PNAS

RESEARCH ARTICLE | POPULATION BIOLOGY

Survey-based inference of continental African elephant decline

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Edited by James Clark, Duke University, Durham, NC; received February 22, 2024; accepted August 24, 2024

Long-term quantification of temporal species trends is fundamental to the assignment of conservation status, which in turn is critical for planning and targeting management interventions. However, monitoring effort and methodologies can change over the assessment period, resulting in heterogeneous data that are difficult to interpret. Here, we develop a hierarchical, random effects Bayesian model to estimate site-level trends in density of African elephants from geographically disparate survey data. The approach treats the density trend per site as a random effect and estimates a parametric distribution of these trends for each partitioning of the data. Data were available from 475 sites, in 37 countries, between 1964 and 2016 (a total of 1,325 surveys). We implemented the model separately and in combination for the African forest (*Loxodonta cyclotis*) and savannah (*Loxodonta africana*) elephant species, as well as by region. Inference from these distributions indicates a mean site-level decline for each species over the study period, with the average forest elephant decline estimated to be more than 90% compared to 70% for the savannah elephant. In combination, there has been a mean 77% decline across all sites; but in all models, substantial heterogeneity in trends was found, with stable to increasing trends more common in southern Africa. This work provides the most comprehensive assessment undertaken on the two African elephant species, illustrating the variability in their status across populations.

African elephant | density trend | conservation status

Significance

Despite the conservation importance of documenting temporal population trends of African elephants, we lack a comprehensive assessment of recent changes in the world's largest terrestrial mammal. This assessment summarizes site-level trends in density over five decades from hundreds of surveys conducted across Africa on the forest and savannah elephant species. Both species have experienced substantial declines at the majority of survey sites. Forest elephant sites have declined on average by 90%, whereas savanna elephant sites have declined by 70% over the study period. However, savannah elephants have also demonstrated some increases, indicating that the threats and challenges elephants face are not the same everywhere. From the successes, we can learn how to better protect elephants across their range.

Global biodiversity decline (1, 2) is accelerating and undermines the environmental systems of the planet (3). Large bodied, long-lived mammals, which can have disproportionate impacts on ecosystem functioning (4, 5), are among the most threatened taxa (6, 7), and all three extant elephant species (*Loxodonta africana*, *Loxodonta cyclotis*, and *Elephas maximus*) serve as notable examples (8). Their flagship status and the increasingly limited distribution of extant elephant populations have made their conservation a global priority (9).

In Africa, populations of *L. africana* and *L. cyclotis* are becoming increasingly fragmented, and typically tethered to protected areas (9, 10). Human pressures have accelerated over the past 50 years, with major threats including habitat loss caused by land conversion to sustain growing human populations (11, 12), and the commercial trade in elephant parts (13). However, quantifying their population status has been challenging. The habitable area for African elephants is vast, and monitoring has been inconsistent, with different methodologies applied at different sampling sites at different times (9). As such, we lack a systematic assessment of changes in the two species at the continental scale and over an appropriate time period.

Surveys of elephant populations were initiated in the 1960s at a handful of sites due to concerns about the impact of high elephant densities on their ecosystems (14). Efforts to survey elephant populations increased in the 1970s and 1980s in response to unsustainable, illegal exploitation for ivory markets (15, 16). These initial survey efforts serve as valuable, quantitative baselines for population status; though they do not capture the periods of decline and growth in elephant numbers that occurred across Africa in the preceding century (17). While some population specific trends have been compiled (15, 18–21), few attempts have been made to quantify the multidecadal trend across the entire continent. Such an assessment is critical to understand the species conservation status. Furthermore, site-based heterogeneity in the scale of decline or increase can identify areas of concern; this can then underpin local, national, and global conservation decisions (22).

Despite the need for a comprehensive assessment, survey data that differ in timing, spatial extent, and method have complicated the estimation of trends over time. Range loss and the compression of elephants into protected areas has further affected the interpretation of survey counts, since surveys are often deliberately focused on areas of

Author contributions: C.T.T.E., K.S.G., F.M., D.B., R.T., and G.W. designed research; C.T.T.E., K.S.G., F.M., D.B., R.T., and G.W. performed research; C.T.T.E. contributed new reagents/analytic tools; C.T.T.E. and G.W. analyzed data; and C.T.T.E., K.S.G., F.M., D.B., R.T., and G.W. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2403816121/-/DCSupplemental.

