

LETTER

Performance of protected areas in conserving African elephants

Roberto J. Correa¹  | Peter A. Lindsey^{2,3,4,5} | Rob Critchlow^{6,7}  |
Colin M. Beale^{6,7,8}  | Jonas Geldmann⁹  | Andrew J. Plumptre^{1,10} 

¹Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK

²Mammal Research Institute, Department of Zoology, University of Pretoria, Pretoria, South Africa

³Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa

⁴Wildlife Conservation Network, San Francisco, California, USA

⁵Environmental Future Research Institute, Griffith University, Nathan, Queensland, Australia

⁶Department of Biology, University of York, York, UK

⁷Leverhulme Centre for Anthropocene Biodiversity, University of York, York, UK

⁸York Environmental Sustainability Institute, University of York, York, United Kingdom

⁹Centre for Macroecology, Evolution, and Climate, Globe Institute, University of Copenhagen, Copenhagen, Denmark

¹⁰KBA Secretariat, % BirdLife International, Cambridge, UK

Correspondence

Andrew J. Plumptre, KBA Secretariat, c/o BirdLife International, Pembroke St, Cambridge, UK. Email: aplumptre@keybiodiversityareas.org

Funding information

U.S. Fish and Wildlife Service, Grant/Award Number: F19AC00770; The Danish Independent Research council, Grant/Award Number: 0165-00018B

Abstract

Protected areas have been gazetted to protect natural resources and biodiversity, but evaluations of effectiveness rarely include measures of species population change. We compiled annual site-level spending and elephant population data for 102 protected areas conserving either savannah (*Loxodonta africana*) or forest (*Loxodonta cyclotis*) elephants, which showed a median annual population decline of -0.78% across the protected areas. Site-level population change was strongly associated with funding and government effectiveness. Annual funding deficits occurred in 78% of the protected areas, and when comparing necessary levels of annual spend to stabilize elephant populations, we estimate a US\$1.5 billion annual funding deficit across all the protected areas. While financial investment can improve elephant conservation outcomes, there is still a need to identify where and how to best finance elephant poaching interventions, requiring a global commitment to improve the socioeconomic impacts of protected areas on local communities and reduce ivory demand.

KEYWORDS

African elephant, financing, governance, management costs, population trends, protected areas

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1 | INTRODUCTION

The establishment of protected areas has been a key response to global biodiversity declines and the associated threats. To be effective, the global protected area network must achieve two things: (i) represent the full range of biodiversity and (ii) ensure the long-term survival of species (Margules & Pressey, 2000). Several studies have developed ways to identify priority areas for expanding the protected area network (di Minin & Toivonen, 2015). In contrast, the effectiveness of protected areas in conserving the biodiversity they contain has received rather less attention.

Studies on the effectiveness of protected areas have mostly relied on metrics such as habitat conversion, or management effectiveness assessments, rather than explicitly examining how protection affects the size of species populations (Geldmann et al., 2013). Changes in the population size of species that live in a protected area are, however, a more robust metric for evaluating biodiversity conservation outcomes (Geldmann et al., 2021). Changes in population size are sensitive to long-term environmental change, can quantify biodiversity change in a variety of habitats, and are often directly linked to protected-area objectives. They are also valuable in diagnosing extinction risk (Barnes et al., 2016).

Allocating sufficient financial resources to conservation efforts is a key factor underpinning successful interventions for conserving biodiversity (Geldmann et al., 2018; Leader-Williams & Albon, 1988). Studies of population change have, however, rarely been able to account for funding levels and rather focused on the effect of anthropogenic pressures and the socioeconomic context of the region in which the protected area is situated (Barnes et al., 2016; Craigie et al., 2010; Geldmann et al., 2018; Graham et al., 2021). This can be attributed to the lack of collated, comparable data on spending on protected areas (Iacona et al., 2018).

Identifying the expenditure needed to conserve key wildlife populations is critical to help decision-makers improve the allocation of limited resources (McCarthy et al., 2012). This is perhaps most acute in Africa, where wildlife populations in protected areas have been experiencing declines (Craigie et al., 2010) due to lack of conservation spending (Balmford et al., 2003; Lindsey et al., 2018), increasing anthropogenic pressures (Geldmann et al., 2019), and both political and economic instability (Daskin & Pringle, 2018).

