

Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas

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We compiled all credible repeated lion surveys and present time series data for 47 lion (*Panthera leo*) populations. We used a Bayesian state space model to estimate growth rate- λ for each population and summed these into three regional sets to provide conservation-relevant estimates of trends since 1990. We found a striking geographical pattern: African lion populations are declining everywhere, except in four southern countries (Botswana, Namibia, South Africa, and Zimbabwe). Population models indicate a 67% chance that lions in West and Central Africa decline by one-half, while estimating a 37% chance that lions in East Africa also decline by one-half over two decades. We recommend separate regional assessments of the lion in the World Conservation Union (IUCN) Red List of Threatened Species: already recognized as critically endangered in West Africa, our analysis supports listing as regionally endangered in Central and East Africa and least concern in southern Africa. Almost all lion populations that historically exceeded ~500 individuals are declining, but lion conservation is successful in southern Africa, in part because of the proliferation of reintroduced lions in small, fenced, intensively managed, and funded reserves. If management budgets for wild lands cannot keep pace with mounting levels of threat, the species may rely increasingly on these southern African areas and may no longer be a flagship species of the once vast natural ecosystems across the rest of the continent.

lion | *Panthera leo* | Africa | population decline

Large carnivores are generally declining worldwide (1), but trends vary according to geography (2) and the severity of threats posed to humans (3). The African lion (*Panthera leo*) exemplifies the challenges of carnivore conservation: widespread habitat loss (4), extensive prey base depletion (5–7), indiscriminate retaliatory or preemptive killing to protect humans and their livestock (8–10), poorly regulated sport hunting (11–18), and demand for traditional African and Chinese medicines (19). Although lions are relatively well-studied compared with most large felids, regional-scale population estimates remain scant across much of its range (20), and population surveys are generally repeated at irregular intervals because of the inherent difficulty of counting lions (21, 22) and shortage of funds for systematic surveys. No reliable data are available for Angola, Central African Republic, Somalia, South Sudan, and Ethiopia. Furthermore, systematic surveys are absent from large areas of potential lion habitat in countries with a rich tradition of wildlife research, such as Zambia and Tanzania.

With widespread declines in many reserves (23) and rapid deterioration of the lion's status in a substantial portion of the species' range (24), there is growing concern that lion numbers may be declining rapidly, leading to the lion's consideration for listing as threatened or endangered on the US Endangered Species Act. The lion is currently listed as vulnerable on the World Conservation Union (IUCN) Red List and would be considered endangered if numbers were to decline by at least 50% over three lion generations (LGs) (25). Here, we use a

comprehensive dataset of repeated counts to assess lion status, calculate growth rate per population, and estimate broader trends per geographic region. We show that lion populations are rapidly disappearing from large parts of Africa, signaling a major trophic downgrading of savannah ecosystems.

Results

We present time series data for 47 of 67 areas (4) where lions are still known to occur (Fig. 1), with the most recent estimates totaling 8,221 lions (Dataset S1); note that this subsample only excludes areas where the available data are speculative. Almost all lion populations that historically exceeded ~500 individuals are declining (Figs. 2–4). All West Central African populations other than Pendjari ($\lambda = 1.07 \pm 0.13$) are declining (Fig. 2), with lions in Comoé and Mole now likely extinct. A similar pattern is found in East Africa (Fig. 3), with Serengeti ($\lambda = 1.02 \pm 0.02$) being the only large population surveyed that is not decreasing, whereas data from Katavi indicate a dramatic decline ($\lambda = 0.67 \pm 0.11$). Southern African populations do not indicate such a drastic and widespread decline (Fig. 4), but one of the largest (Okavango; $\lambda = 0.97 \pm 0.1$) is, nevertheless, declining. Fenced populations reveal a completely different pattern: none have experienced a sharp decline, and many small fenced populations are increasing (Figs. 3 and 4). Data and model inferences for 47 populations included in our study are given in Figs. S1–S4. When summing posterior densities of growth rates into regional groups, we found that West Central African populations were sharply declining ($\lambda = 0.90 \pm 0.22$) and that East African populations were also declining, albeit less sharply ($\lambda = 0.99 \pm 0.14$). In contrast, southern African

Significance

At a regional scale, lion populations in West, Central, and East Africa are likely to suffer a projected 50% decline over the next two decades, whereas lion populations are only increasing in southern Africa. Many lion populations are either now gone or expected to disappear within the next few decades to the extent that the intensively managed populations in southern Africa may soon supersede the iconic savannah landscapes in East Africa as the most successful sites for lion conservation. The rapid disappearance of lions suggests a major trophic downgrading of African ecosystems with the lion no longer playing a pivotal role as apex predator.

