

# 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- $\lambda$  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.

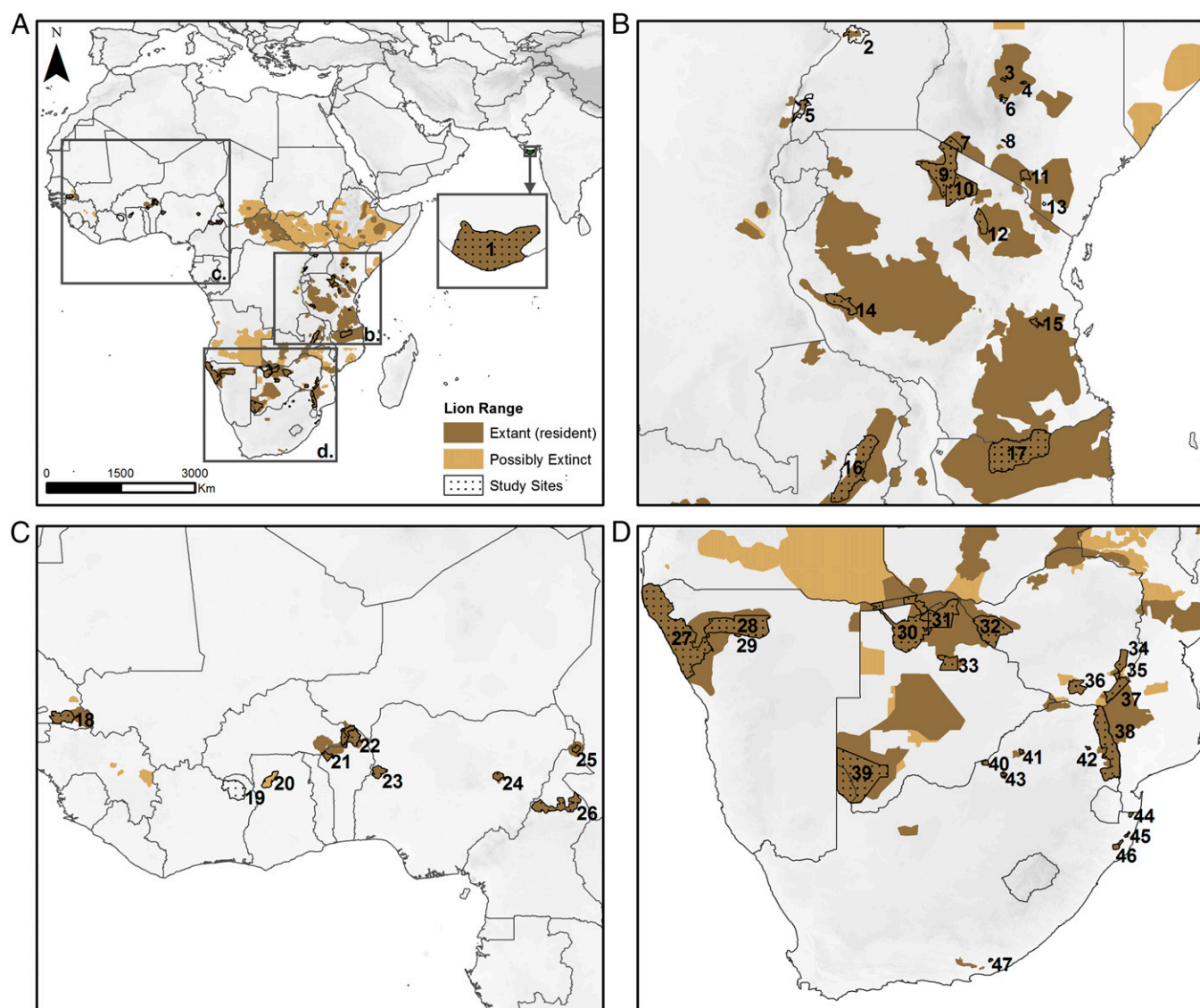
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**Fig. 1.** Distribution map of monitored lion populations; zooming levels: (A) species wide, (B) East Africa, (C) West Central Africa, (D) southern Africa. 1, Gir; 2, Murchison Falls; 3, Laikipia; 4, Samburu; 5, Queen Elizabeth National Park; 6, Ol Pejeta Conservancy; 7, Masai Mara; 8, Nairobi; 9, Serengeti; 10, Ngorongoro; 11, Mbirikani; 12, Tarangire; 13, Taita Hills; 14, Katavi; 15, Matambwe; 16, Luangwa; 17, Niassa; 18, Niokolo Koba; 19, Comoe 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, Bubye 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.