Here, we model how elephant population trends vary in relation to protected area expenditure while also accounting for other contextual factors. African elephants, both savannah (*Loxodonta africana*) and forest (*Loxodonta cyclotis*), while far from a catch-all for biodiversity, are

useful species for assessing funding requirements for protected areas because (i) they have the most comprehensive quantitative database on population abundance time series across multiple sites of any mammal species (Thouless et al., 2016); (ii) they occupy a vast range, with large regional differences in elephant population status (Chase et al., 2016); and (iii) they have been the focus of major conservation efforts due to their key ecological role and significant economic value (Naidoo et al., 2016). Our model estimates the levels of spend necessary to halt the decline of elephant populations within protected areas across sub-Saharan Africa. This in turn allows us to establish relative levels of spend adequacy across protected areas and identify countries where elephant conservation is most underfunded.

2 | METHODS

2.1 | Elephant population data

We first compiled a database of population abundance over time for both species of African elephants for populations in protected areas with at least two population surveys (Table S1, Figure S1). Data were predominantly obtained from the two most recent African Elephant Status Reports at the time of the data compilation in 2020 (Blanc & Barnes, 2007; Thouless et al., 2016), which are the most authoritative and up-to-date compilation of information on numbers and distribution of African elephants. For countries where estimates of elephant numbers had been amalgamated (Botswana $n = 2$, Tanzania $n = 11$), population estimates for individual sites were obtained from gray literature. Populations included where the measured abundance was predominantly within a protected area because these were sites where we were likely to obtain financial data. Annual population change was calculated as the logarithm of the latest population count divided by the population count in the first survey year, divided by the survey interval in years. To improve confidence in the model, we excluded sites with an annual rate of change $>12\%$ (eight sites). This cut-off is based on the maximum theoretical long-term growth rate for stable-aged elephant populations at around 7% per year (Calef, 1988). However, to account for observations of higher growth rates in sites with low population density or those that are recovering from poaching, the threshold was set at 12% (Foley & Faust, 2010).

2.2 | Budget data

The reality of managing protected areas is often very complex. Reflecting this, costs associated with conservation

interventions can cover a very large array of activities (Green et al., 2012). Here, we focused on annual recurrent management costs (i.e., costs associated with maintaining the protected area including [but not limited to] staff salaries, law enforcement, maintenance of infrastructure and roads, habitat management, and engagement with adjacent communities) because these are more directly related to the success or failure of conservation interventions (Geldmann et al., 2018). We compiled a database of sub-Saharan Africa protected area spending (for one or several years between 2005 and 2018) from (i) gray and published literature, (ii) Management Effectiveness and Tracking Tool (METT) assessments, and (iii) personal contacts of experts affiliated with protected areas (Lindsey et al., 2017), including contact with wildlife authorities and other stakeholders directly associated protected area management (see Table S1). Where spend data spanned multiple years, we divided the total amount by years to calculate mean annual spend. Values were converted to US dollars at the average exchange rate in the year reported (XE, 2019) and converted to US dollar equivalents in 2015 to account for inflation (US Bureau of Labor Statistics, 2023). The year 2015 was chosen to align with the date of most of the elephant population time-series data. Finally, we divided the annual spend by reported protected area size to calculate the standardized spending per unit area (km²). Further details on funding sources (Table S1) and the limitations of the budget data are provided in the Supporting Information.

2.3 | Contextual factors

For each protected area, we extracted information on additional covariates known to be associated with the rate of elephant population change (Kuiper et al., 2023). These were grouped into: (i) protected area attributes (Brashares et al., 2001), (ii) local human impacts (Hauenstein et al., 2019), (iii) socioeconomic context (Selier et al., 2016), and (iv) governance (Smith et al., 2015). Descriptions of the explanatory variables, their resolution, and sources are provided in Table S3.

2.4 | Modeling elephant population change

All analyses were carried out using R software version 4.3.1 (R Core Team, 2023). Prior to statistical analysis, the values for management spend, protected area size, surrounding human population density, and agricultural land were log-transformed; all variables were subsequently standardized by subtracting the mean and dividing by the standard deviation. We tested the correlation between each covari-

able by visual inspection of the data and by calculating Pearson's correlation coefficients (Figure S2). Explanatory variables within the same group of covariables were highly collinear (Pearson's correlation coefficient > 0.6). Therefore, we tested each explanatory variable within the same group and selected the variable with the greatest explanatory power based on Akaike information criterion (AICc) values (Dormann et al., 2012). Variables excluded from the final model included Human Development Index, political stability, and accessibility.

