

Current Biology

Poaching of African elephants indirectly decreases population growth through lowered orphan survival

Highlights

- Orphan African elephants have a lower survival probability than nonorphans
- Orphaning of wild African elephants decreases population growth
- Orphan survival is more critical to population growth when there is more poaching
- Poaching both directly and indirectly decreases population growth in elephants

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In brief

Parker et al. find that eliminating adult females from a long-lived mammal population indirectly decreases population growth through orphaning. Orphan African elephants survive less than nonorphans, and elephant population growth is sensitive to the probability of being orphaned. Orphan survival affects population growth more when poaching is common.

Report

Poaching of African elephants indirectly decreases population growth through lowered orphan survival

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SUMMARY

Prolonged maternal care is vital to the well-being of many long-lived mammals.¹ The premature loss of maternal care, i.e., orphaning, can reduce offspring survival even after weaning is complete.^{2–5} However, ecologists have not explicitly assessed how orphaning impacts population growth. We examined the impact of orphaning on population growth in a free-ranging African elephant population, using 19 years of individual-based demographic monitoring data. We compared orphan and nonorphan survival, performed a sensitivity analysis to understand how population growth responds to the probability of being orphaned and orphan survival, and investigated how sensitivity to these orphan parameters changed with level of poaching. Orphans were found to have lower survival compared to nonorphaned age mates, and population growth rate was negatively correlated with orphaning probability and positively correlated with orphan survival. This demonstrates that, in addition to its direct effects, adult elephant death indirectly decreases population growth through orphaning. Population growth rate's sensitivity to orphan survival increased for the analysis parameterized using only data from years of more poaching, indicating orphan survival is more important for population growth as orphaning increases. We conclude that orphaning substantively decreases population growth for elephants and should not be overlooked when quantifying the impacts of poaching. Moreover, we conclude that population models characterizing systems with extensive parental care benefit from explicitly incorporating orphan stages and encourage research into quantifying effects of orphaning in other social mammals of conservation concern.

RESULTS AND DISCUSSION

Mothers of long-lived mammal species continue to provide defense against predators and aggression, improve access to resources, and impart knowledge to their offspring after the offspring are no longer nursing.^{6–10} These benefits are crucial because studies have shown that orphans of some species like spotted hyenas (*Crocuta crocuta*), chimpanzees (*Pan troglodytes*), red deer (*Cervus elaphus*), and killer whales (*Orcinus orca*) survive less than nonorphans even if maternal death occurs post-weaning.^{2–5} However, the effect of reduced orphan survival on overall population growth has not been measured in wildlife systems.

Concerningly, orphan death may contribute to the decline of mammal populations undergoing poaching or hunting that targets adults, as these practices can result in an atypically large number of orphans. Furthermore, orphan survival may become more important during periods when adults are dying at higher

rates because shifts in environmental conditions, such as increased poaching and drought, can alter the contribution of vital rates to population growth.¹¹ Exploring the effect of such shifts is relevant because wildlife populations undergo different levels of poaching and/or hunting.

We sought to quantify the effect of lowered orphan survival on population growth for a long-lived mammal species of conservation concern, the African savanna elephant (*Loxodonta africana africana*).^{12,13} Elephants are highly social, and post-weaning maternal care plays an important role in elephant society.^{12,14–16} African elephants' International Union for Conservation of Nature conservation status is endangered due to habitat loss and poaching; the latter targets both male and female adults for their large ivory tusks.¹³ Understanding how elephant orphaning and subsequent survival affect population dynamics could improve efforts to conserve this ecologically and economically important species.^{17–20} Moreover, determining the indirect effects of adult death can increase our

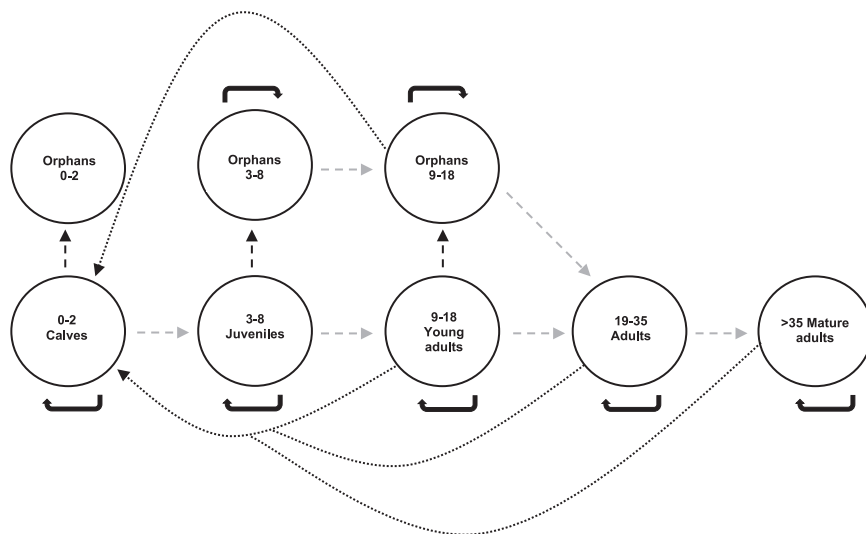


Figure 1. Life cycle diagram for Samburu's elephants

Dashed arrows represent transitions, self-looping solid arrows represent survival, and long dotted arrows represent fertility. The black dashed arrows represent orphaning, i.e. transitions into an orphan class. There is no transition arrow from the orphan 0–2 to the orphan 3–8 stage class because 0–2 dependent orphan calves have never survived. See also [Table S2](#).