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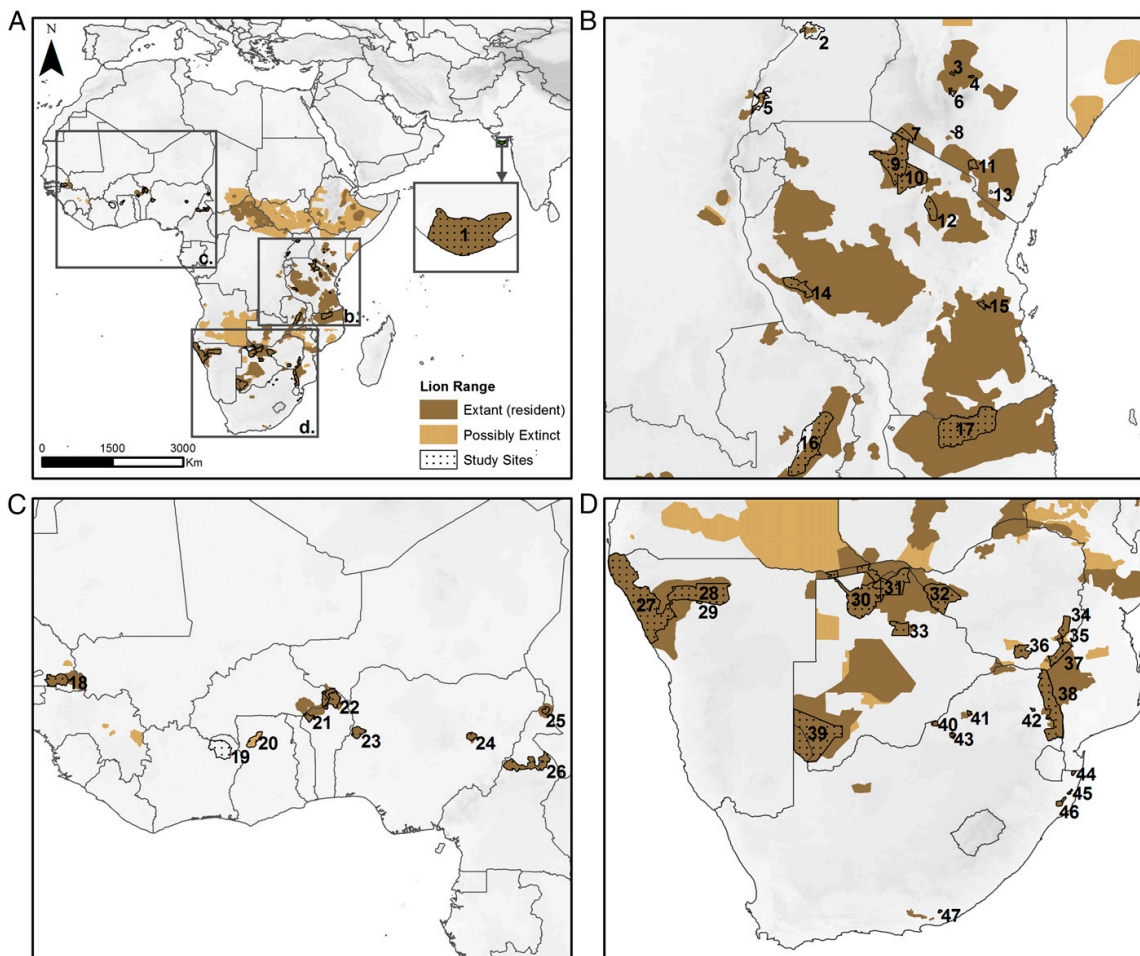


Fig. 1. Distribution map of monitored lion populations; zooming levels: (A) species wide, (B) East Africa, (C) West Central Africa, (D) southern Africa. 1, Gir; 2, Murchison Falls; 3, Laikipia; 4, Samburu; 5, Queen Elizabeth National Park; 6, Ol Pejeta Conservancy; 7, Masai Mara; 8, Nairobi; 9, Serengeti; 10, Ngorongoro; 11, Mbirikani; 12, Tarangire; 13, Taïta Hills; 14, Katavi; 15, Matambwe; 16, Luangwa; 17, Niassa; 18, Niokolo Koba; 19, Comoé National Park; 20, Mole; 21, Pendjari; 22, W; 23, Kainji Lake; 24, Yankari; 25, Waza; 26, Benoue; 27, Kunene; 28, Etosha; 29, Ongava; 30, Okavango Delta; 31, Chobe Kwando; 32, Hwange; 33, Makgadikgadi Pans; 34, Save Conservancy; 35, Malilangwe Conservancy; 36, Bulyebe Conservancy; 37, Gonarezhou; 38, Kruger National Park; 39, Kgalagadi; 40, Madikwe Nature Reserve; 41, Welgevonden; 42, Makalali; 43, Pilanesberg National Park; 44, Tembe Elephant Park; 45, Phinda; 46, Hluhluwe iMfolozi; and 47, Kwandwe.

populations were increasing ($\lambda = 1.09 \pm 0.15$), as the majority were in fenced reserves showing strongest increases ($\lambda = 1.10 \pm 0.14$). Nationally, South Africa was the only African country with growth in every population, all of which were fenced; most were re-established over the past two decades and quickly reached saturation. The Asian population, representing a single contiguous population surviving in the Indian state of Gujarat, has stabilized inside the Gir Reserve (Fig. 2) and expanded in the surrounding countryside (26). Niassa Reserve in Mozambique also increased but is considered as a separate case (Fig. 2) (see below).

When population trends were assumed to remain unchanged in the future and, ignoring process error, were projected over a multiyear timescale (Table 1), we found that four of seven surviving West Central African populations were extremely likely to decline by more than one-half in two decades ($p_{0.5}^{20} > 0.7$) (Table 1). In East Africa, 6 of 14 surviving populations were very likely to decline by more than one-third in two decades ($p_{0.33}^{20} > 0.5$)

(Table 1). In southern Africa, the second largest population (Okavango) was also likely to decline by one-third in two decades ($p_{0.33}^{20} > 0.5$) (Table 1). When considering projected growth rates summed by regional groups, we found that the West Central African group was likely to drop by one-third in 5 y ($p_{0.33}^5 = 0.56$) and very likely to drop by one-half in 20 y ($p_{0.5}^{20} = 0.67$), whereas East African populations also had a bleak future, with $p_{0.33}^{20} = 0.45$ and $p_{0.5}^{30} = 0.43$, respectively. When applying IUCN thresholds, the West Central African group had a probability of projected decline of more than one-half in three LGs of $p_{0.5}^{3LG} = 0.67$, and the East African group had a probability of declining by more than one-half in three LGs of $p_{0.5}^{3LG} = 0.37$.

Discussion

These growth rate estimates represent the best available knowledge of the global trends of lion populations. However, we acknowledge that they are intrinsically imprecise. In some sites, census