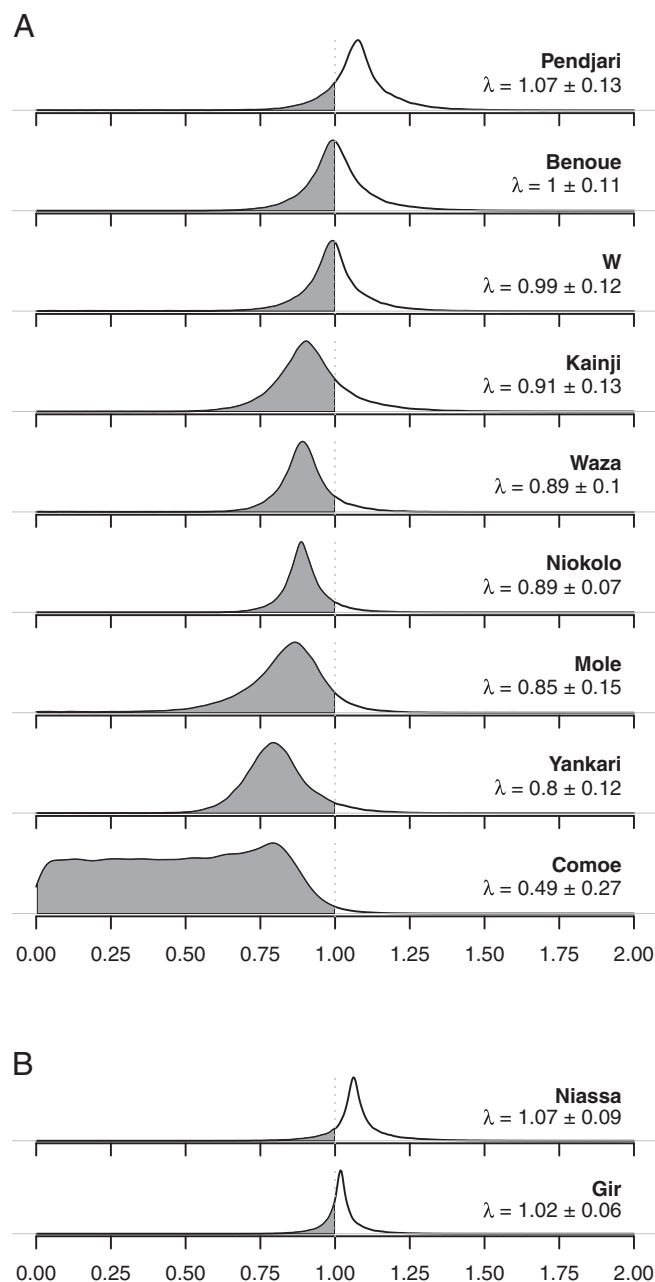
populations were increasing ( $\lambda = 1.09 \pm 0.15$ ), as the majority were in fenced reserves showing strongest increases ( $\lambda = 1.10 \pm 0.14$ ). Nationally, South Africa was the only African country with growth in every population, all of which were fenced; most were reestablished over the 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  $p_{0.5}^{20} = 0.43$ , 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  $p_{0.5}^{3LG} = 0.37$ .