Maternal care clearly sustains a higher probability of survival for weaned juveniles. The estimated probability of survival for a weaned juvenile orphan (0.860) was not only less than that for nonorphans of the same age (0.965), but also less than the estimated survival for a mature adult female (0.904; [Table 1](#)). This is surprising

because mature adults are the most subject to age-related natural mortality and have the largest tusks, making them the preferred targets of ivory poachers.²¹ Furthermore, the survival probability of weaned juvenile orphans may have been more different to nonorphans during the period of more poaching than our findings suggest ([Figure 2B](#)). If a poacher killed an elephant mother and we never saw her calf without her, the calf was counted in non-orphan deaths. In reality, such a calf may have survived a short while as an orphan and died before being observed without her mother. Thus, our estimate of juvenile orphan survival during the period of more poaching was conservative and likely inflated while non-orphan survival was likely deflated. The physiological mechanism of reduced survival in nutritionally independent juvenile elephant orphans is unknown and a subject of ongoing study.

It is less certain whether young adult orphans aged 9–18 have differing survival to nonorphans, as confidence intervals overlapped, especially during the period with more poaching ([Figure 2C](#)). However, the overlap was slight for the period with less poaching, suggesting orphans had a lower probability of survival during those years. K-S tests showed no difference in survival across all years of the study ($D = 0.362$, $p = 0.147$), a significant difference for the period of less poaching ($D = 0.546$, $p = 0.035$), and no difference for the period of more poaching ($D = 0.333$, $p = 0.810$).

Increased poaching presumably equalized young adult orphan and non-orphan survival during the period of more poaching ([Figure 2C](#)) because poaching of younger adult individuals became more common,²¹ affecting both orphans and nonorphans. Under more natural conditions, female elephant orphans seem to suffer lower survivorship than nonorphans into young adulthood ([Figure 2C](#)), which is also the case for philopatric male chimpanzee orphans.⁵ As with juvenile orphans, the physiological mechanism of reduced survival in young adult orphans is currently unknown.

Survival probabilities of orphan and nonorphan elephants

The bootstrapped means and confidence intervals of all calculated vital rates are shown in [Table 1](#). Dependent orphan calves aged 0–2 years had very different survival to non-orphan calves, as they never survived without human intervention ([Figure 2A](#)). Juvenile orphans aged 3–8 years likewise had lower survival probabilities than nonorphans, although confidence intervals overlapped during the period of more poaching ([Figure 2B](#)). The Kolmogorov-Smirnov (K-S) test statistic comparing these survival probabilities demonstrated significant differences across all years of the study ($D = 0.737$, $p < 0.001$) and during years with less poaching ($D = 1.000$, $p < 0.001$), but no difference during years with more poaching ($D = 0.333$, $p = 0.810$).

We used 19 years of individual-based demographic data from a long-term monitoring project in Samburu, Kenya^{21–23} to achieve three main objectives: (1) quantify survival probabilities of both nursing and weaned orphans in the Samburu elephant population and compare with age-matched non-orphan survival probabilities, (2) model the response of population growth to the probability of being orphaned (i.e., orphaning probability) and orphan survival using empirically derived parameters, and (3) examine how orphan survival, and the response of population growth to orphaning probability and orphan survival, differ during periods of less versus more poaching.

We used a robust sensitivity analysis method with Latin Hypercube Sampling that both accounts for the large amount of uncertainty in biological systems and does not isolate parameters,²⁴ basing our model on the life cycle diagram depicted in [Figure 1](#). We found that orphaning not only substantively depresses population growth of wild African elephants, but that the magnitude of orphaning's impact was larger than the impacts of other parameters traditionally viewed as influential in elephants, including the survival probabilities of breeding females.²⁵

Response of population growth rate to orphaning and orphan survival

The bootstrapped mean λ experienced by the Samburu population over all years of the study was 1.000 (95% CI 0.980, 1.016), indicating a stable population. Sensitivity analysis results

