ECOLOGY

Protecting and connecting landscapes stabilizes populations of the Endangered savannah elephant

Ryan M. Huang[1]*, Celesté Maré[1], Robert A. R. Guldemond[1]*, Stuart L. Pimm[1,2], Rudi J. van Aarde[1]

The influence of protected areas on the growth of African savannah elephant populations is inadequately known. Across southern Africa, elephant numbers grew at 0.16% annually for the past quarter century. Locally, much depends on metapopulation dynamics—the size and connections of individual populations. Population numbers in large, connected, and strictly protected areas typically increased, were less variable from year to year, and suffered less from poaching. Conversely, populations in buffer areas that are less protected but still connected have more variation in growth from year to year. Buffer areas also differed more in their growth rates, likely due to more threats and dispersal opportunities in the face of such dangers. Isolated populations showed consistently high growth due to a lack of emigration. This suggests that "fortress" conservation generally maintains high growth, while anthropogenic-driven source-sink dynamics within connected conservation clusters drive stability in core areas and variability in buffers.

INTRODUCTION

African savannahs cover 13.5 million km^2, almost half of the continent, of which 10% is protected (*1*) and 2.2 million km^2 (16%) sustain globally Endangered savannah elephants (*Loxodonta africana*) (*2*). These savannahs are also home to half a billion people, leading to high levels of human-wildlife conflict. How do conservation actions mitigate these threats? One solution, conservation "fortresses," creates relatively small, isolated habitat islands that keep elephants in and humans out. This separation reduces human-wildlife conflict (*3*) but limits dispersal since fences or adjacent human-dominated landscapes prevent movement. An alternative solution found throughout southern Africa is clusters of well-protected areas [International Union for Conservation of Nature (IUCN) categories I to IV] that form a core area connected to less-protected buffer areas (often IUCN categories V and VI) that allow for human activities (*4*). This arrangement embodies UNESCO's Man and the Biosphere Programme concept of multiple land uses (*5*–*7*). Given these contrasting approaches, we ask how elephant populations respond to combinations of landscape size, connectivity, and protected status.

Conservation fortresses are not specific to elephants. Used across the globe, these protected fragments stem from a long history of Western land-use models that emphasized human-free landscapes (*8*, *9*). Such stringent protection reduces forest loss (*10*, *11*), sustains large mammals (*12*–*14*), and provides ecological services to neighboring communities (*15*). For example, separating humans from wildlife using fences reduces conflict (*16*, *17*) and prevents disease transmission from wildlife to livestock (*18*, *19*). However, such protectionism comes with both ecological and social costs.

First, when segregating people and wildlife, evictions and exclusions of local communities foster resentment and poverty, which can undermine conservation efforts (*20*–*22*). Alternatively, the inclusion of communities in conservation decision-making may promote habitat recovery and sustainable use (*23*, *24*), allow equitable distribution of economic benefits (*25*, *26*), and prevent encroachment from external groups (*27*).

Second, conservation fortresses tend to be relatively small and isolated. Metapopulation theory and island biogeography suggest that they will lose species (*28*–*31*). To achieve larger, connected, protected areas, UNESCO proposes a model where a buffer surrounds a well-protected core. This model has instances of social injustice (*8*) but aspires to promote a more sustainable coexistence of people and wildlife. The evidence of its efficacy is mixed (*32*). Designating buffer zones may ease anthropogenic pressure on high-quality core areas but at the cost of habitat degradation in the surrounding areas (*33*). Although there are several known cases where designating biosphere reserves reduces poverty while keeping biodiversity intact, these instances are few (*34*). For example, marine ecosystems show some success; no-take protected areas may sustain fish populations and allow spillover into adjacent fisheries (*35*).

Third, conservation fortresses are isolated. Notwithstanding the pros and cons of the core and buffer model, such an arrangement allows connections between populations. In contrast, fences prevent release from overcrowding (*36*, *37*), disrupt movement (*38*, *39*), and reduce genetic variability (*40*). Reestablishing connections and developing corridors mitigate these consequences (*41*, *42*) and allow for a functioning metapopulation (*43*–*45*). Corridor success is further augmented when including local people (*46*, *47*). Despite metapopulation theory's acceptance in conservation management, empirical evidence of the benefits of connectivity is limited (*41*).

Southern Africa has set aside large portions of land for wildlife protection (*48*) and thus provides a natural experiment to test variations in protected area design. Home to 70% of Africa's savannah elephants (*1*, *2*), these protected areas are a patchwork of fragments, varying in size, level of protection, and connectivity (*38*, *49*). This region can potentially restore a continuous savannah elephant metapopulation and has been studied extensively. Thus, there is abundant literature and surveys on elephant population numbers.

Here, we consider protected landscape arrangements by explaining how combinations of current designations of land use affect elephant population growth rates. We collected 713 survey estimates of elephant population sizes from 103 protected areas from Tanzania southward. We calculated population changes over 24 years (between

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[1]Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa. [2]Nicholas School of the Environment, Duke University, Durham, NC, USA.
*Corresponding author. Email: ryan@ryanmhuang.com (R.M.H.); robert.guldemond@up.ac.za (R.A.R.G.)

1995 and 2020) to identify key spatial drivers of growth. Given the ever-present threat of poaching to African elephants, we also tested how regionally high levels of poaching influence these rates.