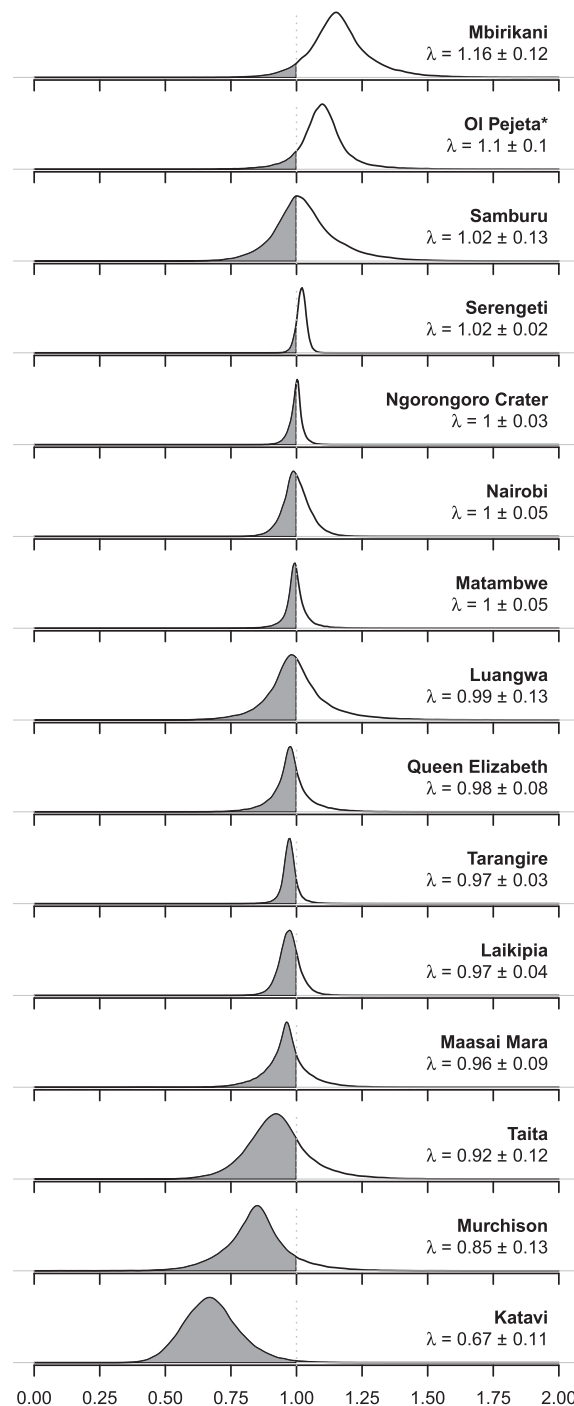
## Discussion

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.

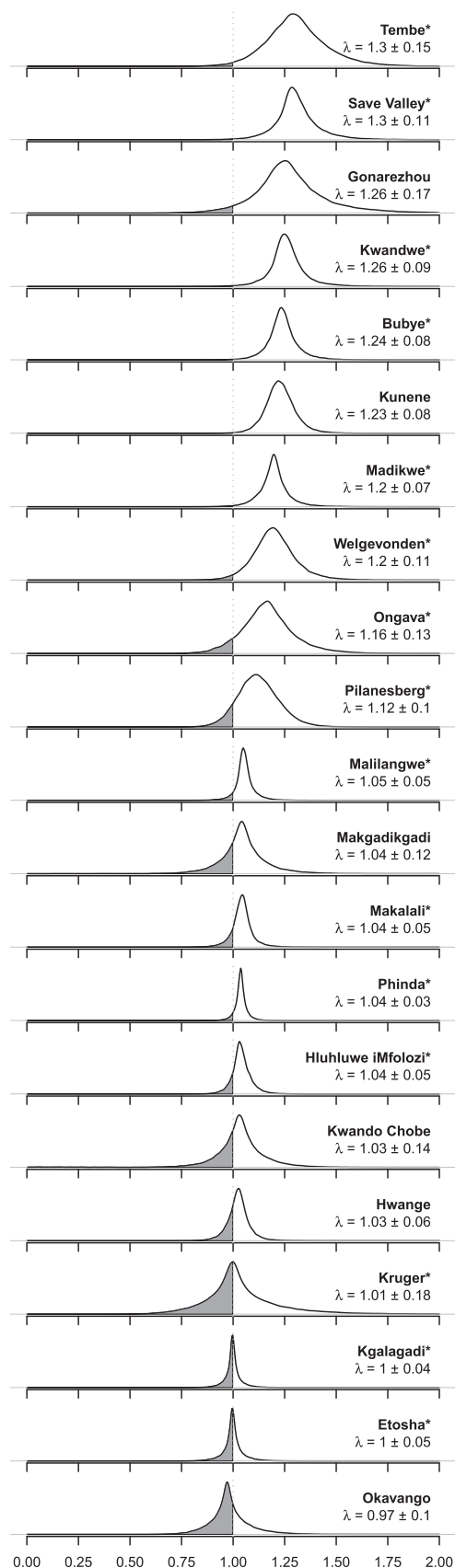
methodology varied between years, although we limited our sample to counts that were consistently based on the most reliable survey techniques, and thus, the regional-scale declines are unlikely to be an artifact of methodological shortcomings. If there is an overall bias in our results, it is probably 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.





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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