Table 1. Summary of site-level survey data per partition, with *n* refering to the number of surveys

Partition	Years	No. of countries	No. of surveys (*n*)	No. of sites	Average *n* per site	Average years per site	Average *n* per year	No. of sites with $n = 1$	No. of sites with $n > 3$
Global	1964 to 2016	37	1,325	475	2.79	14.09	0.20	171	138
Species:									
Forest	1974 to 2015	18	350	150	2.33	11.47	0.20	61	27
Savannah	1964 to 2016	23	975	325	3.00	15.30	0.20	110	111
Region:									
Forest	1974 to 2015	18	350	150	2.33	11.47	0.20	61	27
East	1966 to 2015	8	308	98	3.14	17.71	0.18	33	32
North	1970 to 2015	5	88	34	2.59	15.82	0.16	10	7
South	1964 to 2016	10	579	193	3.00	13.98	0.21	67	72

known high population numbers (23–25). Here, we develop a framework that is able to accommodate these disparate data. It integrates across all available survey count data to estimate a parametric distribution of site-level changes in population density over time. Inference can then be made from the mean expectation of this distribution. We adopted a parsimonious Bayesian modeling approach that intentionally avoided complex assumptions concerning the dynamics at each site and apply this framework to survey data from 475 different sites in 37 countries across the African continent, collected over different time-frames between 1964 and 2016. The bulk of these data is curated in the African Elephant Database (9, 17). Surveys covered an average of 15 y per site (equivalent to 0.2 surveys per year; Table 1), with 138 sites containing more than three surveys. The model was initialized in 1963, giving a 53 y assessment period, and estimates a multiplicative change (trend) in the density over that time period. From the mean trend per site, we infer conservation status for savannah (*L. africana*) and forest (*L. cyclotis*) elephant species, both combined, and at a regional level. We discuss the strengths and weaknesses of our approach, its relationship to species status inferred from International Union for Conservation of Nature (IUCN) Red List categorization criteria, and policy and management implications of our results.

Results

We estimated trends using three different partitionings of the data: the global (continental) population of African elephants (one partition with forest and savannah species combined); each species separately (two partitions); and partitioning into Forest (*L. cyclotis* only), North, East, and South regions (*L. africana* only) of the elephant range (four partitions). Three models were applied with different population dynamic assumptions: constant growth rate (the "constant" model), time-variant linear change in the growth rate (the "linear" model), and density-dependent growth (*SI Appendix, Population Model Derivation*). The density-dependent model did not converge for any of the runs, and we have therefore excluded it from further discussion (*SI Appendix, Model Selection*). The linear model for the regional data partitioning also did not converge and is therefore not included in the final results.

In Table 2, we report posterior estimates of the mean trend. For the global and species-specific partitionings of the data, the constant and linear models yielded similar results, with the linear model generating a small improvement in fit (*SI Appendix, Model Selection*). All trend estimates had a potential scale reduction factor ($\hat{R}$; 26) close to one, consistent with convergence, and a posterior effective sample size (N_{eff}; 27) sufficient for inference. The model fits and posterior distributions of the trend are given in Fig. 1. Because the linear model did not converge for the regional partitioning, we have shown results for the constant model, with a complete set of figures in *SI Appendix, Results*.

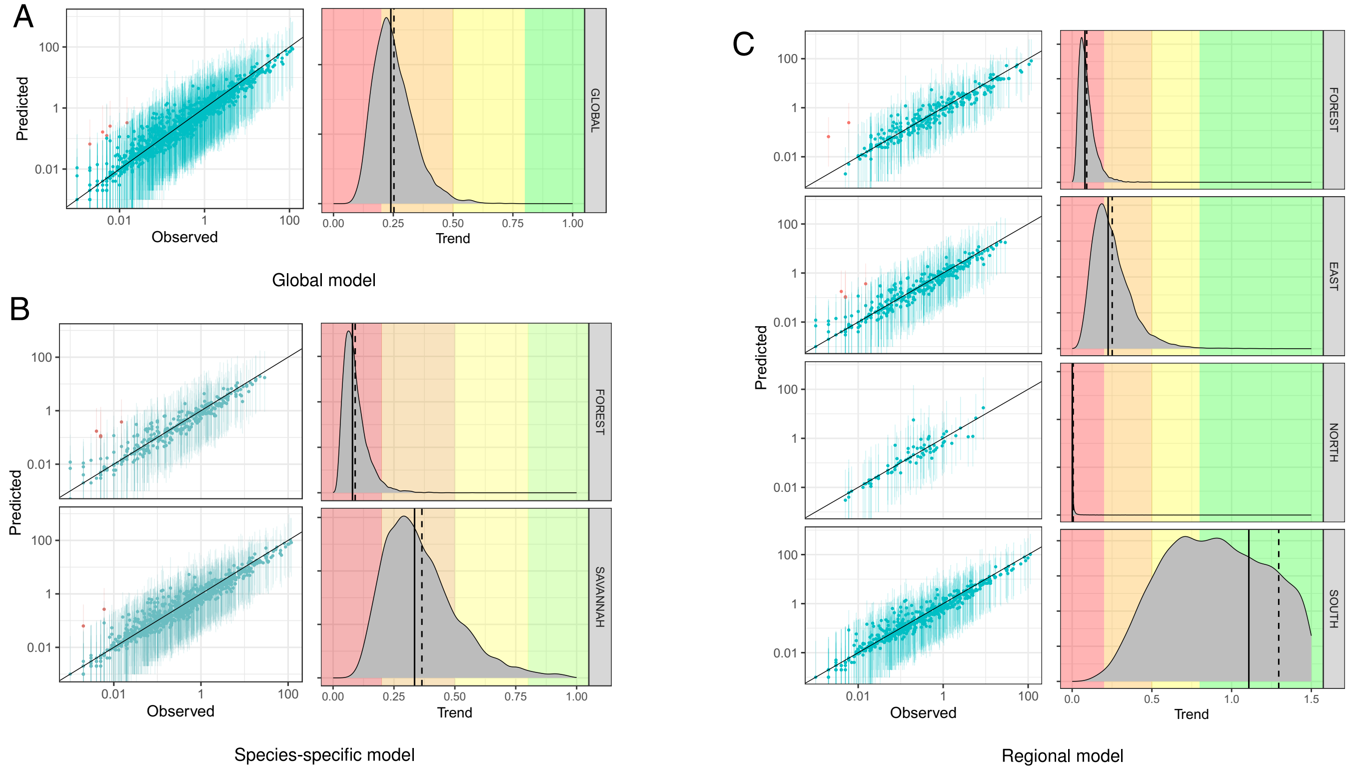
From the global model runs, the average trend per site across the continent between 1963 and 2016 (i.e., the expected change, E[Λ_j]) is estimated to be 20 to 25%, indicating that the average density per site has declined by 75 to 80% over that time (or approximately 3% per year). From the credible intervals of the constant model, there is evidence that the average site has changed by <41% (declined by >59%) with a 97.5% probability. For the species-specific model the average trend is 4 to 10% for the forest elephant and 28 to 36% for savannah; corresponding to average site-level declines of 90 to 96% (5% per year) and 64 to 72% (2% per year) respectively.