RESULTS

In southern Africa, savannah elephants are widely but unevenly distributed across nine conservation clusters (regional groupings of mostly adjacent protected areas) (Fig. 1A) (*4*). These clusters cover an area of 525,957 km^2 and account for over 290,000 elephants across 103 protected areas.

We grouped individual protected areas into one of five categories based on average elephant population size across surveys (<1000 or >1000 individuals), IUCN classification (I to IV as core populations and V, VI, or not reported as buffers), and connectivity (Table 1). We categorize any protected area separated from all others by either human land use or fences as "insular." Most of these display the characteristics of a typical conservation fortress: small in size,

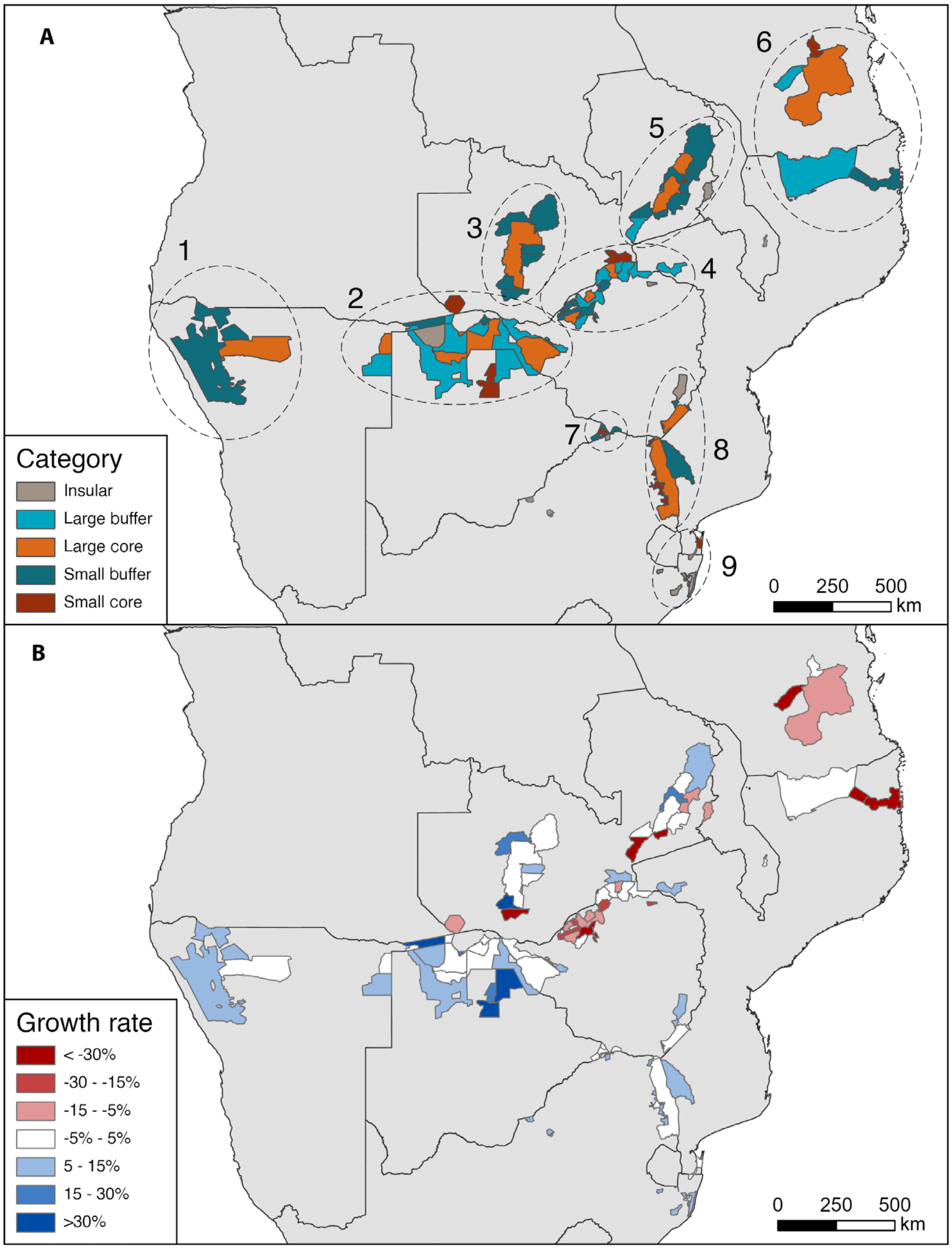

Fig. 1. Map of protected area category designations and their annual elephant population growth rates. We assigned protected areas to one of five categories (**A**) based on average elephant population size across surveys (<1000 or >1000 individuals), IUCN classification (I to IV as core populations and V, VI, or not reported as buffers), and connectivity. We calculated annual elephant population growth rates for each individual protected area from 1995-2020 (**B**). Dashed ovals identify separate clusters (numbers match those in Table 2). This map only displays boundaries for protected areas analyzed (with the exception of Addo Elephant National Park and Niassa-Selous corridor; see the Supplementary Materials). Source: World Database on Protected Areas (*81*).

Table 1. Definitions of protected area categories. We assign protected areas to one of five categories based on three criteria: level of protection (IUCN category), average population size, and connectivity. We defined connected protected areas as any that are open to the movement of individuals with an adjacent protected area. We consider all closed populations that do not exchange individuals with neighboring protected areas as insular.

