al. 2001), and the loss of older individuals can have demographic consequences for a given lineage (Foley et al. 2008). Importantly, the results reported here ignore the inter-relation between survival of parents and their offspring (i.e., covariation in demographic parameters) and, therefore, may underestimate the overall influence of adult survival on population growth.

High predation in tropical large ungulate populations was hypothesized to make population growth more sensitive to adult survival than that shown for temperate ungulates (Owen-Smith and Mason 2005). While elephants have fewer natural predators due to their body size than most large ungulates, results from this study contrasting demographic patterns between periods of high and low human predation support this prediction (Owen-Smith et al. 2005). In answer to our third question regarding the influence of different stage classes on variation in population growth, survival of adults became more influential on population growth when exposed to increased human pressure during the latter half of the study due to greater inter-annual variation in this parameter. Influence also increased for dependent calves and juveniles during the latter half of the study. Human predation of elephants in the study system tended to focus on older adults due to selection for their larger ivory (Wittemyer et al. 2013), which cascaded to their dependent young (elephant calves under 2 yr cannot survive without their mothers in the study system). The influence of the juvenile stage class was particularly amplified in the latter half of the study (Fig. 4). Relatedly, the influence of the young adult stage class, which demonstrated sustained high survival throughout the study and to which population growth was most sensitive, was reduced during the latter half of the study with higher human predation pressure (Appendix S1: Fig. S1), though their survival and fecundity still explained a quarter of the variance in population growth.

Sex-biased survival

While we could not conduct retrospective or prospective analyses on male elephants due to a lack of individual-based reproductive data for the duration of the study, we were able to compare general survival patterns between the sexes. As found among other polygynous species, male survival tended to be lower and more variable than that of females. The degree of differentiation in survival between the sexes, however, appeared to be less than levels reported among other large ungulates (Toïgo and Gaillard 2003), and differences were only found in adult stage classes. Survival of calf, juvenile, and young adult (ages 0–18) stage classes did not demonstrate sex difference, which was surprising given the greater energetic costs of rearing males (Lee and Moss 1986) and may relate to condition-dependent sex ratio adjustment. This lack of sex-related survival differences in younger stage classes has been observed in other savannas (Moss 2001, Gough and Kerley 2006, Foley and Faust 2010) and forest elephant populations (Turkalo et al. 2018). Worth considering was the influence of sampling bias on male demographic rates. It is possible that survival among young adult males is lower than that reported, given dispersing males were truncated from the sample (see Wittemyer et al. 2013 for discussion). However, the fact that males were not reproductively competitive through these stage classes may result in them employing less risky behaviors and, subsequently, surviving better. Additionally, they were not primary targets for ivory poaching. Differences between the sexes in survival were apparent when males became reproductively active, but by about half that reported for other iteroparous species that defend breeding territories (Toïgo and Gaillard 2003)—male elephants employ a roving strategy whereby they defend ovulating females in specific areas (Rasmussen et al. 2008, Taylor et al. 2020). Poaching of older males occurred throughout the study. The lower and more variable survival of males likely resulting from the additive nature of illegal harvest (Péron 2013) during their prime reproductive years is of conservation concern.

Drivers of sex and stage-specific survival

Our multiple regression analyses allowed insight to the hierarchy of demographic impacts

on elephants. Across sex and stage classes, human impacts were more influential than climate (annual rainfall) or the size of the monitored population, where the latter was more influential than climate. The predominance of human influences on demographic processes in the studied elephant populations was expected given the primary predator for elephants is humans and the population experienced moderate to high levels of poaching during the latter half of the study (Wittemyer et al. 2013, 2014). Interestingly, our regression models indicated significantly lower survival for females but not males in the latter half of the study. This is likely related to the fact that males experienced illegal killing throughout the study, while that of females was amplified in the latter half of the study. The marked increase in illegal killing of females in the latter part of the study is likely related to a reduced number of mature males, where the focus of poaching may have switched to females after large males were largely removed from the population (Wittemyer et al. 2011, 2013). Relatedly, survival was lowest among older individuals and regression models showed survival declined faster with age.

Density-dependent influences on tropical ungulates act on both juvenile and adult stage classes (Owen-Smith and Mason 2005), in contrast to findings for temperate ungulates demonstrating primarily juvenile susceptibility (Gaillard et al. 2000). The influence of the monitored population size was our best proxy for density, but the monitored elephants in this study represent less than 10% of the elephants counted in the broader ecosystem (and less than 20% of those in the general dispersal area of the monitored elephants; Wittemyer et al. 2005a) and may not accurately reflect elephant density in the ecosystem. In addition, the broader population size is thought to be lower than historic numbers (Okello et al. 2008). The relatively high survival of calves likely indicates the population is below carrying capacity, though increased drought-induced calf mortality indicated ecological stress is important to structuring population processes (Wittemyer 2011). For females, an interaction between annual rain and population size may suggest density-dependent impacts during low productivity years (droughts), though the interaction was not retained in the top model for

males. As such, it is plausible density-dependent impacts are acting on this population and manifested for females to a greater extent than males.