Table 1. Vital rate means

Age range	Parameter	Bootstrapped mean [95% confidence interval]		
		All years	Less poaching	More poaching
0-2	nonorphan survival	0.951 [0.917, 0.968] a	0.970 [0.954, 0.979] a	0.912 [0.844, 0.961] a
	orphan survival	0	0	0
	transition to 3-8	0.450 [0.371, 0.533] a	0.466 [0.398, 0.534] a	0.418 [0.236, 0.667] a
	orphaning probability	0.032 [0.025, 0.046] a	0.026 [0.020, 0.033] a	0.045 [0.028, 0.081] a
3-8	nonorphan survival	0.965 [0.939, 0.980] a	0.988 [0.984, 0.992] b	0.915 [0.878, 0.952] a
	orphan survival	0.860 [0.820, 0.892] a	0.847 [0.795, 0.885] a	0.886 [0.823, 0.935] a
	nonorphan transition to nonorphan 9-18	0.133 [0.109, 0.162] a	0.138 [0.105, 0.173] a	0.123 [0.092, 0.181] a
	orphan transition to orphan 9-18	0.311 [0.256, 0.369] a	0.299 [0.230, 0.381] a	0.334 [0.235, 0.404] a
	orphaning probability	0.051 [0.037, 0.070] a	0.037 [0.026, 0.051] a	0.082 [0.045, 0.111] a
9-18	nonorphan survival	0.966 [0.952, 0.977] a,b	0.981 [0.972, 0.988] a	0.934 [0.919, 0.954] b
	orphan survival	0.936 [0.914, 0.953] a	0.943 [0.921, 0.963] a	0.923 [0.880, 0.951] a
	nonorphan transition to 19-35	0.080 [0.062, 0.100] a	0.069 [0.051, 0.094] a	0.104 [0.067, 0.133] a
	orphan transition to 19-35	0.054 [0.040, 0.070] a	0.060 [0.042, 0.080] a	0.044 [0.024, 0.065] a
	orphaning probability	0.040 [0.028, 0.057] a,b	0.025 [0.017, 0.036] a	0.073 [0.053, 0.100] b
	nonorphan fertility	0.082 [0.065, 0.099] a	0.083 [0.063, 0.104] a	0.080 [0.048, 0.119] a
	orphan fertility	0.093 [0.071, 0.116] a	0.097 [0.069, 0.129] a	0.085 [0.053, 0.120] a
19 – 35	survival	0.947 [0.922, 0.962] a,b	0.967 [0.956, 0.977] a	0.904 [0.864, 0.937] b
	transition to >35	0.048 [0.035, 0.064] a	0.058 [0.041, 0.075] a	0.027 [0.017, 0.050] a
	fertility	0.115 [0.085, 0.152] a	0.113 [0.082, 0.156] a	0.121 [0.056, 0.190] a
>35	survival	0.904 [0.858, 0.933] a,b	0.943 [0.923, 0.959] a	0.820 [0.745, 0.883] b
	fertility	0.129 [0.092, 0.171] a	0.130 [0.089, 0.170] a	0.129 [0.055, 0.233] a

Bootstrapped means and 95% confidence intervals of vital rates for each stage class for all years, years of less poaching, and years of more poaching. Letters indicate overlap in confidence intervals across each row, with the same letter indicating overlap. See also [Table S1](#).

showed that λ varied negatively with orphaning probabilities and positively with orphan survival ([Figure 3](#); [Table S4](#)). The magnitude of the negative correlation with orphaning into the juvenile orphan stage class was greater than the positive correlation with survival probabilities of adult breeding female stage classes, which are thought of as critical to population growth^{8,25} ([Figure 3](#); [Table S4](#)). Further, λ was more sensitive to the survival of young adult orphans than to the survival of their nonorphan peers.

Being orphaned into the orphan dependent calf stage represents a “dead end” for individuals, after which they can no longer contribute to population growth ([Figure 1](#)), and the orphan juvenile stage had the lowest survival probability among other stages. The relatively strong sensitivity to orphaning into the stages of lowest survival seems to underscore a need for exceptionally high survival in species with slow life histories like the African elephant.²⁶ It also suggests breeding female survival is important largely because it sustains a higher survival probability in young elephant stages.^{8,27}

Sensitivity analysis for years of less versus more poaching

The mean λ experienced by the population during the period of less poaching was 1.021 (95% CI 1.012, 1.033), indicating slight growth, while the mean λ during the period of more poaching was 0.962 (95% CI 0.938, 0.989), indicating decline. The sensitivity of λ to parameters was different between these two periods ([Figure 3](#); [Tables S5](#) and [S6](#)). Sensitivity to orphaning into the orphan juvenile and orphan young adult stages was greater for

the period of less poaching ([Figure 3](#); [Tables S5](#) and [S6](#)). In fact, λ was not significantly sensitive to young adult orphaning for the period of more poaching ([Figure 3](#); [Table S6](#)). Instead, sensitivity to juvenile and young adult orphan survival increased, with λ especially sensitive to young adult orphan survival ([Figure 3](#); [Table S6](#)). Sensitivity to calf orphaning was greater during the period of more poaching, contrary to the pattern of the other two orphaning probabilities ([Figure 3](#); [Tables S5](#) and [S6](#)).

These results indicate that when orphaning is common, growth rate responds less to orphaning itself and more to the fate of individuals who have been orphaned. Of the three orphaning probabilities, only the negative effect of the calf orphaning probability increased in magnitude with more poaching ([Figure 3](#)), likely because there was no survival of orphan calves on which to “offload” sensitivity in response to increased orphaning.

A shift in parameter bounds between poaching periods altered the relationships among population growth and those parameters ([Figure 3](#)). The scale of poaching experienced by the Samburu population was moderate, and poaching in many populations is greater and longer lasting,²⁸ therefore population growth may be even more sensitive to orphan survival in those populations.