Category	Protection	Size	Connectivity
Large core	IUCN I–IV	>1000	Open
Small core	IUCN I–IV	≤1000	Open
Large buffer	IUCN V, VI, NA	>1000	Open
Small buffer	IUCN V, VI, NA	≤1000	Open
Insular	IUCN I–IV*	≤1000*	Closed

*The criteria are a generalization, and there are exceptions.

protected, and isolated from the wider landscape. Last, recognizing that some regions experience higher levels of poaching than others, we categorized protected areas from the Kafue, Luangwa, Niassa, and Zambezi clusters (clusters 3 to 6 in Fig. 1A and Table 2) a priori as regions that experienced relatively higher incidences of poaching (Fig. 2) (*50*–*53*).

Half of the elephants live in core areas, with less than 5% of the region's elephants in insular areas (Table 2). While the buffer areas account for the remaining 45%, elephants have disappeared from some areas entirely (see Supplementary Text). By the most recent estimates, 10 buffer populations and 1 insular population (Mavuradonha Wilderness Area in Zimbabwe) have no remaining elephants. While most of these were small populations (<1000 individuals) that lost a few hundred elephants, the West Petauke Game Management Area in Zambia lost 2500 elephants over 13 years.

After using a density-independent diffusion approximation model (*54*) to calculate growth rates for each protected area (our analytical units), we identified several regions of concern. The Niassa cluster in Tanzania and Mozambique (cluster 6 in Fig. 1A and Table 2) has been particularly hard hit. Its overall decline was 8.6%, but some protected areas declined annually by as much as 90%. Some of these declines are significant, such as the Selous Game Reserve (a large core population in the Niassa cluster), losing nearly 1493 elephants per year for 20 years. Both the Luangwa and Zambezi clusters (clusters 4 and 5 in Fig. 1A and Table 2) also experienced declines of 6.61% and 5.03%, respectively (Table 2 and Fig. 1B), primarily due to high incidences of poaching in these regions (*50*–*52*, *55*).

Despite declines in these three regions, the other six clusters show stable or increasing elephant populations. The Chobe cluster (cluster 2 in Fig. 1A and Table 2), home to 59% of the elephants in southern Africa (Table 2), appears to be the most stable region, with a weighted average growth of 2.71%. The next most populous cluster, Limpopo (cluster 8 in Fig. 1A and Table 2), has the second-highest growth rate at 4.88%, reflecting active protection and management.

Table 2. Summary of average elephant population sizes and weighted annual growth rates by category and cluster. This table displays the sum of the average elephant population sizes for all protected areas within each category for each cluster from 1995 to 2020 (number of protected areas shown in parentheses). The five categories are based on average elephant population size across surveys (<1000 or >1000 individuals), IUCN classification (I to IV as core populations and V, VI, or not reported as buffers), and connectivity. Clusters are regional groupings of protected areas (cluster numbers match the map in Fig. 1). At the right is the weighted growth rate of the clusters based on each protected area's average proportional contribution to the overall cluster. At the bottom are the average growth rates for each category, with standard deviations in parentheses. See Supplementary Text for a detailed description of each cluster and protected area.

Cluster	Insular	Small core	Large core	Small buffer	Large buffer	Total	Weighted growth rate
1. Etosha	–	–	2,281 (1)	665 (1)	–	2,946 (2)	4.78%
2. Chobe	9,329 (1)	1,614 (3)	73,087 (5)	854 (2)	85,459 (10)	170,343 (21)	2.71%
3.* Kafue	–	–	3,011 (1)	979 (7)	–	3,990 (8)	3.83%
4.* Zambezi	45 (1)	894 (1)	8,402 (3)	2,994 (5)	17,716 (7)	30,051 (17)	−5.03%
5.* Luangwa	163 (1)	54 (1)	8,688 (2)	3,408 (6)	1,112 (1)	13,424 (11)	−6.61%
6.* Niassa	–	798 (1)	23,005 (1)	1,330 (3)	15,126 (4)	40,259 (9)	−8.60%
7. Mapungubwe	73 (1)	603 (2)	–	649 (4)	–	1,325 (7)	4.22%
8. Limpopo	1,025 (1)	2,786 (8)	19,738 (2)	1,317 (5)	–	24,866 (16)	4.88%
9. Maputo	945 (7)	215 (1)	–	–	–	1,160 (8)	5.58%
Other	1,789 (4)	–	–	–	–	1,789 (4)	–
Total (*n*)	13,368 (16)	6,963 (17)	138,212 (15)	12,197 (33)	119,413 (22)	290,153 (103)	0.16%
Average growth rate (SD)	2.92% (9.7%)	11.5% (13.2%)	0.8% (7.1%)	−6.3% (27.5%)	−4.4% (19.9%)		

*The cluster experienced higher poaching levels.