The study area is a semiarid ecosystem characterized by stochasticity in ecological conditions driven by rainfall, with a low annual rainfall of 150 mm and a high of 940 mm over the study period. Previous analyses in the study population highlighted the importance of rainfall-driven ecological productivity as a correlate of juvenile mortality (Wittemyer 2011) and reproduction (Wittemyer et al. 2007a, b), but not adult mortality (Wittemyer 2011). As such, the weak effect of annual rainfall in survival models may result from differential impacts on different age classes. However, our stage-specific regression models did not strongly support such differentiation (interactions with rain were not retained in stage-specific models or coefficient values overlapped 0). The physiology of elephants as the largest terrestrial mammal with a hind-gut digestive system may buffer drought impacts to a greater extent than other, smaller bodied ungulates (Owen-Smith 1992). Indeed, during several droughts in the study system, elephants appeared to fair better than many of the other herbivores (G. Wittemyer, *personal observation*). However, large-scale mortality events driven by droughts were observed several times over the study period (Wittemyer et al. 2013) and may reflect the interaction between population size and rain found in the top model of female survival. It is also possible this relationship was partially obscured as mortalities ascribed to human conflict tended to increase during and directly following droughts (Wittemyer 2011). As such, we assume the influence of human impacts was conflated to some degree with that of droughts.

In contrast to other large mammals where rearing young can have a negative impact on survival (Oftedal 1984, Gittleman and Thompson 1988), the presence of dependent young was positively correlated with survival in adult females. Previous work has not found behavioral differences among gestating and lactating females that would support a social mechanism driving this result (Wittemyer et al. 2005b). In elephants, calves are wholly dependent on their mothers for two years and male calves are energetically more expensive to rear (Lee and Moss 1986). Given mature females were generally either pregnant

or with a dependent calf in the study system (Wittemyer et al. 2007a, b), these results suggest survival is lower when pregnant. This may reflect higher fitness individuals are able to bring neonates to term, where individuals in poorer condition are not able to survive the extended gestation period. As such, elephant reproductive costs may be borne by the breeding adult and manifest at different stages of reproductive allocation from that reported in other large mammals. The increased survival when lactating may also reflect a change in behavior, where females demonstrate greater risk aversion when with small calves. Future analyses could inspect differences in movement tactics in relation to calf age and reproductive state to investigate potential behavioral mechanisms for this result.

Conservation implications

Human impacts were the predominant correlate of survival in the Samburu elephants, but human impacts differed across stage classes. Surprisingly, environmental impacts were markedly weaker than those from humans. This highlights the importance of efforts to understand elephant population demography using poaching monitoring, and our presentation of age-specific information on survival and reproduction is particularly pertinent to such attempts (Wittemyer et al. 2014). Our analysis indicated elephant demographic processes were least sensitive to mortality of the oldest stage class, which was the most impacted by humans due to age selective harvest for ivory. These results indicate elephant demography, at least as parameterized in the study population, is more resilient to selective ivory harvest than previously noted (Lusseau and Lee 2016). The poaching filter targeting older individuals and males has less impact on demographic processes than mortality of younger individuals, which may underpin reported elevated population growth in populations recovering from poaching or culling (Freeman et al. 2009, Foley and Faust 2010, Wittemyer et al. 2013). However, extensive poaching not only drives population size down (reduces survival) but also can inhibit future reproduction through reduction of ages for which reproductive output is greatest and potentially elevate stress that inhibits reproduction (Barnes and Kapela 1991). We note our insights were derived from a population

experiencing moderate poaching levels for a relatively short period (4–5 yr) and thus may have less relevance for populations experiencing sustained or extreme harvest. In addition, our strictly numerical assessment does not account for the behavioral impacts of altered age structure on elephant population processes as discussed previously and likely underestimates the value of prime age adults to elephant behavior and demography (Slotow et al. 2000, McComb et al. 2001, Goldenberg and Wittemyer 2018).

In light of the different contexts facing the conservation of elephants across Africa, these data provide insight to population management (i.e., life history stages populations are most and least sensitive too which can be used to target interventions). Elephants are declining precipitously in some areas (Bouche et al. 2011, Maisels et al. 2013, Wittemyer et al. 2014), while in other areas high elephant densities are a concern (Owen-Smith et al. 2006, Scheiter and Higgins 2012). Given the overwhelming influence of humans on the demographic processes assessed here, implications of this study for elephant populations not subject to human predation can only be deduced. But the demographic rates from the first half of the study, particularly for females, provide insight to demographic processes when human impacts are minor. Heavy human impacts on elephant demographic processes, particularly survival of adults, exert different selective pressures than the species has faced evolutionary, which could influence life-history evolution as noted in other systems (Kuparinen and Festa-Bianchet 2017). Our results highlight the potential impacts of ivory poaching on the demographic processes of the species and provide information that can help design more targeted and effective management strategies.

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and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication. There are no conflict of interests associated with this work.

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DATA AVAILABILITY

Data are available in Appendix S3 and from the Mountain Scholar data repository at Colorado State University: <http://doi.org/10.25675/10217/232636>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3720/full>