Synthesis and future directions

Our population model exposed indirect impacts of ivory poaching on African elephants by incorporating the mathematical effects of a social behavior fundamental to the species, prolonged

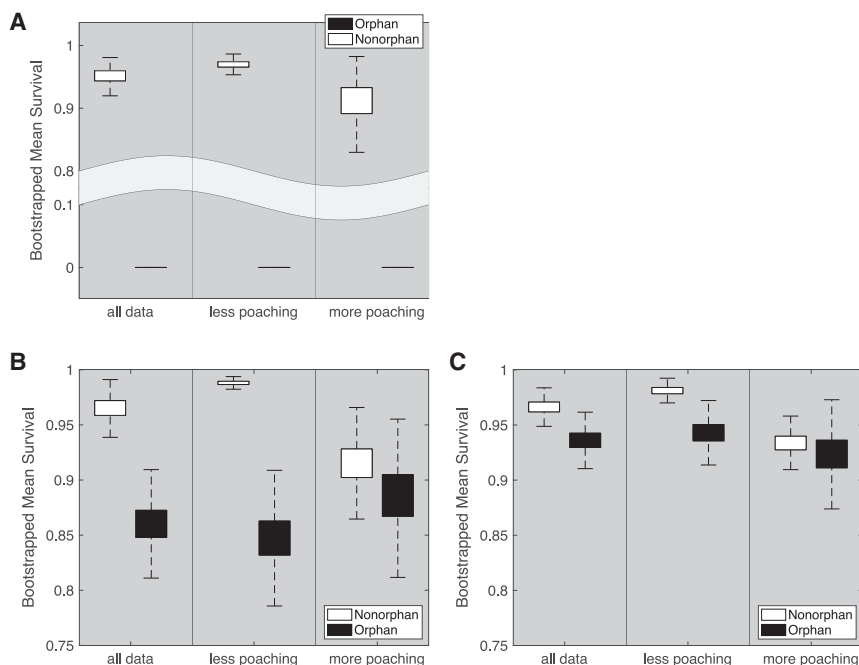


Figure 2. Nonorphan versus orphan survival

Bootstrapped means and 95% confidence intervals for nonorphan versus orphan survival using data from all years, data from years with less poaching, and data from years with more poaching for (A) 0- to 2-year-old calves, (B) 3- to 8-year-old juveniles, and (C) 9- to 18-year-old young adults. Note that the y axis of (A) differs from the y axes of (B) and (C).

maternal care.^{12,14} More widely incorporating key social behaviors into species-specific models may lead to additional new insights. For example, Pitt et al.²⁹ weaved territorial behavior into a population model of coyotes (*Canis lupus*) and found that transient, non-territorial individuals exerted an unexpectedly large influence on population growth. Explicitly representing effects of social interactions among individuals may be especially important for species with slow life histories, in which social behavior fundamentally influences survival.²⁶ These species are also often those of conservation concern.³⁰ A population model investigating the sensitivity of population growth to orphaning in endangered mountain gorillas (*Gorilla beringei beringei*) would be especially interesting in light of recent research showing that adoption buffers the negative effects of maternal loss for gorilla individuals,³¹ suggesting orphaning may not influence gorilla population growth to the same degree as in elephants.

Including only females in demographic population models is common³² and arguably reasonable for polygynous species like the African elephant, yet single-sex models assume both sexes have equal vital rates and male availability does not affect fertility.³³ While our study thoroughly investigated the impacts of orphan death on population growth, we did not account for males in general or effects of orphaning on males. Accurately quantifying male elephant survival is difficult because males disperse anywhere from age 5 to 18,²¹ and sometimes it is impossible to discern whether a male has died or merely dispersed. In species such as chimpanzees, male orphan survival is lower than female orphan survival,⁵ indicating that sexes may be affected differently by the loss of maternal care. If this is true in elephants, our model may either under- or overestimate the immediate effects of orphaning on population growth.

As surviving orphans in Samburu age, we will compare fertility and longevity between orphans and nonorphans. This represents an important avenue for future research, as Gaillard et al.³⁴ state that sensitivity models benefit by incorporating

long-term “cohort effects” because successive life stages are not independent of previous stages. We already know orphan elephants suffer lasting social consequences in that they have less access to matriarchs and receive more aggression after being orphaned and joining a new family.^{15,16} This seems to manifest itself physiologically³⁵ and could be associated with phenomena like faster reproductive aging and shorter lifespans, known responses to stress in Asian elephants (*Elephas maximus*)³⁶ and Asian and African elephants in zoos.³⁷ Once we can empirically determine whether orphans should be kept in separate stages as adults and mature adults, we will determine whether orphaning has additional impacts on population growth. We may also observe and incorporate intergenerational effects of orphaning, as Zippel et al.³⁸ found the offspring of orphans had reduced survival in some primate species.

Conclusion

Using African elephants as a model species, we have provided data-based, quantitative evidence that orphan death resulting from the death of reproductive adults is important to consider when managing and conserving species with prolonged maternal care. Collateral mortality of orphans influenced the Samburu elephant population’s growth more when poaching increased, such that young adult orphan survival became particularly influential to population trends. We recommend that the effects of orphaning be modeled for other long-lived mammal populations to increase our understanding of how it affects population growth in varying environments and across species.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE