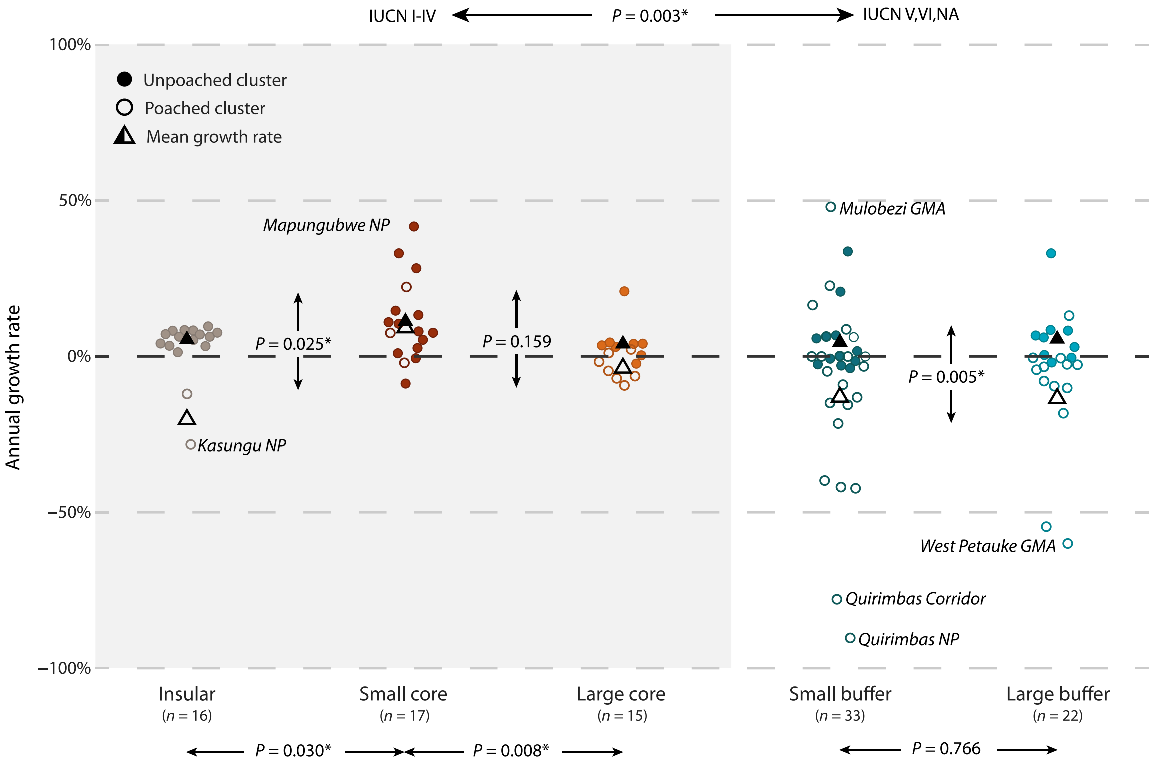

Fig. 2. Comparison of elephant growth rates by category. Dot plot showing annual growth rates for 103 protected areas categorized based on size, IUCN category, connectivity, and regional poaching levels (open versus closed icons). Triangles indicate the mean growth rate for each category. Annotated *P* values show the results from ANOVA analyses described in the main text (* indicates statistical significance). The shaded area specifies the categories under IUCN I to IV protection.

Growth rates between different categories

Level of protection

When comparing protected areas by spatial attribute categories, we find hierarchal effects of landscape arrangement on elephant populations. First, protection plays a significant role ($F_{1,101} = 9.26$, $P = 0.003$; Fig. 2). Areas with IUCN protection I to IV (core and insular areas) have a significantly higher average annual growth rate (5.99%) than buffer areas (IUCN V, VI, or not reported) that allow human activities, which declined by 5.71%. Buffers also show more variation across annual growth rates, ranging from an increase of 48% to a decline of 90%.

After accounting for protection, we subdivide the protected areas into our five categories (large and small cores, large and small buffers, and insular areas), each with high and low levels of regional poaching. Using a series of two-way analyses of variance (ANOVAs), we examine the nuanced and sometimes opposing ways size, connectivity, and poaching affect growth.

Regional poaching

Although we categorized protected areas as having high or low levels of poaching from the literature, our calculated declines generally support previous findings (Fig. 1 and Table 2) (*50*–*53*). However, these population declines are not universal but depend on the level of protection.

Among core protected areas, there is no significant difference between whether they are located in a more poached region or not ($F_{1,29} = 2.09$, $P = 0.159$; Fig. 2). In contrast, for buffer areas, there is a strongly significant difference ($F_{1,52} = 8.73$, $P = 0.005$; Fig. 2).

The most reasonable explanation for this is that stronger protection mitigates or prevents the consequences of poaching. Of concern, however, is the apparent effect of poaching in insular populations ($F_{1,30} = 5.58$, $P = 0.025$; Fig. 2), which generally experience similar protection as cores. This result stems from only two insular protected areas in the poached regions. Possible explanations include more potential points of entry or lack of refuge and escape routes for elephants (*56*, *57*).

Population size

Comparing populations based on average population size reveals another pattern. Growth in large populations (>1000 individuals) is closer to 0% and has smaller standard deviations than their smaller counterparts (Table 2). The difference is significant between core populations ($F_{1,29} = 8.05$, $P = 0.008$; Fig. 2), where small populations have a much higher average growth rate (11.5%) than their larger counterparts (0.8%). Small core growth rates are much higher than the ecological maximum of 6% for elephants by births and deaths alone (*58*). This can only be achieved through immigration. It means that small core populations must be receiving immigrants to achieve growth rates this high. However, large cores do not show the same high rates. This is likely because adding a few individuals to small populations results in larger relative changes in growth. It is more difficult for larger populations in the thousands to receive a proportionally similar number of immigrants.