We assessed predictors of variation in elephant population change using a generalized linear mixed-effect model (GLMM) to account for the hierarchically nested structure of the data using the nlme package (Pinheiro et al., 2020). Country was added as a random effect, to account for country-level effects not captured by the contextual data. We assessed the global model using qq-plots and Cook's distance leverage. From this global model, an average model, ranked by AIC, was estimated using the MuMIn package (Bartón, 2023). Due to the number of variables involved relative to the number of sites with data, we did not explore interaction terms among predictors. To calculate the amount of variance explained in the averaged model, we calculated the conditional and marginal variance explained for each term from all candidate models individually, and weighted these contributions by the relative AIC of each model.

2.5 | Estimating necessary expenditure

We used the averaged model to estimate the necessary annual spend per km² to stabilize elephant populations (i.e., annual rate of population change = 0) in protected areas, while holding all other variables static. For each protected area, we multiplied the predicted necessary annual spend per km² by the size of the protected area to estimate the necessary total annual spend to stabilize the elephant population in that protected area. Although larger protected areas may benefit from economies of scale, almost 80% of modeled sites had an area of < 10,000 km² with an average size of 6600 km² (Figure S3), suggesting that any potential overestimations of necessary expenditure (relative to average sized protected areas) might only occur for a small proportion of sites.

3 | RESULTS

3.1 | Overall population trends

Across all 102 sites, the annual change in population size was, on average, negative (mean -3.71%, median -0.78%), there was a median interval of 9 years between

TABLE 1 Estimated regression parameters, standard errors, and *P*-values for the average model (values are standardized). Percentage of variance explained for each term is the mean variance explained across each model used in the averaged model weighted by the model Akaike information criterion (AIC).

Terms	Estimate	Std. error	<i>P</i> -value	% variance
Intercept	-5.45	1.62	<0.01	
Spend (US\$ km ⁻² yr ⁻¹) ^a	5.19	1.40	<0.001	12.84
Protected area size (km ²) ^a	-0.40	1.48	0.79	0.15
Human population density (people per km ⁻²) ^a	0.40	1.37	0.77	0.25
Per capita GDP (2015 US\$) ^a	-1.37	1.88	0.47	0.35
Government effectiveness	4.38	1.75	<0.05	12.48
Agricultural land use	-1.62	1.41	0.26	1.06
Random effect (County)				20.23

^aNatural logarithm-transformed (ln [x+1]).

the population censuses (Figure S4). Mean annual elephant population trends were less negative across southern Africa (-0.58%) and eastern (-4.95%) than in Central Africa (-10.77%), the mean trend across West African sites was positive (3.32%). In contrast, median rates of change were positive in Eastern (0.41%), Southern (1.41%), and Western Africa (3.3%), compared to Central sites (-6.95%).

3.2 | Model results

The total overlap between population times series and protected area budget consisted of 80 protected areas across 25 countries, representing > 40% of the combined forest and savanna elephant populations. We used repeated population surveys to estimate annual change in elephant population size across these 80 protected areas. The full model included protected area size, annual spend per unit area, government effectiveness, human population density, and per capita GDP and explained 52% of the variation in annual population change (Figure 1). For the average model, we found a strong positive relationship between elephant population growth rate and conservation spend with an additional but smaller positive effect of government effectiveness (Table 1). Most of the variance explained by the model came from country effects (21.3%), followed by spend (12.8%) and government effectiveness (12.5%; Table 1). Protected area size, human population density, agricultural land use, and per capita GDP did not explain any significant variation in elephant population growth.

Our model estimated, across all sites, a median necessary spend per unit area of US\$1034 km⁻² yr⁻¹ to stabilize elephant populations (i.e., annual rate of change = 0%). There was considerable variation across protected areas, ranging between US\$67 km⁻² yr⁻¹ and US\$1242 km⁻² yr⁻¹ (Figure 2b, Table 2). Botswana, Ethiopia, and Namibia

had the lowest estimated necessary spend to stabilize elephants with a median < US\$200 km⁻² yr⁻¹. In contrast the Central African Republic, Democratic Republic of the Congo (COD), Nigeria, and South Sudan had the highest estimated necessary spend with a median of > US\$15,000 km⁻² yr⁻¹. Although conservation projects can incur considerable costs, we capped the maximum necessary spend at US\$10,000 km⁻² yr⁻¹ to align our maximum necessary spend levels closer to previous estimates (Balmford et al., 2003; Lindsey et al., 2018; McCarthy et al., 2012). By taking the estimated necessary annual spend per km² and multiplying it by the size of the protected area, we predict that the 80 assessed protected areas would require US\$1.75 billion annually to stabilize their elephant populations.