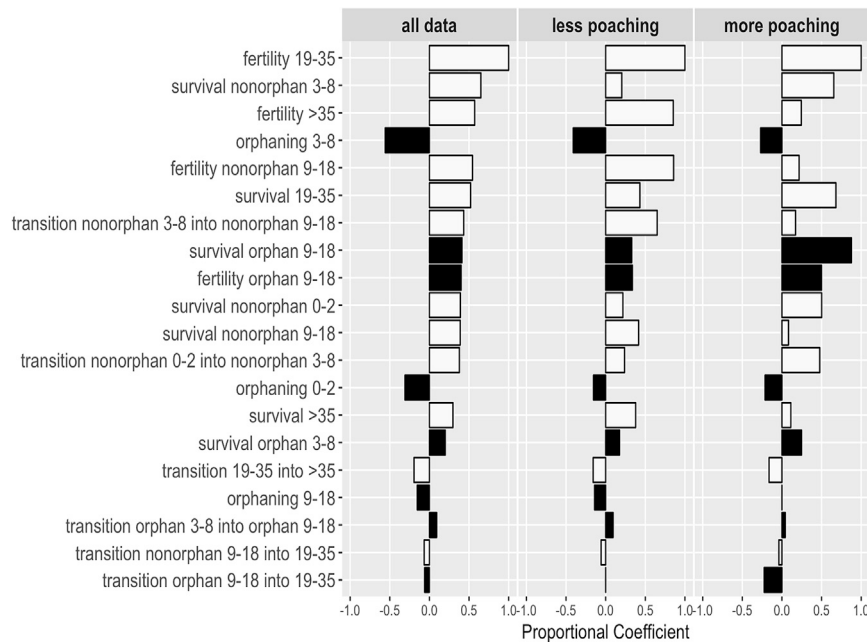


Figure 3. Population growth's sensitivity to vital rates

Estimated linear regression coefficients with a p value ≤ 0.05 , displayed proportionally, from the sensitivity analyses parameterized using all data, data from years with less poaching, and data from years with more poaching. Nonorphan and adult mortality parameters are filled in white, while parameters corresponding to orphan stage classes are filled in black. For the “all data” panel, parameters are ordered greatest to least magnitude effect size from top to bottom. See also [Tables S4–S6](#).

● **RESOURCE AVAILABILITY**

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- Data and code availability

● **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

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- Ethics statement

● **METHOD DETAILS**

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- Demographic data to determine ages, births and deaths
- Sampled individuals

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- Sensitivity analysis
- Years of less versus more poaching
- Projection matrix – additional information
- Correlations – additional information

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.06.091>.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.M.P., C.T.W., and G.W.; data curation, J.M.P., D.D., S.Z.G., J.L., D. Letitiya, D. Lolchuragi, C.L., and G.W.; formal analysis, J.M.P., C.T.W., and G.W.; funding acquisition, J.M.P., S.Z.G., I.D.-H., and G.W.; investigation, J.M.P., D.D., S.Z.G., J.L., D. Letitiya, D. Lolchuragi, C.L., and G.W.; methodology, J.M.P., C.T.W., and G.W.; project administration, I.D.-H. and G.W.; supervision, D.D. and G.W.; validation, J.M.P., C.T.W., visualization, J.M.P., C.T.W., and G.W.; writing – original draft, J.M.P.; writing – review and editing, C.T.W., S.Z.G., and G.W.; resources, I.D.-H.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
MATLAB (R2020a)	MathWorks ³⁹	mathworks.com/products/matlab.html
Statistics and Machine Learning Toolbox (version 11.7)	MathWorks ⁴⁰	https://www.mathworks.com/products/statistics.html
vif(X) MATLAB function	Daniel Vasilaky ⁴¹	https://www.mathworks.com/matlabcentral/fileexchange/60551-vif-x
Other vital rate parameters code	Harvard Dataverse	https://doi.org/10.7910/DVN/IAUEXR
Poaching period comparisons code	Harvard Dataverse	https://doi.org/10.7910/DVN/PX89P9
Sensitivity analysis code	Harvard Dataverse	https://doi.org/10.7910/DVN/ELC2IP
Supplemental code	Harvard Dataverse	https://doi.org/10.7910/DVN/HQHFD4
Survival comparisons code	Harvard Dataverse	https://doi.org/10.7910/DVN/IVHK82
Other		
Non-monotonicity check graphs	Harvard Dataverse	https://doi.org/10.7910/DVN/3XRZC5

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Jenna M. Parker (jennaparker13@gmail.com).

Materials availability

This study did not generate any new unique reagents.

Data and code availability

The data and attached Excel sheets used to calculate annual vital rates reported in this study cannot be deposited in a public repository due to the conservation status of the African elephant. To request access to these data and/or formulas relating to Equations 2 – 10 of the [method details](#) in the [STAR Methods](#), please e-mail the lead contact.

All original code has been deposited in Harvard Dataverse under the title “Poaching of African elephants indirectly decreases population growth through lowered orphan survival” and is publicly available as of the date of publication. DOI’s are listed in the [key resources table](#).

Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Animals

This study was centered around the long-term monitoring of wild, free-ranging African savanna elephants (*Loxodonta africana*) from vehicles in the Samburu and Buffalo Springs National Reserves of Kenya. We included individually identified female elephants of all ages in analysis. Further information on the study population and subjects can be found in the [Method Details](#).

Ethics statement

Although our analysis did not use GPS collar data, some of the subjects were collared for related studies. Immobilization and collar fitting were led by Kenya Wildlife Service (KWS) veterinarians and followed standard protocol.

METHOD DETAILS

Study area and population

Data collection for our study took place in the Samburu and Buffalo Springs National Reserves of Kenya. These reserves lie just north of the equator at 0.3 – 0.8° N and 37.0 – 38.0° E, separated by a semi-permanent river called the Ewaso N’giro.²¹ Together they encompass 220 km² of semiarid terrain.²¹ Rainfall in the ecosystem averages 350 mm per year, usually falling during two wet seasons from November – December and April – May.²¹ The end of September / beginning of October marked the most consistent separation

between dry and wet seasons across study years,²¹ therefore we structured our analyses by designating years ecologically as beginning on the calendar date October 1 and ending on calendar date September 30. For example, data from October 1, 1999 – September 30, 2000 were binned together as an ecological year of 2000. Unless otherwise specified, henceforth when referencing year(s) we are referring to ecological year(s).