The difference in growth rates between large and small buffer areas does not show the same significance ($F_{1,52} = 0.09$, $P = 0.766$), given the wide variation of growth rates among buffers. Again, given that many of these rates are above the maximum ecological rate from births alone, this variation is likely due to fluctuations in elephant numbers from immigration and emigration. Such movements are often in response to external threats such as poaching and land conversion, which are more common in buffer areas than core areas (*51*, *52*, *59*).

As expected, population size correlates with area ($r^2 = 0.413$, $P < 0.001$; Fig. 3). This suggests that area size has a similar effect on growth rates as average population size. The larger a protected area is, the more elephants it is likely to have and to sustain the population at a stable growth rate of 0%.

Connectivity

Last, given the subsuming effects of protection and size, we compare the growth rates of insular populations versus their most similar equivalents, small cores, to reveal the effect of connectivity. On average, insular populations grow at 2.92% annually, whereas similar-sized connected populations have a significantly higher growth rate (11.5%, $F_{1,30} = 5.16$, $P = 0.030$). As described previously, this high growth rate in small cores must be partly driven by dispersal, which is impossible in closed, insular protected areas. (A few insular population growth rates may also exceed the limit from births alone following the occasional translocation of individuals.) Notable is the strong consistency of growth rates among the unpoached, insular protected areas. Without the two poached, insular protected areas, the average annual growth rate of the remaining populations is 5.40%, close to the effective maximum growth rate in closed populations. This is a realistic result, given the lack of dispersal opportunities for these individuals.

Growth rate variation within individual populations

An advantage of the diffusion-approximation approach to calculating growth rates is that it allows one to measure the variability in growth between surveys. Rather than assuming that deviations from a smooth curve are measurement errors about the model fit, we can test whether connectivity affects the variability in population growth. Some of the variability may reflect counting errors, but some suggests movements of elephants in and out of the population.

An analysis of covariance (ANCOVA) of log $_{10}$(standard deviation of interannual rates within a population) against the overall growth rate and core/buffer/insular status shows a statistically significant effect ($F_{3,99} = 14.72$, $P < 0.001$; Fig. 4A). For a given population growth rate, insular populations show the most consistent year-after-year growth. For instance, Madikwe Game Reserve, an insular population in South Africa, has an overall positive annual growth rate of 7%. Its survey estimates rarely stray far from this average (Fig. 4B). Populations in these isolated fragments may only change through births, deaths, and translocations of individuals [which occurred in Madikwe (*60*) and explains a growth rate above 6%].

Conversely, buffer areas show the most variation year to year due to several possible effects. Immigration and emigration with nearby populations may cause large changes in growth rates between years, even when the overall growth rate is close to 0%, such as the case in Mahenye in Zimbabwe (Fig. 4C). In other instances, immigration may drive growth rates well above what is possible by births alone, as seen in the Malapati Safari Area of Zimbabwe, where the overall growth rate is 21% (Fig. 4D). Last, many buffer populations, like the Sichifulo Game Management area in Zambia, exhibit large interannual growth variability and declines due to the sudden loss of elephants by emigration, poaching, or both (Fig. 4E). Admittedly, sampling error may be higher for surveys in buffer areas than in insular areas that are often more actively managed. This may increase variability in the reported buffer populations. However, dispersal is a parsimonious explanation for the observed interannual variation and observed growth rates between categories.

Core populations display an intermediate amount of interannual growth rate variability. These areas are less subject to poaching and human activities than their neighboring buffers, suggesting a more consistently suitable environment for elephant populations. Unlike insular populations, cores are connected to other areas. They are subject to immigration and emigration, as evidenced by the average small core growth rate well above the maximum birth and survival rate. This connectivity can result in short-term fluctuations of population numbers.

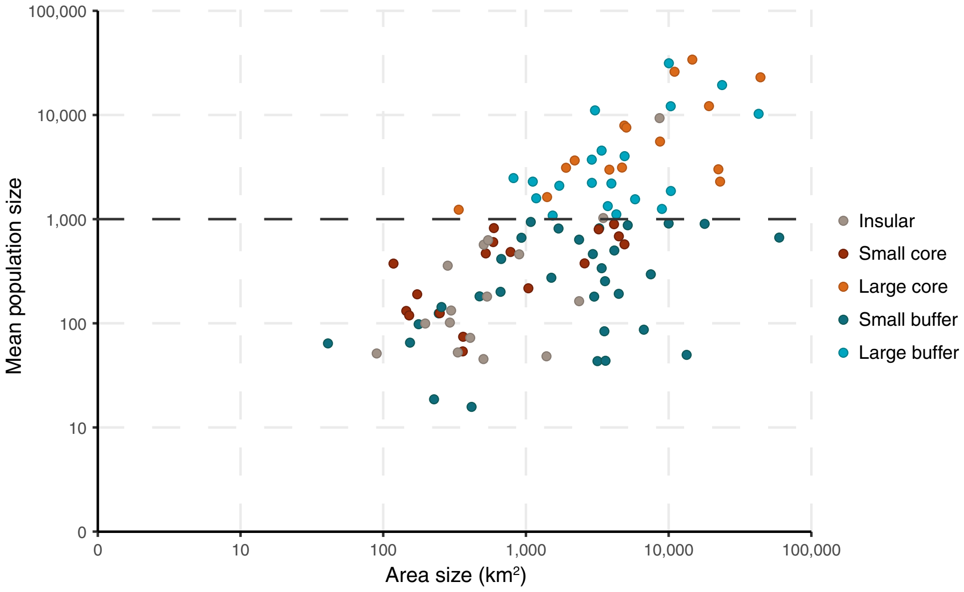

Fig. 3. Mean elephant population size against protected area size. Protected area size is strongly positively correlated with mean population size ($r^2 = 0.413$, $P < 0.001$). Dashed horizontal line indicates the threshold between small and large populations (<1000 or >1000 individuals). Both axes are plotted on a log$_{10}$ scale. Area data provided by World Database of Protected Areas (*81*).