For the regional model there were strong differences in the estimated average trend between regions, with posterior estimates of 8 to 9% for Forest (average decline of approximately 4% per

Table 2. Posterior estimates of the trend (E[Λ_j]) for global, species-specific, and regional partitions, assuming either a constant growth rate or linear change in the growth rate over time

		Posterior			
Partition	Model	Mean	Median	95% CI	N_{eff}
Global	Constant	0.25	0.24	(0.14,0.41)	6,176
	Linear	0.24	0.20	(0.07,0.56)	2,758
Species:					
Forest	Constant	0.09	0.08	(0.03,0.18)	6,911
	Linear	0.10	0.04	(0.00,0.39)	4,091
Savannah	Constant	0.36	0.33	(0.17,0.66)	5,736
	Linear	0.36	0.28	(0.09,0.91)	3,662
Region:					
Forest	Constant	0.09	0.08	(0.03,0.19)	8,283
	Linear	–	–	–	–
East	Constant	0.25	0.23	(0.10,0.49)	9,507
	Linear	–	–	–	–
North	Constant	0.01	0.00	(0.00,0.02)	9,936
	Linear	–	–	–	–
South	Constant	1.30	1.11	(0.43,2.76)	9,626
	Linear	–	–	–	–

The posterior effective sample size (N_{eff}) is also shown, from a total of $N = 10{,}000$ retained posterior samples. All reported trend estimates had a potential scale reduction factor of $0.995 < \hat{R} < 1.005$. The linear model with regional partitioning did not converge and is excluded (*SI Appendix, Model Selection*).



Global model

Species-specific model

Regional model

Fig. 1. Fit of the constant growth rate model to empirical survey numbers per site and year (*Left* panel) and posterior distribution for the trend $E[\Lambda_j]$ (*Right* panel), per partition for: (*A*) global (i.e., continental scale), (*B*) species-specific, and (*C*) regional model runs. For the model fit, the median and 95% credible intervals of the posterior predicted survey numbers are plotted against the observed survey numbers on a log-10 scale in units of one thousand individuals. Predicted values that do not contain the observed value within their credible interval are colored in red. For the posterior distribution of the trend, intervals representing the magnitude of the trend are shaded in green (>80%), yellow (80 to 50%), orange (50 to 20%), and red (0 to 20%). The posterior mean and median values for $E[\Lambda_j]$ are shown as dashed and solid lines respectively.

site per year), 23 to 25% for East (approximately 3% per site per year), 0 to 1% for North (>10% decline per site year), and 111 to 130% for South (<1% increase per site per year; Table 2). Spatial heterogeneity was also evident in the distribution of site-specific trends within each region, with the greatest heterogeneity observed in the South (Fig. 2). Using the posterior median of the estimated trend per site (Eq. **2**), we categorized sites by the magnitude of their decline. The number of sites in each category is given in Table 3. For the South, 42% of sites demonstrated a density increase over the modeled period. In contrast, only 10% of East sites are estimated to have increased, and none in the North. In the North 97% of sites exhibit a trend of 0 to 20% (with 0% equivalent to extinction at that site). Among Forest sites, only 3% of sites are estimated to have increased, with 92% exhibiting a trend of 0 to 20%.