The elephant population using the reserves (hereafter the “Samburu population”) has been studied since 1998.²³ Over 1,000 elephants have been identified. For this study, known elephants were monitored daily between October 1, 1998 – September 30, 2017 by long-term researchers who recognized each elephant individually using age, sex, ear markings, tusk configurations and other notable features^{21,42} pictured in a continually updated photo identification file. Once a group of elephants was found, each individual was recorded, and the accuracy of the record rated according to whether observers were certain they could record every individual present.⁴³

Demographic data to determine ages, births and deaths

At the beginning of the long-term study, adult ages were estimated using shoulder heights and physical appearances according to guides established from molars of dead elephants.^{44,45} Later analysis using dental molds of darted Samburu individuals found these age estimates were accurate to within ± 3 years for 75% and ± 5 years for 95% of measured individuals.⁴⁶ Due to more distinguishable size and age markers for calves younger than 10 years old, it was easy to estimate their age within 1-2 years.⁴⁵ We knew ages for calves born during the study period because newborn calves are generally sighted within three weeks or less of birth.²¹

Most elephant families included in our study were seen at least once a month and usually multiple times a week, therefore we considered females and non-dispersing male calves as dead if their mother and core family group were recorded without them for three consecutive observations when all group members were seen.²¹ Carcasses reported by the community or discovered by the monitoring team confirmed death for roughly a third of individuals.²¹

Sampled individuals

Since the Samburu and Buffalo Springs Reserves encompass less than 10% of the area used by the Samburu population,²² we included only elephants who frequented the reserves for this study. We also included only females because males disperse between the ages of 5 and 18,²¹ making it more difficult to track their mortality and reproductive output. Calves were born with a sex ratio of 64 males: 77 females throughout the study period, or roughly 4 males: 5 females, with a total of 705 calves, 320 males and 385 females. Importantly, because the assumption that calves were born with a sex ratio of 1:1 was not met, this means we assumed male survival and reproduction do not affect population growth dynamics.^{32,33}

Our sample size over the 19 years totaled 645 female individuals. Among this sample of focal females, one family of 8 individuals was truncated from the sample in 2016 on account of a range shift out of the core study area⁴⁷ that made them unobservable. In addition, 6 individuals comprising two families shifted their ranges into the study area and were added to the sample the year of their immigration.

An “orphan” was defined as a prepubescent female elephant whose mother died before the orphan reached maturity, with maturity marked by giving birth. Sometimes orphans joined unrelated families, which meant 7 unknown orphan individuals (2 young adults and 5 juveniles) entered the population at various points during this study. When these unknown orphans were continuously observed with a known family, their age was estimated following established protocols⁴⁵ and they were included in orphan survival calculations beginning the year they were first seen.

Increased poaching (see below for quantification of the increase) in the study area from 2009 – 2014²¹ generated a large number of individually known orphaned elephants. Although droughts occur relatively regularly in the semi-arid study area, there were two severe droughts during these years that also increased orphan numbers. The number of females who became orphans at some point over the study’s 19 years was 162, and over half of orphaning events (57%) occurred during the 6 years of heavy poaching and two severe droughts spanning 2009 to 2014.

QUANTIFICATION AND STATISTICAL ANALYSIS

Calculation of annual vital rates

We organized individuals into stage classes for each year of the study by birth year assuming a post-breeding, or retrospective, census.³² We defined the stage classes (Figure 1) according to elephant life history: elephants are nutritionally dependent upon their mother until the age of 2, are juveniles between the ages of 3 and 8, and give birth with an average interbirth interval of 4 years beginning anywhere from age 9 to 18.²¹ Adult females are in their prime from ages 19 to 35, and tend to lead families starting around age 36, meaning their presence at that age is especially important to the well-being of their family.⁸ Although we know survival and fertility significantly drop around the age of 50 years in African elephants,²⁵ selective poaching^{21,48} meant our annual sample size of females > 50 years old (range: 1 to 15, mean 5.89, Table S1) was not large enough to reasonably estimate average vital rates for an oldest stage class of > 50 years. Therefore we binned the oldest females with individuals aged 36 – 50 (Figure 1).

We included orphaned individuals in separate stage classes. Transitions between life history stages were based on age, but transitions from nonorphan to orphan stages were event-based, occurring if an elephant’s mother died when they were in the 0-2 (calf) or 3-8 (juvenile) stage class, or in the 9-18 (young adult) class if they had not yet given birth. Orphans in the young adult stage class reentered a common pool with nonorphans when they turned 19 years old (Figure 1) because we do not yet have enough data on

older orphan cohorts to know if orphan vital rates differ later in life. Population dynamics were calculated using a common stage-structured model,

$$\mathbf{n}(y + 1) = \mathbf{A}\mathbf{n}(y), \quad (1)$$

where $\mathbf{n}(y)$ is the vector of abundances in each stage at year y ³² and \mathbf{A} is a projection using vital rates to estimate abundances for each stage class in year $y + 1$, as depicted in [Table S2](#) (see penultimate subsection of [STAR Methods](#) for more about the projection matrix).