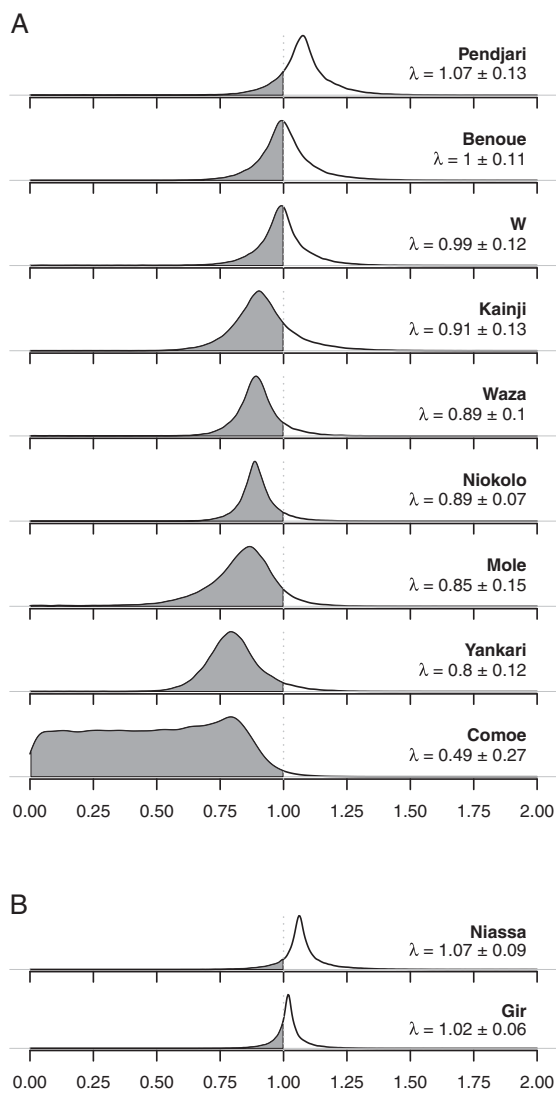


Fig. 2. Posterior densities of growth rates for (A) West Central Africa lion populations and (B) special cases. The gray areas under the curves indicate the probabilities of decline. Values shown are medians \pm SDs of growth rate estimates.

methodology varied between years, although we limited our sample to counts that were consistently based on the most reliable survey techniques, and thus, the regional-scale declines are unlikely to be an artifact of methodological shortcomings. If there is an overall bias in our results, it is probably toward optimism: our sample populations were all monitored in areas with at least partial protection, and research sites are known to be generally avoided by poachers and encroachers (27). Concomitantly, a clear pattern emerged that the most severely declining populations were the least well-monitored (Fig. S5). In fact, it seems likely that unmonitored unfenced populations across much of Africa will have suffered even greater rates of decline than

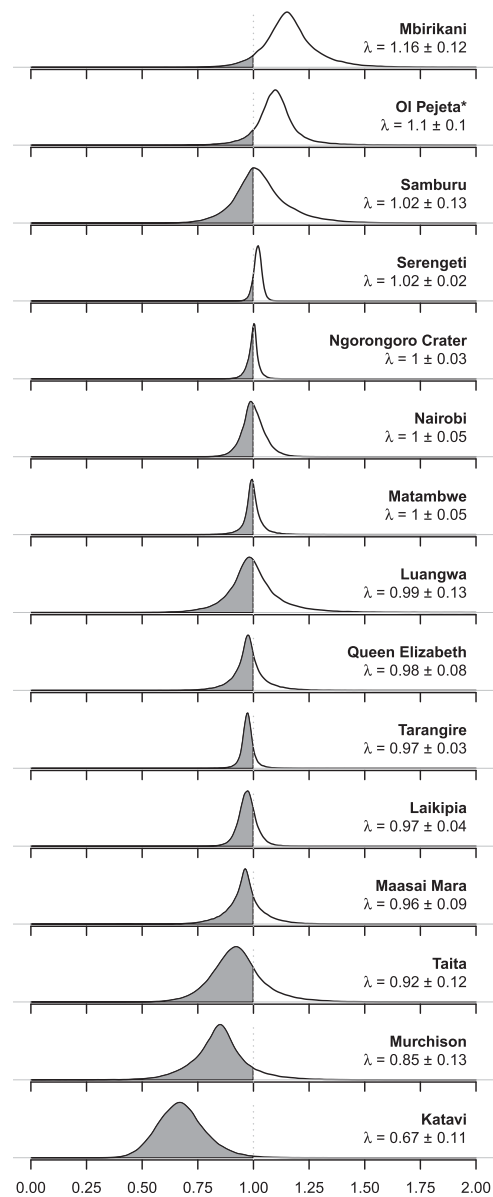


Fig. 3. Posterior densities of growth rates for East Africa lion populations. The gray areas under the curves indicate the probabilities of decline. Values shown are medians \pm SDs of growth rate estimates. *Fenced populations.

reported here, because lack of monitoring generally reflects a lack of conservation effort. The deteriorating conservation status of lions across much of the continent is further emphasized by the apparent extirpation of lions in 12 African countries, with possible recent extirpation in another 4 countries (25).

Niassa (Mozambique) was treated as an outlier because of the exceptional postwar situation, with the return of rule of law coinciding with increased scavenging opportunities resulting from high

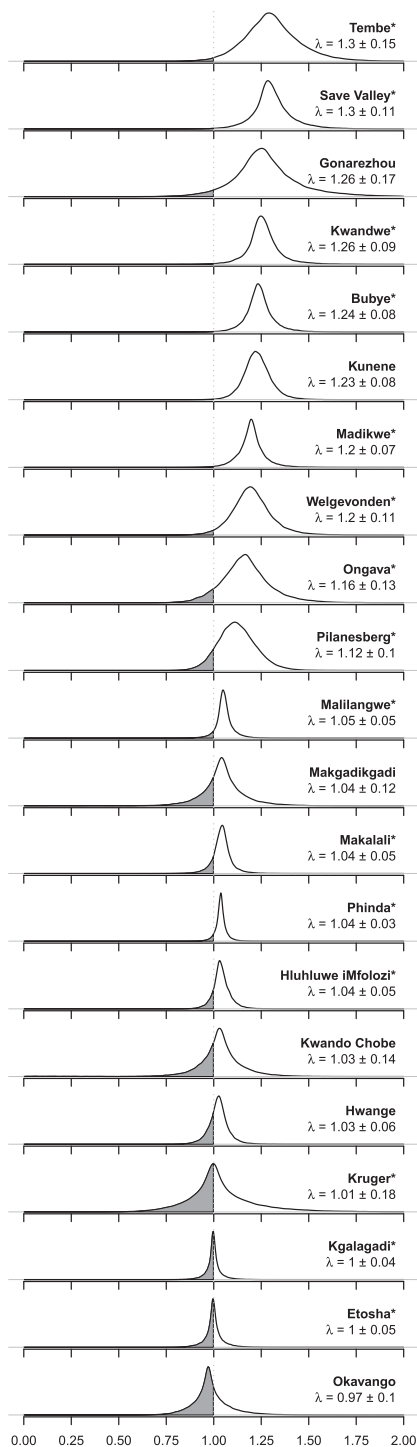


Fig. 4. Posterior densities of growth rates for southern Africa lion populations. The gray areas under the curves indicate the probabilities of decline. Values shown are medians \pm SDs of growth rate estimates. *Fenced populations.

levels of elephant poaching. Human population density is relatively high in Mozambique, and therefore, unless management is further strengthened, this lion population may also experience declining prey abundance in the near future, which is common in most of Africa.