Discussion

African elephants are iconic species, and their decline highlights the detrimental impacts of habitat loss (28) and overconsumption of wildlife parts (29). While the threats are known and debated in policy circles (30–32), an explicit characterization of their conservation status has been lacking, despite decades of surveys and monitoring. Historic efforts to aggregate and model survey data have provided insight into trends that occurred in the 1970s and 1980s (15, 33), and trends have also been derived over shorter recent periods (13, 19, 21, 34). However, a comprehensive evaluation of trend information from African elephant populations over the past half-century has been a critical outstanding scientific need necessary for informing debate around the species management and conservation (9, 35, 36). The results presented here fulfill this need.

Our results complement, and are consistent with, the IUCN Red List Assessments for African elephant (35, 36). In both instances, we modeled the site-level density trend. However, for the IUCN Red List Assessments, guidelines required an estimate of the change in species-level population abundance over time (37), which was calculated as an abundance-weighted average of the site-level density trend. In the current study, we instead present an estimate of the overall change that is obtained from the central tendency of the distribution of density trends across sites (Eq. **13**).

The average trend across sites does not allow direct inference of changes in the total population size. This would require each density trend to be converted to numbers using a population area size assumption, which we have not attempted to do here. Given that both the survey area and the area occupied by each surveyed population are known to have changed over the study period, converting estimated trends in density to numbers is difficult without invoking further assumptions, and therefore has the potential to undermine the strength of our conclusions. While changes in overall abundance are often reported in ecological studies, we consider our presentation of the distribution of trends in density to be more defensible in this instance. Furthermore, it provides an arguably more representative picture of the status of Africa's elephants across the continent. Since a few large populations can dominate trends in abundance, large regional differences in abundance can bias estimates of the overall trend toward the trend at sites with the largest populations. In cases where there is strong heterogeneity in population size across

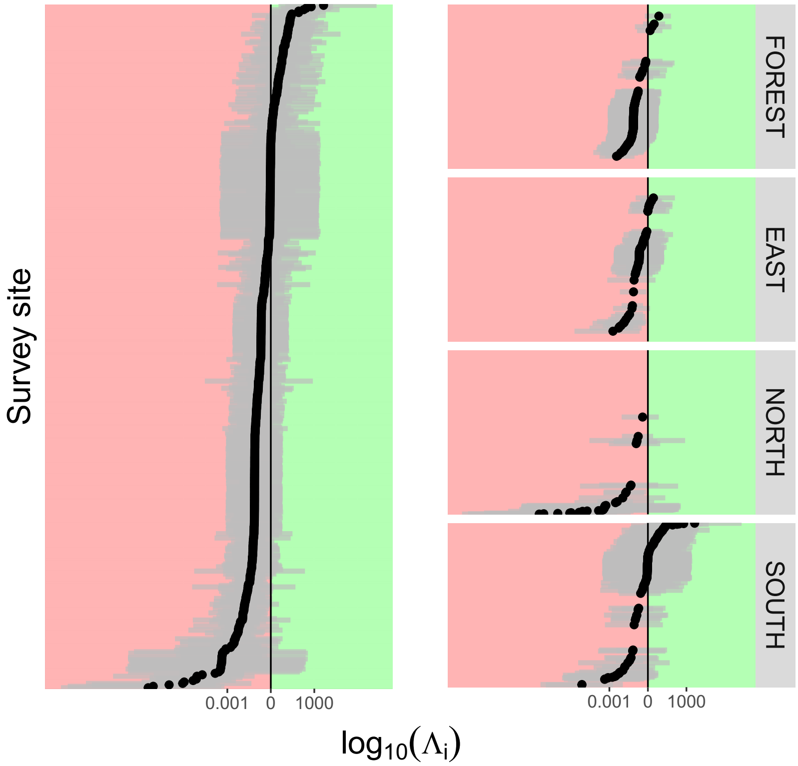


Fig. 2. Distribution of estimates of the decline per site, Λ_i (Eq. **2**) estimated from the constant model with regional partitioning. Points represent the posterior median value per site, with 95% credible intervals in grey. In the *Left* panel, all sites are shown; in the *Right* panel, sites are shown per region. The vertical axis is the same for all plots, with the estimated decline omitted for sites not in a particular region. Results are on a log-scale. Estimates of the decline per site are further listed in *SI Appendix*, Table S2.

the range of a species, with African elephant species being two examples, the current approach provides an alternative means of inferring conservation status.