Assuming vital rates are a function of the aforementioned stages,⁴⁹ we calculated annual vital rates for orphan and nonorphan classes, appropriately discounting any lost individuals and / or individuals who had not yet entered the population (as discussed above in the “Sampled individuals” section) from denominators of the following equations. Equation 2 calculated survival probability, S_x , for nonorphan stage x in year y , where $n(y)$ denotes the number of nonorphans alive at census y and $p(y)$ denotes the number of non-orphan individuals at $y - 1$ orphaned over the course of y :

$$S_x(y) = \frac{n(y)}{n(y-1) - p(y)}. \quad (2)$$

Survival probabilities of older stages were calculated in the same way, but the denominators of the equations differed as they did not involve the subtraction of orphaned individuals, i.e., with i equal to number of individuals in stage x :

$$S_x(y) = \frac{i(y)}{i(y-1)}. \quad (3)$$

[Equation 4](#) calculated survival probability, V_x , for orphan stage x with $o(y)$ equal to the number of orphans alive at census y :

$$V_x(y) = \frac{o(y)}{o(y-1) + p(y)}. \quad (4)$$

Age-based transition probability, T_x , from nonorphan stage x into subsequent nonorphan stage $x + 1$ was calculated according to [Equation 5](#), where d is the number of oldest nonorphans to transition into $x + 1$:

$$T_x(y) = \frac{d(y)}{n(y-1) - p(y)}. \quad (5)$$

Age-based transition probabilities, T_x , of older stages were calculated in the same way, but again the denominators of the equations differed as they did not involve the subtraction of orphaned individuals. [Equation 6](#) calculated the age-based transition probability, U_x , from orphan stage x into subsequent stage $x + 1$, with e as the number of oldest orphans to transition into $x + 1$:

$$U_x(y) = \frac{e(y)}{o(y-1) + p(y)}. \quad (6)$$

All age-based transitions were multiplied by survival of the originating stage x within the projection \mathbf{A} to calculate $\mathbf{n}(y+1)$, see penultimate subsection of [STAR Methods](#) and [Table S2](#).

[Equation 7](#) calculated Z_x , the probability of being orphaned and moving into orphan stage x from nonorphan stage x :

$$Z_x(y) = \frac{p(y)}{n(y-1)}. \quad (7)$$

This event-based orphaning probability, Z_x , was multiplied by the survival probability of the orphan stage into which orphaned individuals were entering, V_x , within \mathbf{A} (see [Table S2](#)). Finally, we calculated the fertility F_{9-18} of the nonorphan stage of ages 9-18 according to [Equation 8](#), with c denoting the number of female calves born to nonorphans during y :

$$F_{9-18}(y) = \frac{c(y)}{n(y-1) - p(y)}. \quad (8)$$

Fertilities of the older stage classes, F_x , were calculated according to the same method with reduced denominators:

$$F_x(y) = \frac{c(y)}{i(y-1)}. \quad (9)$$

The fertility for the young adult orphan stage, G_{9-18} , was calculated according to [Equation 10](#) below, with c denoting the number of female calves born to orphans during y :

$$G_{9-18}(y) = \frac{c(y)}{o(y-1) + p(y)}. \quad (10)$$

Our calculations produced 20 vital rate vectors, each corresponding to an arrow in [Figure 1](#) (the 20 vital rates are also specified in [Table S2](#)). Vectors for most parameters consisted of 19 data points (one for each year 1999 – 2017), but we excluded data points

calculated from annual sample sizes of less than 5 individuals (see [Table S1](#) for average annual sample size per stage class). Therefore the orphan 3-8 and orphan 9-18 vital rates had 18 and 17 data points, respectively.

Orphan and nonorphan survival comparisons

We compared transformed (see below under “Sensitivity analysis” for method of transformation) orphan and nonorphan survival probability vectors of the juvenile and young adult stage classes by bootstrapping the means of each⁵⁰ (see `bootstrap.txt` of “Survival comparisons code” linked in the [key resources table](#)) and examining the degree of overlap in resulting confidence intervals. As an additional test, we ran the Kolmogorov-Smirnov (K-S) test³⁹ (see `K_S_tests.txt` of “Survival comparisons code” linked in the [key resources table](#)) to compare the same orphan and nonorphan survival probability vectors. (We further bootstrapped the means and confidence intervals of all other vital rates, see `boot_other_parameters.txt` of “Other vital rate parameters code” linked in the [key resources table](#).)

Sensitivity analysis

For the sensitivity analysis, we created beta distributions for each of the 20 vital rates with MATLAB’s (version 2020a)⁴⁰ Distribution Fitter App of the Statistics and Machine Learning Toolbox⁵¹ (see [key resources table](#)). To account for variable sample sizes ([Table S1](#)) and because our data contained some 0 and 1 values that cannot be included when fitting a beta distribution, we transformed each data point following Smithson and Verkuilen:⁵²

$$w' = \frac{w * (q - 1) + .5}{q}, \quad (11)$$

with q as the number of individuals in a stage class at the end of the previous year (i.e., the number of individuals used in the denominator of calculations in Equations 2 – 10), then input the transformed data vectors. Resulting alpha and beta parameters for each beta distribution can be found linked in the [key resources table](#) (see `beta_parameters.txt` of “Sensitivity analysis code” linked in the [key resources table](#)).