The striking contrast between countries in southern Africa and the rest of the continent is congruent with differences in human population density, which has been shown to be an important explanatory variable for population status (23). Another important determinant is prey abundance (28, 29), which is increasingly under threat from an unsustainable and increasingly commercialized bushmeat trade (6). Lion trends are consistent with time series data on their main prey species: whereas herbivore population sizes increased by 24% in southern Africa, herbivore numbers declined by 52% in East Africa and 85% in West Central Africa between 1970 and 2005 (5). Another important determinant is management budgets and capacity to protect parks, all of which are higher in the well-maintained populations in southern Africa (23). Packer et al. (23) showed that management budget and the presence of wildlife-proof fencing were the two most important determinants of short-term lion population trends across Africa. Although the results presented in Figs. 3 and 4 are consistent with the benefits of fencing, we cannot present a formal analysis because of the negative relationship between data availability and rates of population decline (Fig. S5) and the lack of data on management budget for many of 47 sites in this analysis.

Nevertheless, our results clearly confirm widespread declines in West Central Africa and support the regionally critically endangered listing for West Africa (24). Moreover, they suggest that the lion is regionally endangered in East Africa, where lions have traditionally been abundant across large ecologically intact mosaics of landscapes (4). The rapid disappearance of lions from recently identified strongholds (4) also signals a major trophic downgrading of African ecosystems, with the lion no longer playing its ecological role as apex predator (30). The decline of lions was first apparent in West Central Africa (24) and is now apparent in East Africa. This decline is consistent with a broader pattern of defaunation (31), with multiple megafauna species experiencing massive declines (32).

Our results indicate that greatly increased intervention efforts are required to maintain viable and ecologically effective populations in most large “lion conservation units” (33, 34). Effective lion conservation requires management capacity and sizeable budgets (23), but most African reserves operate on low levels of funding and management capacity (23). Declining populations require immediate increases in financial support and improved governance and management capacity to reverse current trends, and cost-effective monitoring will be essential in all of the important remaining lion populations. Accurate estimates of short- to medium-term changes require frequent counts, because time series data consisting of only two to three surveys can inevitably only provide very weak information on long-term trends (Figs. S1–S4). These results emphasize the importance of consistent, rigorous large-scale surveys conducted by independent agencies, particularly in countries like Tanzania, which has previously been assumed to hold a significant proportion of Africa’s remaining lion populations.

Fenced reserves in Kenya and southern Africa are very effective, but these reserves include many small populations that require metapopulation management, euthanasia, and contraception and only make limited contributions to ecosystem functionality and conservation outcomes (23, 35, 36). Effective management of lions in large landscapes is also possible (9, 37) but has rarely been implemented at sufficiently large scale, except in southern Africa (21). Unless political and funding commitments are scaled up to address mounting levels of threat (23), lions may disappear from most of Africa.

Table 1. Cumulative probabilities of projected lion population decline by one-third (33%) and one-half (50%) in periods of 5, 10, 20, and 30 y and three LGs defined according to the IUCN

Population	Size	$p_{0.33}^5$	$p_{0.5}^5$	$p_{0.33}^{10}$	$p_{0.5}^{10}$	$p_{0.33}^{20}$	$p_{0.5}^{20}$	$p_{0.33}^{30}$	$p_{0.5}^{30}$	$p_{0.33}^{3LG}$	$p_{0.5}^{3LG}$
Western-Central											
Yankari	11	0.87	0.76	0.91	0.88	0.93	0.92	0.94	0.93	0.93	0.92
Niokolo	16	0.72	0.33	0.85	0.76	0.89	0.86	0.9	0.89	0.89	0.87
Waza	17	0.68	0.35	0.82	0.72	0.87	0.84	0.88	0.86	0.87	0.84
Kainji	32	0.56	0.33	0.69	0.6	0.75	0.71	0.76	0.74	0.75	0.71
W	64	0.2	0.1	0.34	0.23	0.44	0.36	0.48	0.42	0.45	0.37
Benoue	200	0.17	0.08	0.3	0.2	0.39	0.32	0.42	0.37	0.39	0.33
Eastern											
Taita	15	0.5	0.3	0.65	0.54	0.72	0.67	0.74	0.71	0.72	0.68
Samburu	26	0.15	0.07	0.25	0.17	0.32	0.27	0.35	0.31	0.33	0.28
Nairobi	30	0.06	0.01	0.19	0.08	0.34	0.23	0.4	0.31	0.35	0.24
Laikipia	60	0.1	0.01	0.37	0.15	0.59	0.43	0.66	0.56	0.6	0.45
Luangwa	94	0.21	0.1	0.36	0.24	0.45	0.38	0.49	0.44	0.46	0.39
Matambwe	112	0.03	0.01	0.12	0.05	0.26	0.14	0.36	0.23	0.28	0.15
Murchison	132	0.78	0.6	0.86	0.81	0.88	0.86	0.89	0.88	0.88	0.87
Queen Elizabeth	144	0.16	0.06	0.36	0.2	0.54	0.4	0.6	0.51	0.55	0.41
Tarangire	157	0.04	0.01	0.28	0.06	0.63	0.36	0.73	0.58	0.65	0.39
Maasai Mara	286	0.26	0.1	0.5	0.31	0.65	0.54	0.69	0.63	0.66	0.56
Southern											
Kgalagadi*	115	0.03	0.01	0.11	0.04	0.21	0.13	0.28	0.19	0.22	0.13
Kwando Chobe	285	0.11	0.06	0.19	0.13	0.25	0.2	0.27	0.23	0.25	0.21
Makgadikgadi	327	0.1	0.05	0.16	0.12	0.21	0.17	0.23	0.2	0.21	0.18
Etosha*	457	0.05	0.01	0.14	0.07	0.26	0.16	0.33	0.23	0.26	0.17
Okavango	1107	0.2	0.09	0.38	0.24	0.55	0.42	0.59	0.52	0.55	0.44
Kruger*	1672	0.2	0.12	0.3	0.22	0.37	0.31	0.39	0.35	0.37	0.32

Population sizes show most recent estimates of lion numbers. Extinct populations or populations unlikely to decline are not shown.
*Fenced population.