In general, we have sought to maintain parsimony in our analysis: A simple model allowed us to include a large amount of noisy and inconsistent data that could not support a more highly parameterized model. Density dependence could not be estimated from the survey count data (there were three or fewer surveys reported in over 70% of sites; Table 1) and was also unjustified from an ecological perspective, with the majority of sites likely far below carrying capacity (some protected sites in southern Africa being likely exceptions). Instead, we have assumed that trends per site are a product of density-independent intrinsic growth and anthropogenic mortality only. Our analysis suggested that an assumption of a constant growth rate was sufficient to describe the data. Although higher-resolution temporal changes may have occurred, more complex models offered little additional explanatory power.

Such a parsimonious approach is inclusive, since it maximizes the quantity of data that can be utilized and therefore ensures the relevance of our analysis at the continental scale. Inclusivity was furthered by treating site-specific trend estimates as random effects. This allowed information to be shared between sites, with the most informative sites (i.e., sites with the highest quantity of data showing a consistent pattern) contributing most to the overall trend estimate. A strength of the approach is that it can provide a trend estimate for those sites with limited information (other than knowledge that elephants are present) without influencing, or otherwise degrading the overall result.

While our analysis spans 53 y, it represents less than the lifetime of a long-lived elephant and only two elephant generations. It does not offer insight into longer-term trends in either species, despite interest and speculation regarding historical erosion of elephant range (10). Information on the dynamics of elephant populations in the time period that predates this analysis is largely anecdotal given a sparsity of systematic monitoring. Ivory harvesting is thought to have reduced during the interwar period, potentially offering a respite from harvest-driven declines (17, 38) though regional differences are thought to have existed (25). Human population shifts, rapid growth, and land conversion began to accelerate toward the end of World War II, which in turn led to the compression of elephants into newly created protected areas (14, 24, 39, 40). As a result, hypotheses about elephant population trends prior to 1970 vary (17, 24, 40). Trends were likely not similar across the range given variation in the intensity and flux of different pressures and protections, but if comparable survey data existed for a longer period of time, it is plausible that an intervening period of population growth could have lessened our estimate of the decline at some sites.

Despite the uncertain changes that occurred prior to the availability of survey data, there are reasons to suggest that our results could underestimate the decline over the period we have analyzed. In particular, survey data have been overwhelmingly collected from nationally protected areas. Protected areas typically contain the highest quality data and are therefore likely to be the most influential in our analysis. In addition, unprotected areas in Africa are known to have harbored elephant populations into the 1970s and early 1980s that were subsequently extirpated, either due to intensive ivory harvest or on account of habitat conversion. These areas outside of protected areas were often not systematically surveyed. Expert opinion has documented the presence and roughly estimated the size of some of these populations, but such

Table 3. Number of sites per discrete category of Λ_i (Eq. 2) for the constant growth rate models

Partition	>1.0	1.0 to 0.8	0.8 to 0.5	0.5 to 0.2	0.2 to 0.0
Global	83	10	28	201	153
Species:					
Forest	4	0	3	5	138
Savannah	85	8	19	136	77
Region:					
Forest	4	0	3	5	138
East	10	2	8	53	25
North	0	0	0	1	33
South	82	64	6	8	33

Categorizations were based on the posterior median estimates. The total sites per partition is given in Table 1.

anecdotal information could not be included in our analysis. Where survey data have been collected, survey effort has often been reduced as the population declines so as to rationalize costs. For these reasons, less threatened populations are overrepresented in the survey data used in our analysis, which may have led us to underestimate the average decline.

Overall, our analysis provides a much-needed quantitative assessment of conservation status for African elephants using survey data from the past half century. While the mean site-level decline has been striking, particularly in the northern savannah region, many sites experienced growth. The heterogeneity was most notable for savannah elephants, which experienced markedly different trends both within and between regions (i.e., broad scale declines across most sites in the North and East regions and stability or increase in over half of the sites in the South; Table 3 and Fig. 2). For forest elephants, severe declines were registered at most sites across the species range, but 3% of sites were estimated to have increased. These results indicated that conservation efforts are succeeding in some sites across regions of Africa. Such heterogeneity offers opportunities to identify key factors related to the efficacy of conservation efforts, that may ultimately protect the viability of wild elephant populations. Our results highlight strongholds for the species, including sites that have increased while embedded in regions of decline (e.g., Pendjari National Park in Benin is a rare example of an increasing forest elephant trend). The consistency of our approach across sites makes these comparisons valid. Such sites, where the associated populations are believed to be demographically viable, may merit greater attention and investment given their importance for the species.

Materials and Methods

Due to differences in resources for monitoring across sites and the development of new techniques over decades of data collection, surveys varied widely in respect to method, effort, and frequency. More specifically, the methodology and temporal range of data differed between sites; and at any one site, surveys may have used different methods, with different associated levels of observation error, and with different survey area sizes that may or may not have included the complete elephant population. We further lacked information on intrinsic demographic rates of growth or carrying capacity, which change across the continent due to environmental conditions. These limited and inconsistent data constrained our analytical approach in three important ways. First, we modeled elephant density rather than numbers since the survey area size was not constant over time for most survey sites. Second, we were able to fit only the simplest exponential population model: A logistic model of density-dependent growth did not converge. Third, we lacked overlapping, comparative data across sites that would allow us to calculate an overall measure of population change directly from estimated site-specific trends.