Next, we created 10,000 projection matrices with each vital rate parameter drawn at random from its estimated distribution under a Latin Hypercube sampling (LHS) design using custom code (see `LHS_draws.txt` and `LHS_matrices.txt` of “Sensitivity analysis code” linked in the [key resources table](#)),^{24,41,53} Because orphaning probabilities are necessarily dependent on the survival of females with calves, we calculated the correlation between data points for each of the four breeding female stage classes’ survival probabilities and the three orphaning probabilities, then used conditional statements to achieve similar correlations among parameter draws while still preserving the LHS design (see final subsection of [STAR Methods](#) for more on these correlations). The complete correlation matrix among LHS parameter draws after inducing correlation can be found in [Table S3](#).

We subsequently calculated the dominant eigenvalue for each constructed projection matrix (see `eigenvalues.txt` of “Sensitivity analysis code” linked in the [key resources table](#)). Then, we standardized each vector of LHS draws for the 20 vital rate parameters and the corresponding vector of dominant eigenvalues into z-scores. We regressed the standardized eigenvalue vector, corresponding to population growth rate (λ), against the standardized 20 vital rate parameter vectors (see `linear_regression.txt` of “Sensitivity analysis code” linked in the [key resources table](#)). Resulting coefficients provided a measure of sensitivity.

Before running the regression analysis, we plotted each parameter against the dominant eigenvalues to check for non-monotonicities and did not find anything of concern (see `check_for_non_monotonicities.pdf` of “Non-monotonicity check graphs” linked in the [key resources table](#)). Additionally, variance inflation factors calculated from the regression output with the `vif(X)` function in MATLAB⁵⁴ (see [key resources table](#)) were all lower than 10, indicating multicollinearity was not an intractable issue despite the correlations we induced between adult survival and orphaning probabilities.^{55,56}

Years of less versus more poaching

The larger Samburu ecosystem is designated a Convention on the International Trade in Endangered Species (CITES) site for the Monitoring of Illegal Killing of Elephants (MIKE), therefore elephant carcasses are monitored and each calendar year the Proportion of Illegally Killed Elephants (PIKE) is estimated by dividing the number of illegally killed carcasses by total carcasses found.²¹ PIKE increased from an average of 0.275 from calendar years 2002 – 2008 to 0.515 from calendar years 2009 – 2014, falling again to 0.360 from calendar years 2015 – 2017.²⁷ To analyze periods of high versus low poaching, we divided data into two groups: those from ecological years of the study corresponding to calendar years with less (1999 – 2008 and 2015 – 2017) and more (2009 – 2014) illegal killing. We then compared orphan versus nonorphan survival, created vital rate beta distributions, and reran the regression sensitivity analysis separately for each period. Notably, the study system is prone to drought, and two especially severe droughts overlapped with the period of higher PIKE from 2009 – 2014 and contributed to the larger number of adult deaths as mentioned above.²¹

To ensure we were comparing a period of growth versus a period of decline, especially given the slight discrepancy in calendar versus ecological years, we calculated mean growth rates experienced by the population for all (ecological) years, for the designated period of less poaching, and for the designated period of more poaching by creating 17 projection matrices from the transformed data vital rate vectors, using only years during which all stage classes had an adequate sample size. We then calculated the dominant eigenvalue (λ) associated with each matrix, and bootstrapped the means and confidence intervals of all 17 eigenvalues, the 11 eigenvalues corresponding to years of less poaching, and the 6 eigenvalues corresponding to years of more poaching (see `lambdas.txt` of “Poaching period comparisons code” linked in the [key resources table](#)).

Projection matrix – additional information

Notably, the three orphaning probabilities within the matrix, from 0-2 years into orphan 0-2 years (“ Z_{02} ”), 3-8 years into orphan 3-8 years (“ Z_{38} ”), and 9-18 years into orphan 9-18 years (“ Z_{918} ”), are distinguished from other transition rates because they are multiplied by the survival rate of the stage class which they are entering as opposed to the previous stage class (Table S2). This is because these orphaning transitions occur at any time during the year, as opposed to the other “pulsed” age-based transitions, and we wanted to properly capture the death of orphan individuals who were both orphaned and died during the same year.

Orphan calves under the age of 2 have never survived within the Samburu population.²¹ The lack of an outlet from the orphan 0-2 class made our projection matrix *reducible*, meaning it contained *at least one stage that cannot contribute, by any developmental path, to some other stage or stages*.³² There are concerns about reducible matrices and their use in sensitivity analyses.⁴⁹ We tested whether the reducibility of our matrix was problematic by assigning the 0-2 orphan class stage a very low survival rate (see `beta_parameters_irr.txt` of “Supplemental code” linked in the [key resources table](#)), such that the matrix was irreducible, and re-running the described sensitivity analysis. The results were nearly identical to our primary model results, indicating reducibility is not a cause for concern in this instance.

Correlations – additional information

The correlations in our model between adult survival and orphan survival draws were lower than observed in the data (Table S3). We originally attempted to correlate variables using the method of Iman and Conover,⁵⁷ but the data-derived correlation matrix was not positive definite, and correcting it to be so gave correlations further from the data-derived correlations than the conditional method we devised (see `LHS_draws.txt` of “Sensitivity analysis code” linked in the [key resources table](#)).