Materials and Methods

We compiled and analyzed data from 47 lion populations representing the best available knowledge of the species from the past two decades (23, 25) (Dataset S1). Population estimates were obtained by diverse methods, including total count, individual identifications, total or sample inventory using calling stations, radio telemetry, photo databases, transects, spoor counts, and density estimates based on direct observations corrected for patrol effort (20, 22, 24, 38). We excluded population estimates that were based on extrapolation of lion densities in adjacent areas and unpublished guesstimates by experts. There is a wide discrepancy between populations regarding the intensity of monitoring: some have only been monitored two times during the period of our study, others have been monitored more regularly, and a few are monitored annually.

We used a Bayesian state space model to estimate the growth rate λ of each population (39). Theoretically, a hierarchical approach could be used to explain the growth rate of each population with hyperparameters (40, 41) describing, for example, broad geographic location (southern, East, or West Central Africa), human population density, whether the reserve is fenced, conservation efforts, or governance scores (23). What is often referred to as “borrowing strength” by modeling parameters in the data model as random variables at the group level drawn from a hyper-distribution would allow a more informative posterior parameter estimate than a separate analysis of each dataset (42–44). However this approach was ill suited for this analysis, because populations were not exchangeable since populations with small amounts of data were not random draws from the overall distribution of lambda (Fig. S1): growing populations are well-monitored, whereas declining populations are often poorly monitored. Two-thirds of the populations that are missing more than one-half of the data are declining, whereas two-thirds of the populations missing less than one-half of the data are increasing. Thus, a posthoc analysis confirmed that posterior median estimates of population growth rates were positively correlated with the number of years of data in each time series ($P < 0.05$). A hierarchical approach would, therefore, bias the posterior estimates of growth rate toward the information-rich growing populations and thus, provide spurious inferences about overall population dynamics, because the model would attempt to fit the data from the declining populations by increasing individual random effects without capturing any biological mechanisms.

Our process model assumes that true population size at time t (N_t) follows a log-normal distribution of the deterministic prediction of the median population size at time t (μ_t) with a stochastic process error on the log scale σ_{proc} . The deterministic prediction results from exponential growth with rate λ :

$$\begin{cases} \mu_t = \log(\lambda \cdot N_{t-1}) \\ N_t \sim \text{lognormal}(\mu_t, \sigma_{\text{proc}}) \end{cases}$$

We link this process model to census data with an observation model, where the count of lions at time t ($N_{\text{obs}t}$) is Poisson-distributed, with mean ψ_t , itself drawn from a Gamma-distribution with mean equal to the prediction of the process model and an SD for observation error $\sigma_{\text{Nobs}t}$. This hierarchical formulation allows the uncertainty in the data to exceed the variance of the Poisson parameter ψ_t (45):

$$\begin{cases} \alpha_t = \frac{N_t^2}{\sigma_{\text{Nobs}t}^2} \\ \beta_t = \frac{N_t}{\sigma_{\text{Nobs}t}^2} \\ \psi_t \sim \Gamma(\alpha_t, \beta_t) \\ N_{\text{obs}t} \sim \text{Poisson}(\psi_t) \end{cases}$$

For each population, we ran six Monte Carlo Markov Chains (100,000 iterations thinning by 10 after adapting and updating for 50,000 iterations) with JAGS (46) and R (47) and checked convergence (48).

Forty-seven unweighted posterior density distributions of growth rate (one per population) were summed across three sets to provide geographic conservation-relevant estimates of demographic trends. The four African regions defined by the IUCN regional lion conservation strategies (33, 34) constituted three sets after we lumped West and Central Africa because of similar genetic characteristics and conservation threats.

We estimated the projected probability of decline over T years by 33% [$p_{0.33}^T = P(\lambda^T < 0.67)$] and 50% [$p_{0.5}^T = P(\lambda^T < 0.5)$] for each population (without making inferences on true population size M , with T equal to 5, 10, 20, or 30 y). Because the IUCN Red List mandates an appraisal of species' population trends over the longer time period of three generation lengths (GLs) or 10 y (49), we also calculated $p_{0.33}^{3GL}$ and $p_{0.50}^{3GL}$, where $T = 3 \times \text{GL}$. GL = 7 is defined by $\text{GL} = R_{\text{span}} \times Z + \text{age of first reproduction}$, where age of first

reproduction is 3.5 y (50), $R_{span} = 12$ [the number of years that females are reproductive (50)], and $Z = 0.29$ [a constant calculated as the slope of the linear regression between GL and R_{span} for 221 mammalian species (51)] as recommended by the IUCN. Two populations are presented separately from any grouping: the Gir populations in India and Niassa Reserve in Mozambique, which is considered an outlier (*Discussion*).

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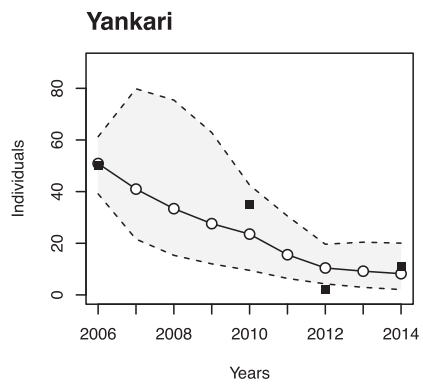


Fig. S1. West Central African populations: model fitted to time series (black squares are data, white circles are medians of the model-inferred true population sizes μ_t , and gray areas between dashes lines are 95% credible intervals).