3.3 | Protected area spend

Our sampled protected areas receive a minimum of US\$226 million (Table 2). Annual spend per unit area varied widely between sites, ranging from US\$20 to US\$17,423 km⁻² yr⁻¹, with a median annual spend of US\$254 km⁻² yr⁻¹ (Figure 2a, Table 2). At a national level, protected areas in Kenya, Rwanda, South Africa, and Eswatini received high median spends of > US\$2000 km⁻² yr⁻¹, while countries with the lowest mean spending included Angola and Botswana (< US\$50 km⁻² yr⁻¹). Several countries, for example, Mozambique and Tanzania, were characterized by widely varying levels of annual spend per unit area between sites (Figure 2, Table 2).

In comparing current levels of spend with estimated necessary spend, we predicted a total annual deficit of US\$1.5 billion (Table 2). Funding deficits occurred in 78% of the protected areas assessed (Figure 2c). Of the 25 countries assessed, 20 (80%) had at least one protected area experiencing a spend deficit. All protected areas assessed

TABLE 2 Current and estimated necessary spend required to stabilize elephant populations across protected areas (PA) by region.

Region	Country	PA (no.)	Total area of PAs sampled (km ²)	Median spend (US\$ km ⁻² yr ⁻¹)			Total spend (US\$ million)		
				Current	Necessary	Deficit	Current	Necessary	Deficit
Central	Cameroon	7	15,404	162	1587	-1181	4.782	23.261	-18.478
Central	CAF ^a	3	31,242	27	84,788	-84,761	2.802	312.42	-309.618
Central	Chad	1	3000	753	3899	-3146	2.258	11.698	-9.439
Central	COD ^a	5	46,700	90	54,451	-54,377	7.423	467	-459.577
Central	Gabon	2	8732	256	1110	-854	1.306	12.547	-11.241
Central	COG ^a	3	22,743	251	935	-802	5.678	22.195	-16.517
East	Ethiopia	3	15,287	61	124	-45	1.013	2.419	-1.406
East	Kenya	5	23,584	1959	1275	NA	41.743	48.024	-6.281
East	Rwanda	1	1122	2206	489	NA	2.475	0.549	NA
East	South Sudan ^a	1	540	1827	15,208	-13,381	0.986	5.4	-4.414
East	Tanzania	8	127,120	208	3615	-3427	33.73	606.444	-572.715
East	Uganda	4	8055	378	374	NA	3.05	3.012	NA
South	Angola	1	22,610	30	1050	-1,020	0.686	23.739	-23.053
South	Botswana	1	10,600	21	113	-93	0.221	1.202	-0.981
South	Malawi	3	3845	332	673	-174	2.071	2.557	-0.486
South	Mozambique	4	59,686	155	726	-571	9.638	51.17	-41.532
South	Namibia	2	26,783	425	105	NA	7.083	3.543	NA
South	South Africa	5	22,253	3445	203	NA	76.767	14.206	NA
South	Zambia	5	44,349	161	669	-512	7.071	36.36	-29.289
South	Zimbabwe	8	29,715	217	2253	-1812	10.19	72.82	-62.63
South	eSwatini	2	379	5064	1011	NA	1.906	0.381	NA
West	Benin	1	2755	829	775	NA	2.284	2.134	NA
West	Burkina Faso	2	3110	228	218	NA	0.656	0.755	-0.099
West	Liberia	2	2782	62	766	-703	0.209	2.106	-1.897
West	Nigeria ^a	1	2254	155	17,052	-16,897	0.349	22.54	-22.191
	All countries	80	534,650	19,302	193,469	-183,756	226.377	1748.48	-1591.84

^aCountries whose estimated necessary annual spend per unit area to stabilize elephant populations was capped at US\$10,000 km⁻² yr⁻¹ when calculating total spend (US\$ million).