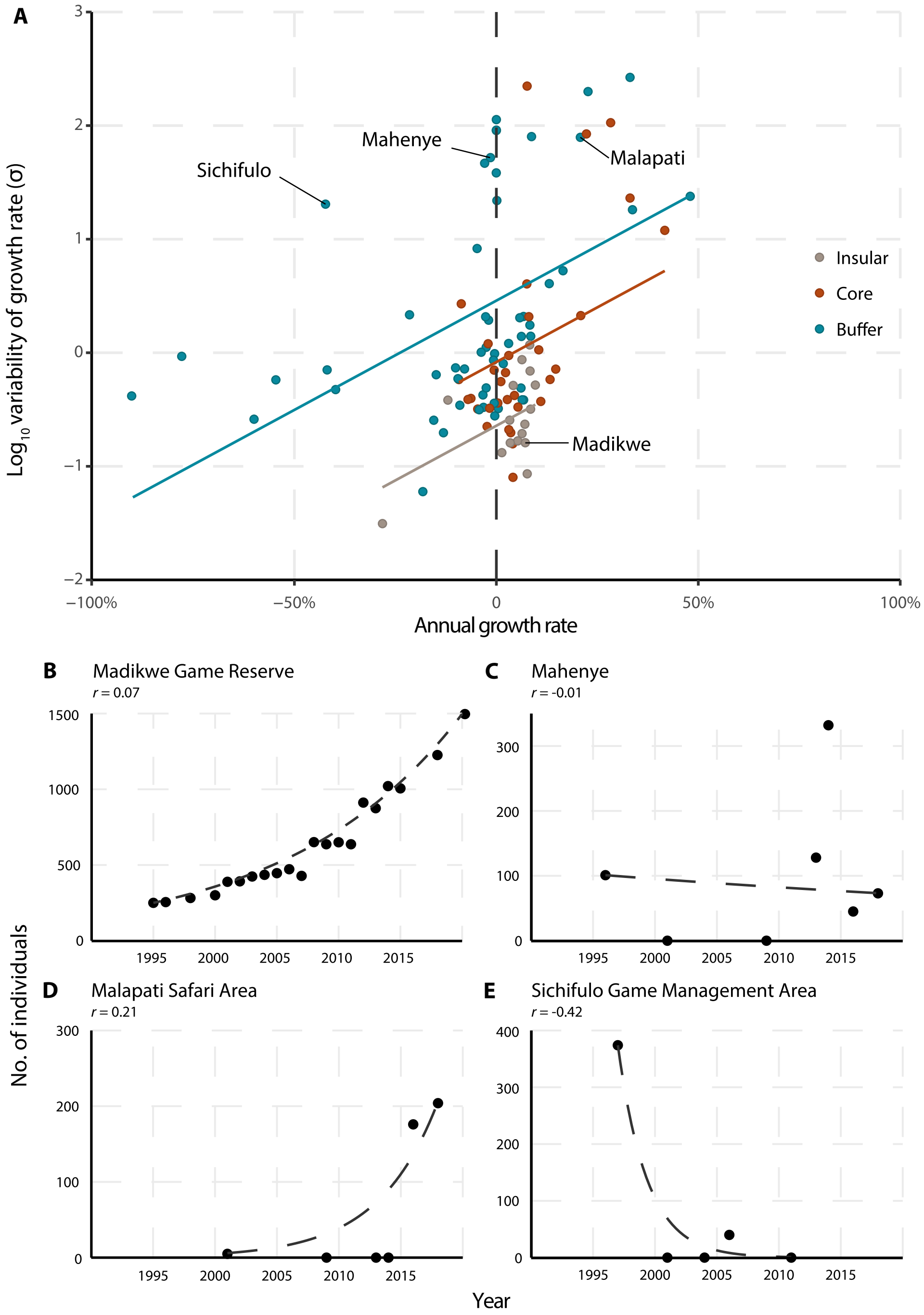

Fig. 4. Covariance analysis evaluating interannual growth rate variability among core, buffer, and insular populations. (**A**) The ANCOVA results of log $_{10}$(standard deviation of interannual rates within a population) against the population's overall growth rate and type of population ($F_{3,99} = 14.72$, $P < 0.001$). The regression lines show a population type's variability for a given growth rate. The bottom charts show the survey estimates from 1995 to 2020 for (**B**) Madikwe Game Reserve in South Africa, (**C**) Mahenye in Zimbabwe, (**D**) Malapati Safari Area in Zimbabwe, and (**E**) Sichifulo Game Management Area in Zambia. The dashed line shows the projected growth according to the population growth equation: $n(t) = y0 \times e^{rt}$.