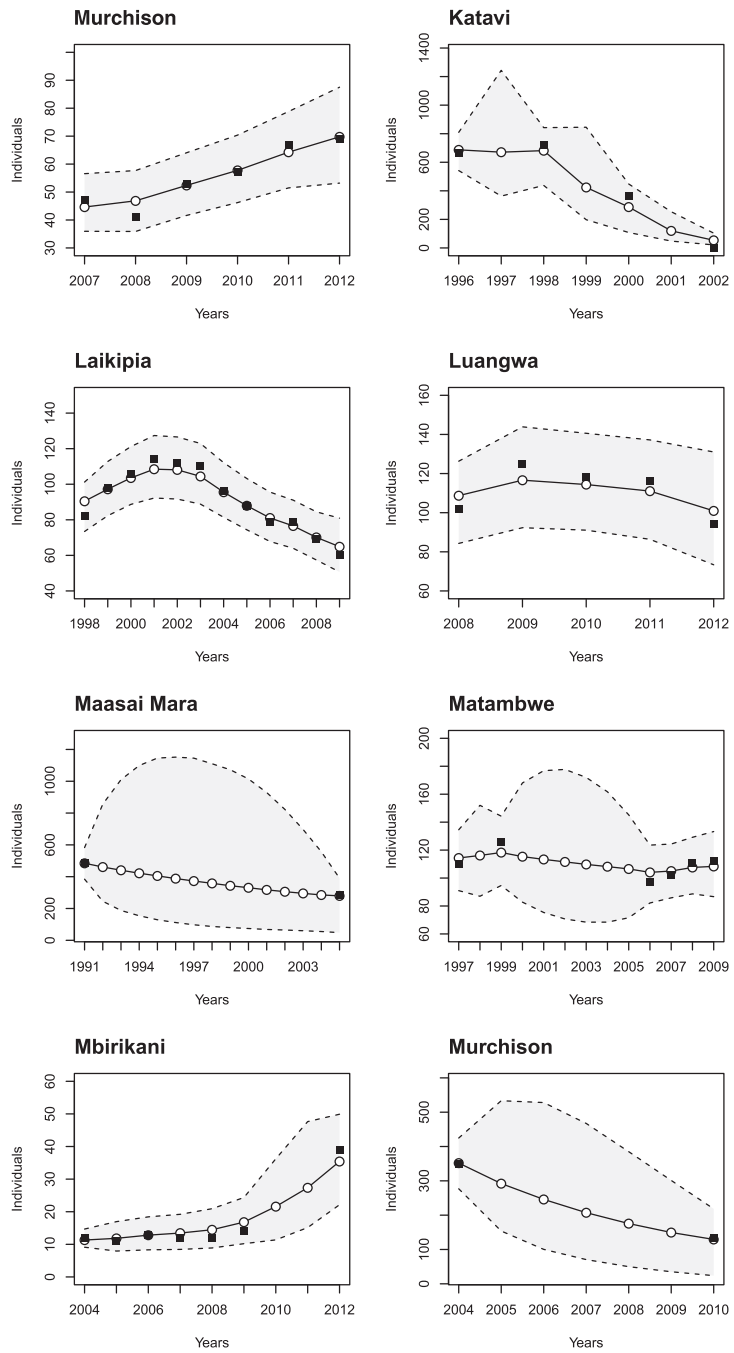


Fig. S2. (Continued)

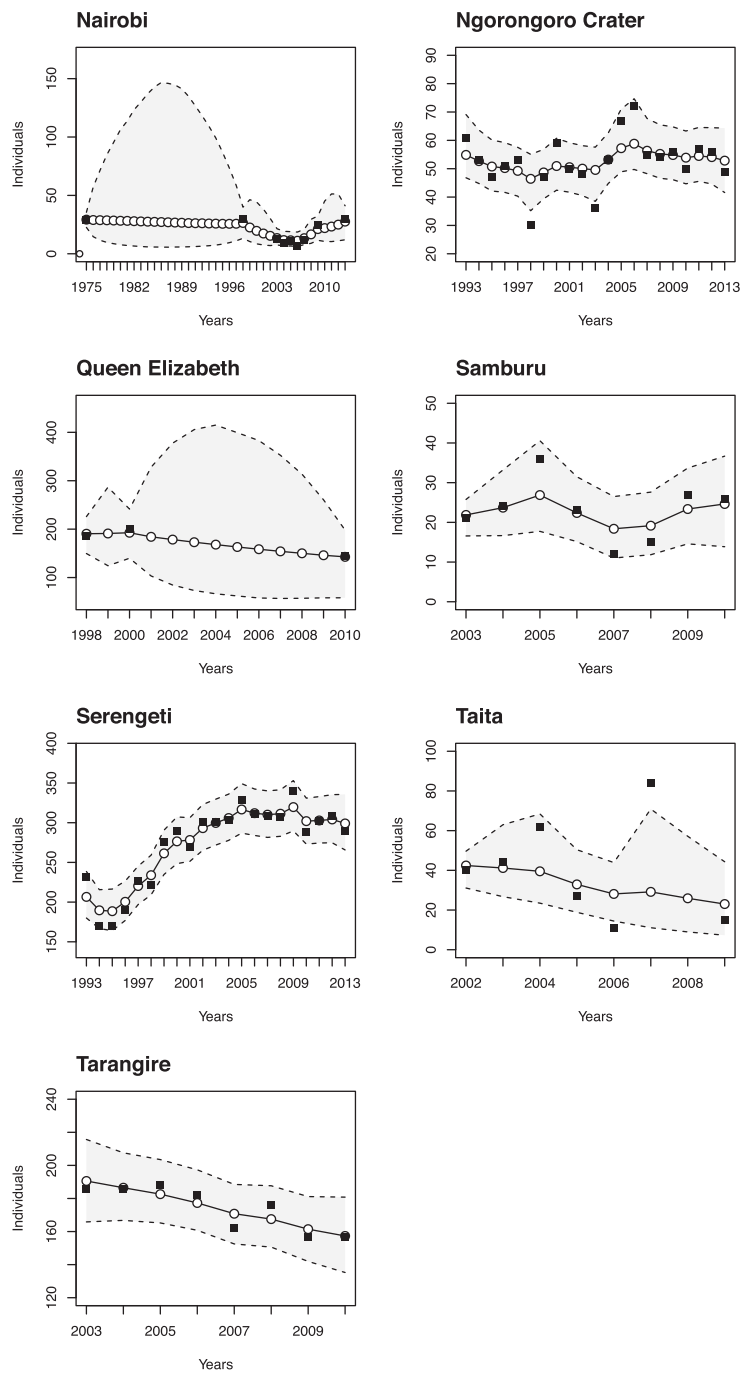


Fig. S2. East African populations: model fitted to time series (black squares are data, white circles are medians of the model-inferred true population sizes μ_t , and gray areas between dashes lines are 95% credible intervals). *Fenced populations.