The model assumed African elephant population dynamics were a function of site-specific growth rates $\lambda_{i,t}$, which describe the rate of change in population density at survey site i using a simple multiplicative relationship:

$$x_{i,t+1} = x_{i,t} \cdot \lambda_{i,t}, \qquad [1]$$

where $x_{i,t}$ is the density at time t and $x_{i,t+1}$ is the density in the following year (*SI Appendix, Model Derivation*). For an initial condition $x_{i,0}$ at $t = 0$, the population change per site from $t = 0$ to $t = T$ is the product of each sequential change:

$$\Lambda_i = \prod_{t=0}^{T-1} \lambda_{i,t}. \qquad [2]$$

In order to estimate a global, species-specific, or regional trend, we are required to combine estimates of Λ_i from multiple populations (survey sites), each with different data characteristics. A weighted average (e.g., refs. 35 and 36) or summation (e.g., ref. 41), could be used. Weights could be constructed from survey estimates of the population size, or the survey area sizes could be used to convert the density trend in Eq. **2** to a numbers trend per site. However, neither population size estimates nor survey area sizes were available for overlapping years across all sites. An alternative approach was therefore required, and we instead characterized the distribution of density trends across sites. Specifically, we used an analytical derivation of the probability distribution of Λ_i, basing our inference directly on this distribution.

We show that it is possible to use the distribution of Λ_i to construct an index of the average density trend, which can be used to infer conservation status in the absence of comparable abundance data across sites. The contribution of each site to the index does not need to be weighted but is determined only by the information content of the data at that site. Furthermore, the distribution of Λ_i can be obtained directly from a simple model of the population dynamics, and uncertainty in the estimated component parameters retained in the final output. In our description of the approach, we write the model in Eq. **1** as a regression and show how the estimated coefficients can be used to define the distribution of Λ_i.

Data. The primary source of African elephant population survey estimates is the IUCN/Species Survival Commission (SSC) African Elephant Specialist Group (AfESG) African Elephant Database (AED), a comprehensive repository of data from survey reports and questionnaires from 37 African elephant range states beginning in 1992 through 2016. Site-specific data on elephant numbers predating the AED were compiled from original sources (primarily survey reports) largely found in the IUCN/SSC AfESG African Elephant Library.

Data cleaning involved the following steps: 1) Exclude surveys with incomplete information including missing site labels, number estimates, survey area, year of survey, or country of survey site; 2) Unify site names so that surveys from the same site are matched; 3) Delete duplicate survey records; 4) Exclude survey records for which estimates were based on extrapolation to a wider (unobserved) area than originally surveyed; 5) Exclude survey records recorded as having low reliability in the AED; 6) Sum subsectioned survey records when site surveys from the same survey effort were reported independently per site.

The data covered 475 survey sites with a total of 1,325 surveys between 1964 and 2016 (Table 1; 42). Based on coverage of the data, the models were initialized in 1963 (i.e., $t = 0$ in this year) and terminated in 2016 (total elapsed time: $T = 53$). Quantitative information on the observation error was not consistently available across surveys and was therefore not used in the analysis.

Model Structure. We developed regression models with estimated coefficients related directly to the rate of population change $\lambda_{i,t}$ (Eq. **1**). Population change refers to the aggregated effects of birth, natural mortality, and anthropogenic mortality, which are assumed multiplicative and density-independent. Density-dependent models did not converge (*SI Appendix, Model Selection*) and were arguably unnecessary given depleted and declining elephant populations over much of the continent. We could however allow $\lambda_{i,t}$ to change over time in a density-independent manner. For the purposes of the modeling, each site was assumed to be closed (i.e., no movement of individuals between sites).

The following notation was adopted:

- $i \in \{1, 2, \cdots, 475\}$ and $t \in \{0, 1, \cdots, 53\}$ subscripts refer to the survey site and time (in years) respectively;
- j refers to a partition that contains a nonoverlapping collection of sites.

We further define notation $i|j$ as referring to a site nested within partition j. The definition of the partition depends on the model run. For example, if the model is partitioned into two elephant species, then $j \in \{1, 2\}$ refers to the species, and $i|1 \in \{1, 2, \ldots, 150\}$ and $i|2 \in \{151, 152, \ldots, 475\}$ refer to the sites for forest and savannah elephant species respectively.

- $y_{i|j,t}$ is the observed elephant numbers per survey (the number of surveys and the temporal range of the surveys per site are listed in *SI Appendix*, Table S2);
- $A_{i|j,t}$ is the survey area size in square kilometers;
- $x_{i|j,t}$ is the estimated density (numbers per square kilometer);
- $\lambda_{i|j,t}$ is the multiplicative rate of change in $x_{i|j,t}$;
- $\eta_{i|j,t}$ is the model predicted elephant counts.