DISCUSSION

The spatial arrangement and designation of conservation lands determine the fate of elephants and their landscapes. Elephant population growth rates across southern African protected areas follow several patterns:

1) Across sites, more strictly protected areas—i.e., IUCN I to IV—hold populations that typically grow and are much less likely to show sharp declines than populations in buffer areas—i.e., IUCN V, VI, not reported (Table 2 and Fig. 2). In regions with historically high incidences of poaching, protection appears to prevent population

declines. Protected sites also show more consistent changes in numbers from year to year than buffer areas (Fig. 4A).

2) Larger areas hold more elephants (Fig. 3). Across sites, this results in more consistent growth rates (Fig. 2), likely because they are proportionally less affected by immigration and emigration. Among small populations, the arrival or departure of a single herd of a dozen individuals will have an outsized effect on apparent annual growth rates.

3) When considering connectivity, insular populations grow quickly and consistently across sites and years (Figs. 2 and 4 and Table 2). With few exceptions, these growth rates are near the maximum possible by births and deaths alone. Alternatively, small core sites sometimes show very high growth rates (Fig. 2) and more variable increases from year to year, likely due to immigration from areas nearby since they far exceed the rate at which populations can increase otherwise. Some buffer populations show rapid increases in numbers, sometimes exceeding those in comparable cores (Fig. 2). These increases, plus the more variable year-to-year growth rates within buffer sites (Fig. 4), can also reflect movements into these populations.

In short, large, well-protected, and connected areas provide the best solution to conserving elephants and their landscapes. That said, large, strictly protected areas contain only 48% of the region's elephants.Our results have several implications for conservation.

First, across most of Africa, habitat degradation and intensive and chronic poaching for ivory threaten the persistence of many elephant populations (*53*, *61*–*64*). The Kafue, Niassa, Luangwa, and Zambezi regions have been hard hit by illegal ivory poaching, causing steep declines in numbers (Fig. 1). We recognize that chronic poaching and other illegal activities may drive the apparent patterns, induced by socioeconomic rather than ecological limitations in some buffer populations (*65*). We do not foresee a scenario where such limitations will disappear soon.

This said, across six of the nine conservation clusters analyzed, covering 320,000 km^2, elephant populations are numerically stable or increasing (*65*–*69*) (Table 2). These six clusters account for 60% of Africa's savannah elephants (*1*). While savannah elephants across the continent may be listed as Endangered given the myriad of threats they face (*70*, *71*), southern African elephants show a stable growth of 0.16% for the past quarter century. This is remarkable, given that 45% of these elephants cohabitate with humans in buffer areas.

Second, conservation activities directed at Africa's elephants should recognize the importance of space and connectivity for the long-term stability of populations (*43*).

Insular populations seem to flourish (Figs. 2 and 4). That said, they may induce undesirable elephant population growth and eventual densities that initiate management interventions—such as contraceptives or culling—and cause societal conservation conflicts (*37*, *72*). Without the ability to disperse naturally or through management interventions, unrelenting population increases may eventually lead to transient overcrowding (*36*, *37*). The damage to the habitats during such transitions may be long-lasting (*73*).

As illustrated here, clusters of connected, protected areas with various land-use options can stabilize elephant numbers. Buffers serve a useful conservation function. These areas are the first to face land cover conversion and overexploitation, but their connectivity to other buffer and core populations results in a source-sink dynamic. As elephants become threatened, they may quickly shift to a nearby buffer or core area. They may just as easily flow back when living conditions change or when high densities become problematic. Thus, connectivity drives stability in the core areas and variability in buffers, an important addition to the limited empirical support of metapopulation theory for conservation management.

Such anthropogenic-driven source-sink dynamics within clusters of conservation areas under various levels of protection may be considered the new baseline for species management. Our call for spatially connecting large, protected areas has been introduced previously. Still, we consider this evidence for managing savannah landscapes to stabilize elephant populations across large swaths of the continent to be the most comprehensive to date.

MATERIALS AND METHODS

Study area

We delineated nine clusters of protected areas spread across nine countries in southern Africa (Namibia, Angola, Botswana, South Africa, Zimbabwe, Zambia, Malawi, Mozambique, southern portion of Tanzania; Fig. 1A and Supplementary Text) (*4*, *74*). Each cluster is a regional grouping of protected areas (e.g., national park or game management area). This analysis includes four populations not associated with any cluster due to their isolation: Addo Elephant National Park, Madikwe Provincial Reserve, Pilanesberg Provincial Reserve of South Africa, and Liwonde National Park in Malawi.

Data collection and filtering

We collated population estimates and counts of elephant populations from the African Elephant Database (*75*), peer-reviewed publications, and gray literature (*65*, *69*) (see the Supplementary Materials). We only used estimates that met reliability criteria A or B of Thouless *et al.* (*1*), excluded estimates from wet season surveys, and excluded populations with fewer than three surveys or only reported zero elephants. Where discrete populations were surveyed in their entirety, estimates were retained, even if survey areas may have differed slightly. We combined survey results for some areas to match larger areas reported previously. Our assessment spanned the period from 1995 to 2020 and therefore constitutes one elephant generation [~24 years (*76*)] to reflect the recent history of populations and to exclude trends that may have been driven by large-scale culling operations and by periods of civil unrest in parts of southern Africa before 1994. We restricted our analysis to southern Africa (Tanzania southward) since this region contains the majority of savanna elephants, is well documented and surveyed, and contains a large number and variation of protected areas, which allows us to test combinations of spatial characteristics. In total, we use 713 surveys from 103 protected areas for our analysis.