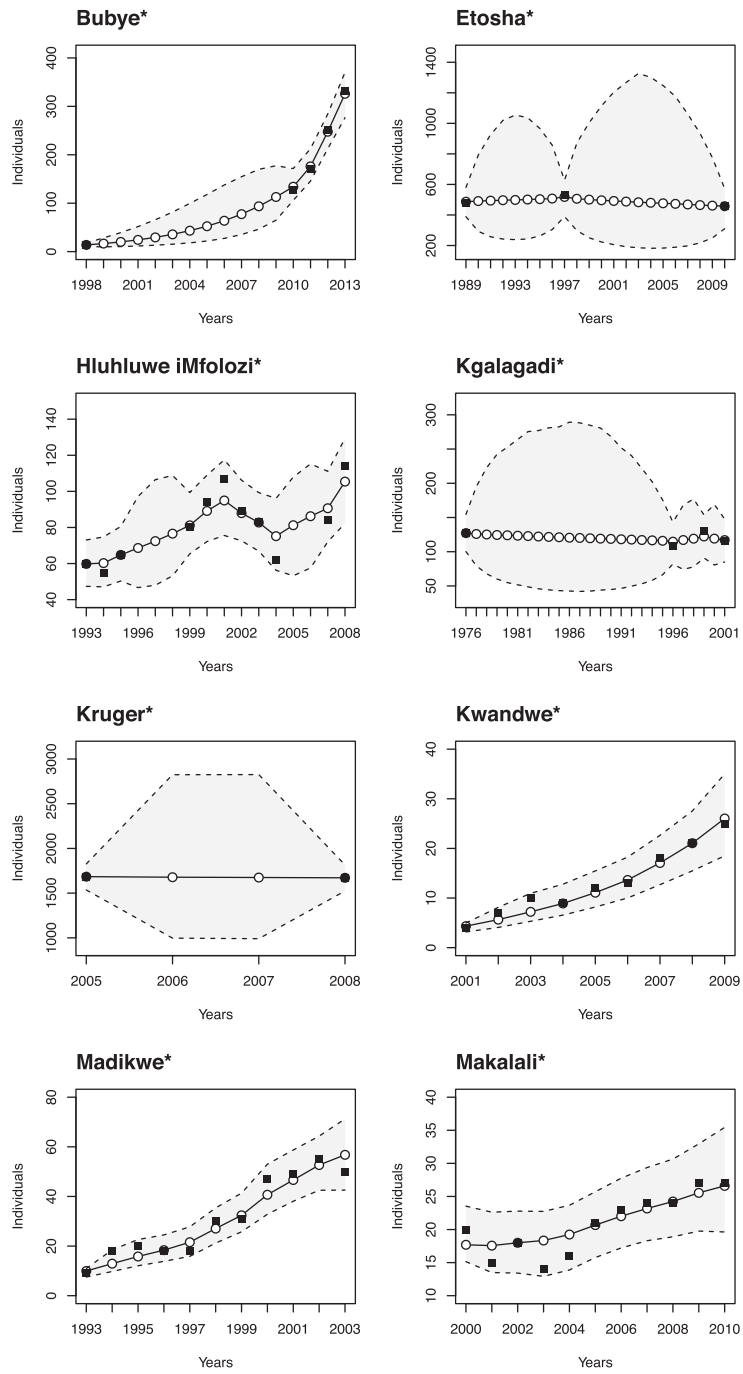


Fig. S3. (Continued)

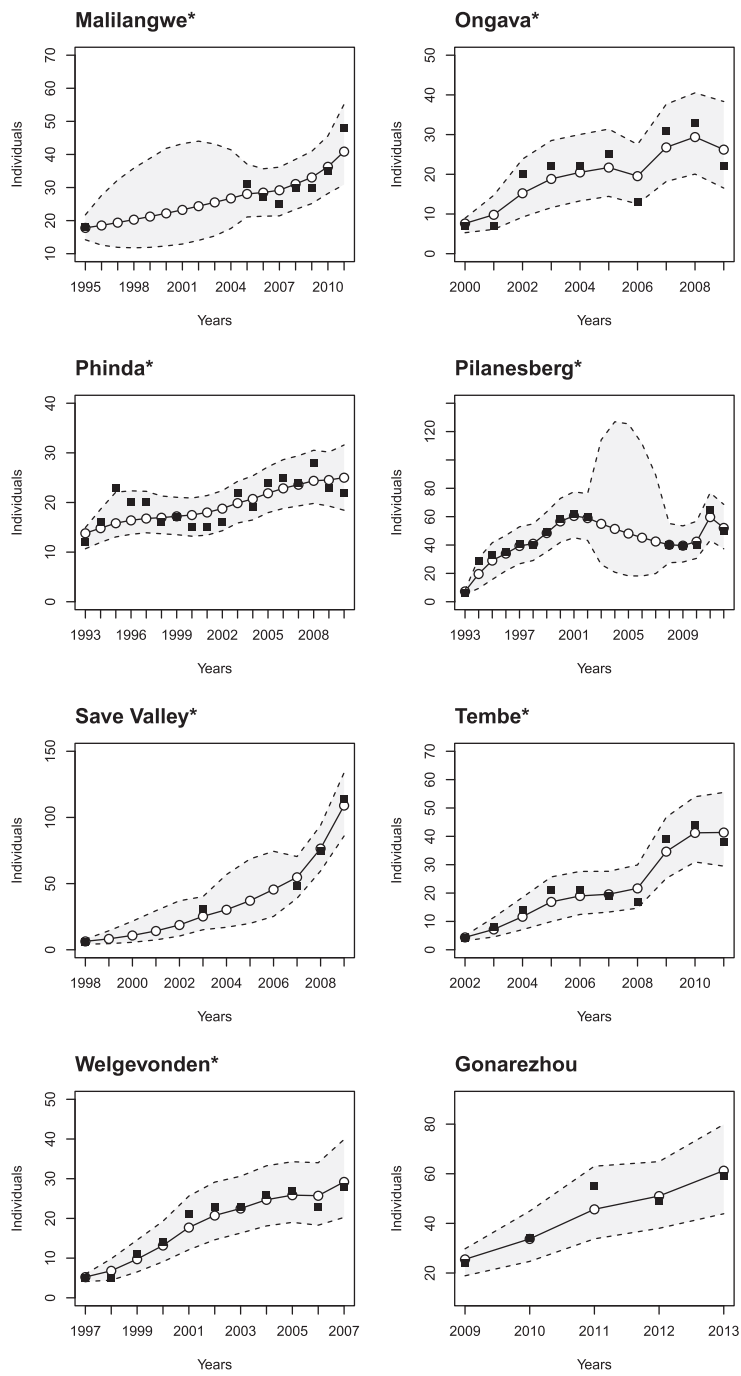


Fig. S3. (Continued)