The process and observation models can be written in log–linear form for $t > 0$:

$$\ln\left(x_{i|j,t}\right) = \ln\left(x_{i|j,0}\right) + \sum_{z=0}^{t-1} \ln\left(\lambda_{i|j,z}\right), \qquad \mathbf{[3a]}$$

$$\ln\left(\eta_{i|j,t}\right) = \ln\left(x_{i|j,t}\right) + \gamma \cdot \ln\left(A_{i|j,t}\right), \qquad \mathbf{[3b]}$$

where z is an index referring to time $z \in \{0, \cdots, t-1\}$. The observation model includes the stability parameter $\gamma > 0$. Surveys are not random but centered on known elephant populations. Assuming placement of the survey in a region of highest known density, the count per unit area would be expected to decrease as the survey area expands toward the spatial limit of the population. This can be accommodated by an estimated value of $0 < \gamma < 1$, which would stabilize the predicted numbers at high $A_{i|j,t}$. Inclusion of a partition-specific γ parameter did not yield any noticeable improvement in the fit to the data (*SI Appendix, Model Selection*), and further exploratory runs with a fixed value of $\gamma = 1$ gave similar results to those reported here.

Two regression submodels were constructed, assuming that the rate $\lambda_{i|j,t}$ was either constant or linearly changing over time. Assuming a constant rate of change:

$$\ln\left(\lambda_{i|j,t}\right) = \alpha_j + \alpha_{i|j}, \qquad \mathbf{[4]}$$

where estimated coefficients are the rate of change per partition α_j, and the nested random effect $\alpha_{i|j}$ per survey site. Assuming a linearly time-dependent rate of change gives a second model:

$$\ln\left(\lambda_{i|j,t}\right) = \alpha_j + \alpha_{i|j} + t \cdot \left(\beta_j + \beta_{i|j}\right), \qquad \mathbf{[5]}$$

with additional coefficients β_j and $\beta_{i|j}$. These are referred to as the "constant" and "linear" models respectively.

Model Fitting. The survey data $y_{it} \geq 0$ were counts, which we described using a Negative Binomial probability mass function:

$$p\left(y_{i|j,t}\right) \propto \left(\frac{\phi}{\phi + \eta_{i|j,t}}\right)^{\phi} \cdot \left(\frac{\eta_{i|j,t}}{\phi + \eta_{i|j,t}}\right)^{y_{i|j,t}}, \qquad \mathbf{[6]}$$

parameterized using the overdispersion parameter ϕ and the model predicted expected value $\eta_{i|j,t}$ (Eq. **3b**). The overdispersion is assumed to be constant across all sites and estimated within the model. Inclusion of a partition-specific ϕ parameter did not yield any noticeable improvement in the fit to the data (*SI Appendix, Model Selection*). The likelihood represents both process and observation error, but since an observation error estimate was not consistently available from the surveys, it was not explicitly included in the likelihood. We note that this will have artificially increased our confidence in the estimated trend at any given site but is unlikely to have biased the trend in any one direction.

Model fitting was conducted within a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling (43–46). The fixed effects α_j were given a weak normal prior centered on zero. The random effects terms $\alpha_{i|j}$ were assumed to follow an exponential scale-mixture normal distribution:

$$\alpha_{i|j} \sim Normal\left(0, \tau^2_{\alpha_j}\right), \qquad \mathbf{[7a]}$$

$$\tau^2_{\alpha_j} \sim Exponential\,(1), \qquad \mathbf{[7b]}$$

that is equivalent to a Laplace distribution for $\alpha_{i|j}$ with location at zero and scale parameter $1/\sqrt{2}$ (47, 48), representing a prior assumption that $\alpha_{i|j} = 0$. The number of τ_{α_j} parameters is equal to the number of partitions. For example, if $j \in \{1, 2\}$ then we estimate parameters τ_{α_1} and τ_{α_2}. Similarly for τ_{β_j}. The same prior assumptions were used for β_j and $\beta_{i|j}$ for the linear model, with τ_{β_j} hyperparameters.

Random effect terms will be distributed around each α_j (and β_j) coefficient, and this hierarchical structure allowed trend information to be shared across sites. This prevented the need for preselection of sites based on the perceived information content of their data. For sites with little informative data, $\alpha_{i|j} \to 0$ (and $\beta_{i|j} \to 0$) which allowed us to make inferences about sites with limited surveys from the shared α_j (and β_j) terms.

The stability parameter was given a gamma prior, because it is bounded at zero, with a prior value of one:

$$\gamma \sim Gamma(1, 1), \qquad \mathbf{[8a]}$$

and the overdispersion a half-normal prior on the inverse of ϕ:

$$\phi^{-1} \sim Normal^{+}(0, 1), \qquad \mathbf{[8b]}$$

which represents a prior assumption that there is only a small degree of overdispersion (as $\phi^{-1} \to 0^{+}$ the data more closely resemble a Poisson distribution).