Calculating and comparing growth rates

We calculated population growth rates for each protected area from the collected survey estimates using the density-independent diffusion approximation method (*54*, *77*). This method is advantageous for addressing missing survey years and temporal autocorrelation and does not assume that residuals are uncertainty in the model, but possibly true variation over the time period (*78*). This method requires first calculating the population change between each successive estimate. The growth rate is then the slope of a zero-intercept ordinary least-squares regression of the ln-transformed population change and the square root of the year interval. We calculate weighted growth rates for each cluster by first calculating the mean population size for each protected area and then a total for each cluster. The proportion each population contributes to the cluster total is the proportional weight of their growth rate to the overall cluster rate.

Assigning protected area categories

We selected four factors a priori that may drive changes in elephant growth rates: level of protection, size, connectivity, and regional poaching.

Level of protection

We categorized levels of protection as either well-protected (IUCN categories I to IV) or less-protected (IUCN V, VI, or not reported). Most southern African countries recognize the IUCN management categories (*79*). South Africa, however, defines protected areas according to the National Environmental Management (NEM) Protected Areas Act, Act no. 57 of 2003, section 9. We followed Paterson (*80*) to assign IUCN categories to the protected areas of South Africa.

Size

As a measure of size, we distinguish between large and small populations by calculating average population size across surveys (<1000 or >1000 individuals). We could not use area or density as variables as there are several protected areas that either have a high proportion of land unsuitable for use by elephants (e.g., Makgadikgadi Pans National Park) or have been depopulated by poaching or emigration (e.g., West Petauke Game Reserve). Thus, neither area nor density would accurately reflect the underlying drivers. Furthermore, average population size is a more mechanistically direct driver of the observed variation in growth rates. Nonetheless, the strong positive correlation between the $\log_{10}$ (average population size) and $\log_{10}$ (area size) suggests that average population size may function as a proxy for area. The data on area size come from shapefiles provided by the World Database of Protected Areas (*81*).

Connectivity

We consider any protected areas that are directly adjacent to another protected area and allow free movement of individuals between protected areas as connected (this includes connections to adjacent protected areas not included in this analysis due to lack of surveys). Should fences or other barriers such as human land use prevent movement to any other protected areas, we classify the protected area as insular. A unique example of this is the Seronga area of the Chobe cluster (cluster 2 in Fig. 1A), which, despite being surrounded by protected areas, does not have free movement because of fences and the Okavango delta (*36*).

Level of poaching

Last, recognizing that different regions experience varying levels of poaching, which may influence population growth, we assigned populations to higher or lower levels of historical poaching. After reviewing the literature (*50*–*53*), we expected that populations from the Kafue, Luangwa, Niassa, and Zambezi clusters (clusters 3 to 6 in Table 2 and Fig. 1) experienced higher levels of poaching.

Using these definitions, we assigned protected areas to one of five categories (Table 1): (i) large cores—large, well-protected, and connected; (ii) small cores—small, well-protected, and connected; (iii) large buffers—large, less-protected, and connected; (iv) small buffers—small, less-protected, and connected; and (v) insular—unconnected. Most insular areas we analyzed are well-protected and small (fewer than 1000 individuals on average).

Statistical analyses of growth rates

Through a series of ANOVAs run in R version 4.2.2 (*82*), we create a custom hierarchical model. At the highest level, we test the effect of protection using a one-tailed, one-way ANOVA between the well-protected areas (cores and insular protected areas together) and the less-protected buffers. Next, we subset the data into our five categories and ran two-way ANOVAs to examine the effects of poaching and size on growth rate (between large and small cores, and large and small buffers). Last, we use a two-way ANOVA to test for the role of connectivity and poaching between small cores and insular protected areas. Given their small and well-protected nature, insular areas may only be compared to small cores, which differ only in their connectivity. For our ANOVAs, we did not correct for the experiment-wise error rate since each is an independent a priori comparison.

Finally, we ran an ANCOVA evaluating the differences in the $\log_{10}$ (standard deviation of interannual growth rates for each site) between core, buffer, and insular populations while accounting for the overall growth rate. We assumed normally distributed residuals about regression lines or treatment means in our models. The outliers in buffer areas of the F-tests likely reject this assumption, but their removal would not alter the inferences we draw.

Although many of the population surveys may have sampling errors, we do not expect them to significantly alter our results. Such errors are unlikely to be unidirectional (they may either overcount or undercount) and instead simply increase variation in the data. ANOVAs account for this variation when estimating the P value. However, the same may not be true for the ANCOVA analysis given that variation is the dependent variable. One could expect insular protected areas with more management to have less sampling error than the less intensively managed buffers and thus less interannual variability. Although we recognize this possible bias, we interpret our ANCOVA results in context with the ANOVA results.

Supplementary Materials

This PDF file includes:

Supplementary Text
Figs. S1 to S14
Legends for tables S1 to S10
Tables S11 to S15
References

Other Supplementary Material for this manuscript includes the following:

Tables S1 to S10

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