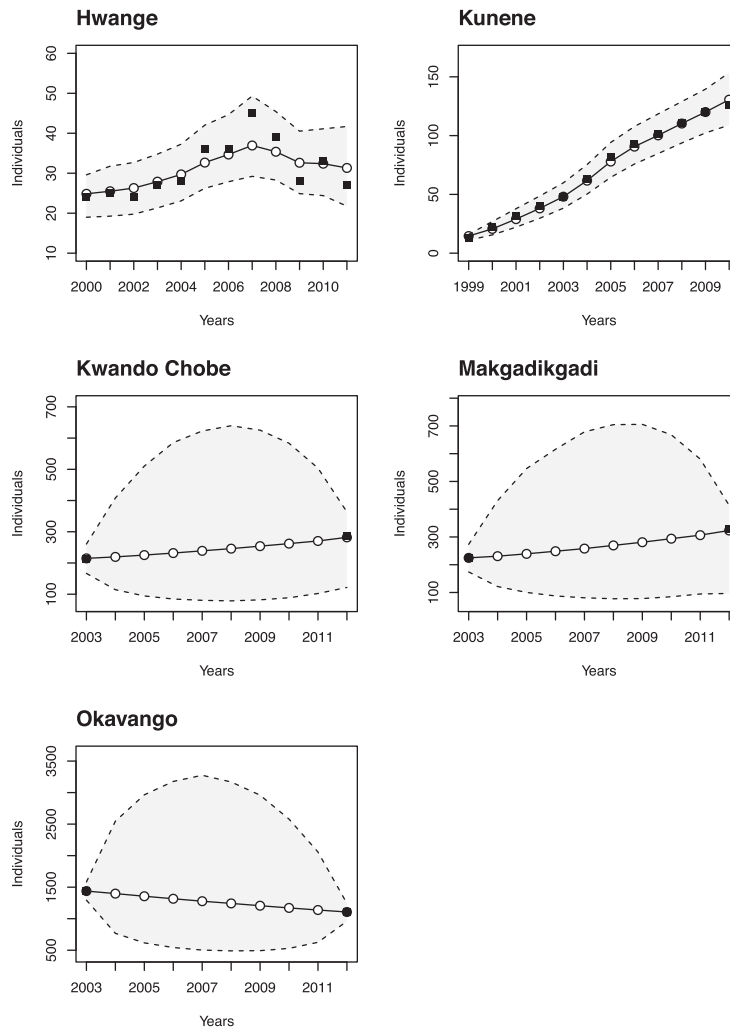


Fig. S3. Southern African populations: model fitted to time series (black squares are data, white circles are medians of the model-inferred true population sizes μ_t and gray areas between dashes lines are 95% credible intervals). *Fenced populations.

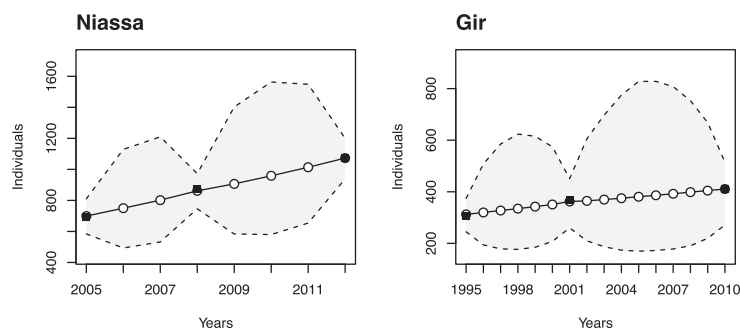


Fig. S4. Other populations: model fitted to time series (black squares are data, white circles are medians of the model-inferred true population sizes μ_t and gray areas between dashes lines are 95% credible intervals).

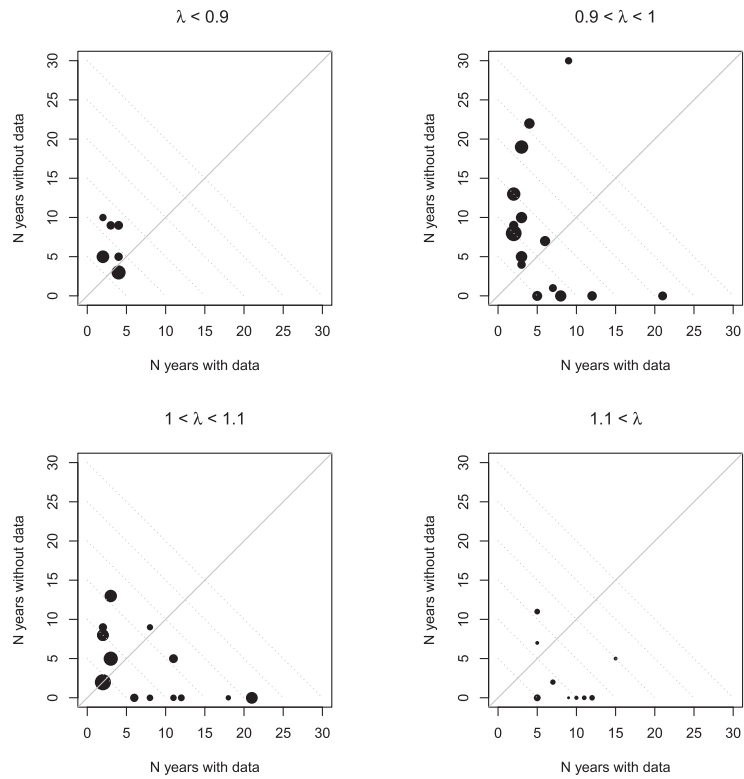


Fig. S5. Patterns of information in the time series data. Each site is represented by the number of years with and without data in its time series, and each point is scaled according to population size. Populations are grouped according to our modeled growth rate estimates. The area above the solid diagonal line indicates populations with times series that lack data for more than one-half of the years. The area below the solid diagonal lines indicates populations with data from more than one-half of the years in the time series. Dotted diagonal lines indicate the overall span of each time series. For example, a 10-y time series (including years with missing data) is indicated by the line having 10 as x and y intercepts.

Dataset S1. Monitoring data for 47 lion populations (23)

[Dataset S1](#)