Trend Estimation. The overall trend per site is $\Lambda_{i|j}$ (Eq. **2**), and we describe the distribution of this trend using estimated model parameters. We could then derive an overall trend statistic as the central tendency of this distribution. To do this, we write $\Lambda_{i|j}$ in terms of the sequential, multiplicative growth rates $\lambda_{i|j,t}$, summed on the log-scale:

$$\Lambda_{i|j} = \exp\left(\sum_{t=0}^{T-1} \ln\left(\lambda_{i|j,t}\right)\right). \qquad \mathbf{[9]}$$

Using the relationships in Eqs. **4** and **5**, the priors in Eq. **7** allowed us to define the distribution of $\ln\left(\lambda_{i|j,t}\right)$ for any collection of sites within partition j. For the constant model:

$$\ln\left(\lambda_{i|j,t}\right) \sim Normal\left(\alpha_j, \tau^2_{\alpha_j}\right), \qquad \mathbf{[10]}$$

and for the linear model:

$$\ln\left(\lambda_{i|j,t}\right) \sim Normal\left(\alpha_j + t \cdot \beta_j, \tau^2_{\alpha_j} + t^2 \cdot \tau^2_{\beta_j}\right), \qquad \mathbf{[11]}$$

Since $\ln\left(\lambda_{i|j,t}\right)$ is a normally distributed random effect, the distribution of the sum over time is also normally distributed. We use the notation:

$$\sum_{t=0}^{T-1} \ln\left(\lambda_{i|j,t}\right) \sim Normal\left(\mu_j, \sigma^2_j\right), \qquad \mathbf{[12]}$$

for site i in partition j. For the constant model:

$$\mu_j = \alpha_j \cdot T,$$

$$\sigma^2_j = \tau^2_{\alpha_j} \cdot T,$$

and for the linear model:

$$\mu_j = \alpha_j \cdot T + \beta_j \cdot T \cdot (T+1)/2,$$

$$\sigma_j^2 = \tau_{\alpha_j}^2 \cdot T + \sum_{t=0}^{T-1} t^2 \cdot \tau_{\beta_j}^2.$$

If the sum of $\ln\left(\lambda_{i|j,t}\right)$ is normal, then $\Lambda_{i|j}$ is log-normal, with an expected change across sites within a partition equal to:

$$\mathrm{E}[\Lambda_j] = \exp\left(\mu_j + \sigma_j^2/2\right). \qquad [13]$$

From our model fit, we were therefore able to obtain a posterior distribution for $\mathrm{E}[\Lambda_j]$, and use this to infer an overall population trend.

Data Partitions. Three partitionings of the data were used, each representing finer disaggregations: 1) Global: all survey data considered in a single partition assessing the continental scale trends of African elephants; 2) Species-specific: survey data partitioned by species: *L. cyclotis* and *L. africana*; 3) Regional: survey data partitioned by region: Forest (*L. cyclotis*), and East, North, South (*L. africana*), based on the precedent of deriving regional estimates of population change (9). The geographic distribution of forest elephant is largely within central Africa, meaning that regional partitioning for this species was not considered useful.

Model Fits and Diagnostics. All analyses and estimation procedures were performed using Bayesian methods within R using the rstan package (43, 44). For each model fit, four MCMC chains were initialized at the maximum a posteriori estimate and run for 10,000 iterations, with every second sample retained and the first half of each chain discarded, yielding a total of 10,000 retained samples. To check performance of the model, the convergence of all parameter and derived value MCMC chains was verified using visual inspection, consideration of the posterior effective sample size, N_{eff}, and the potential scale reduction factor, $\hat{R}$ (26, 27, *SI Appendix, Results*). In addition, posterior prediction of the data was performed to ensure that the model was capable of reproducing the observations.

Reporting of Results. The model outputs posterior distributions for $\mathrm{E}[\Lambda_j]$ for each partition. In characterizing the trend using this summary statistic, we report the posterior mean, median, and 95% equal-tailed credible intervals. In presenting the results we further make use of the discrete categories, analogous to the IUCN Red List of Threatened Species categorization criteria: 0 to 20%; 20 to 50%; 50 to 80%; and $>$80%. Trends of $>$100% indicate population density increase.

Data, Materials, and Software Availability. Anonymized survey abundance estimates and model code have been deposited on Dryad (42, 46). Access to the raw data requires permission from the IUCN/SSC African Elephant Specialist Group (afesg@iucn.org), to which requests should be directed.

ACKNOWLEDGMENTS. Developmental work that contributed to this project was conducted as part of the IUCN Red List Assessments for African Elephant. We are grateful for constructive reviews by James Clark (PNAS and Duke University), Len Thomas (University of St. Andrews), and one anonymous reviewer who substantially improved the quality of the manuscript.

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