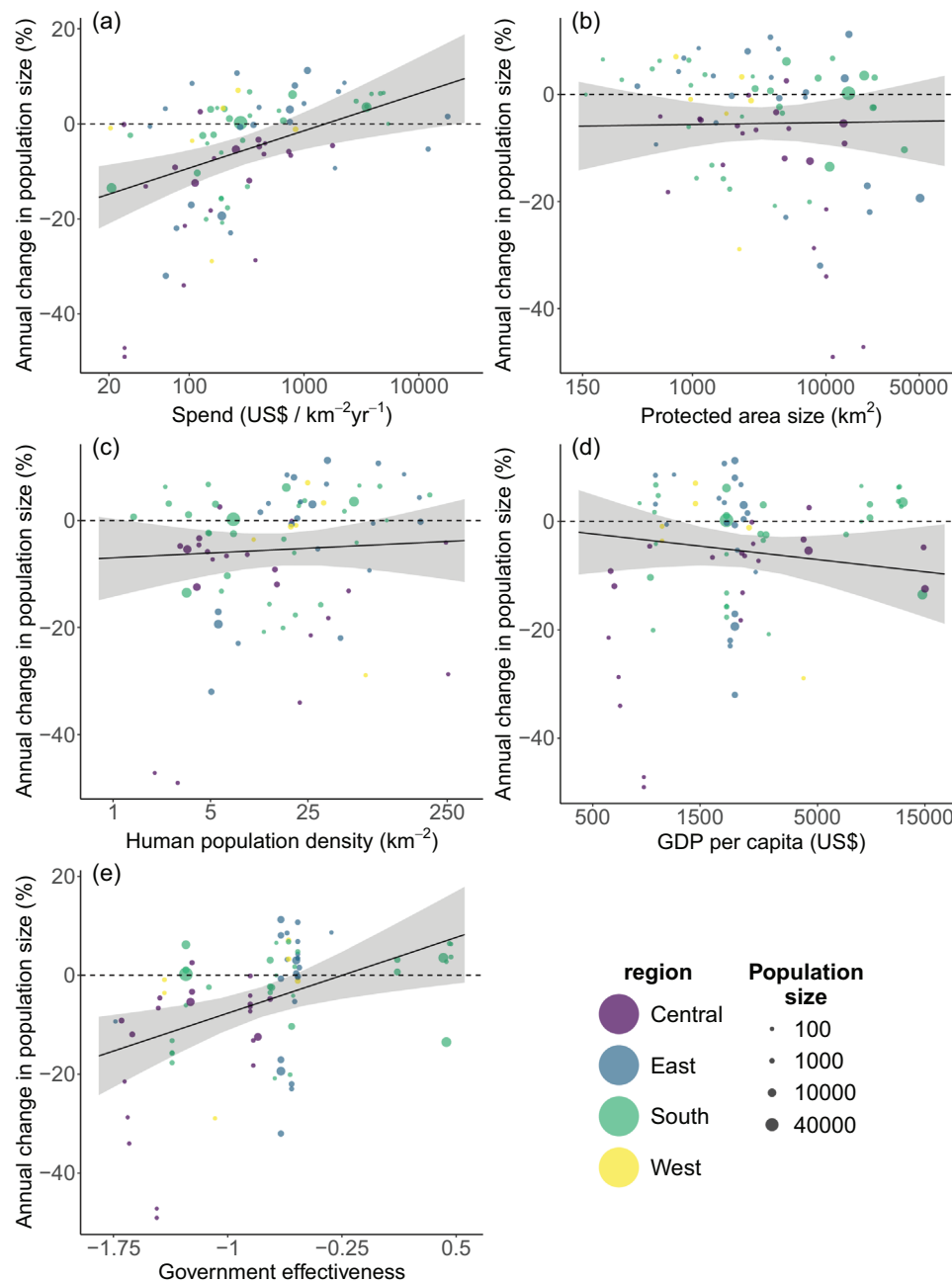


FIGURE 1 Partial-effects plots showing fitted relationships between annual change in population size and (a) annual spend per unit area, (b) protected area size, (c) human population density, (d) per capita GDP, and (e) government effectiveness. Gray ribbon indicates 95% credibility intervals. Population size indicates the most recent census estimate of elephant numbers within protected areas. Assigned region is shown in Figure S1.

in central Africa experienced spend deficits. In western Africa, most protected areas for which we had data were sufficiently funded or had relatively small spend deficits. Protected areas in eastern and southern Africa were characterized by a mixture of sufficiently well-financed protected areas in Kenya, Uganda, Namibia, and South Africa, while countries with the largest protected areas, such as Mozambique, Tanzania, Zambia, and Zimbabwe had large spend deficits.

4 | DISCUSSION

Our results show that investing in protected area management can make a difference, with higher annual funding per km² on the management of protected areas associated with relatively better status of elephant population change. However, there are major deficits in spending on management in protected areas harboring elephants, and that funding must be increased by more than

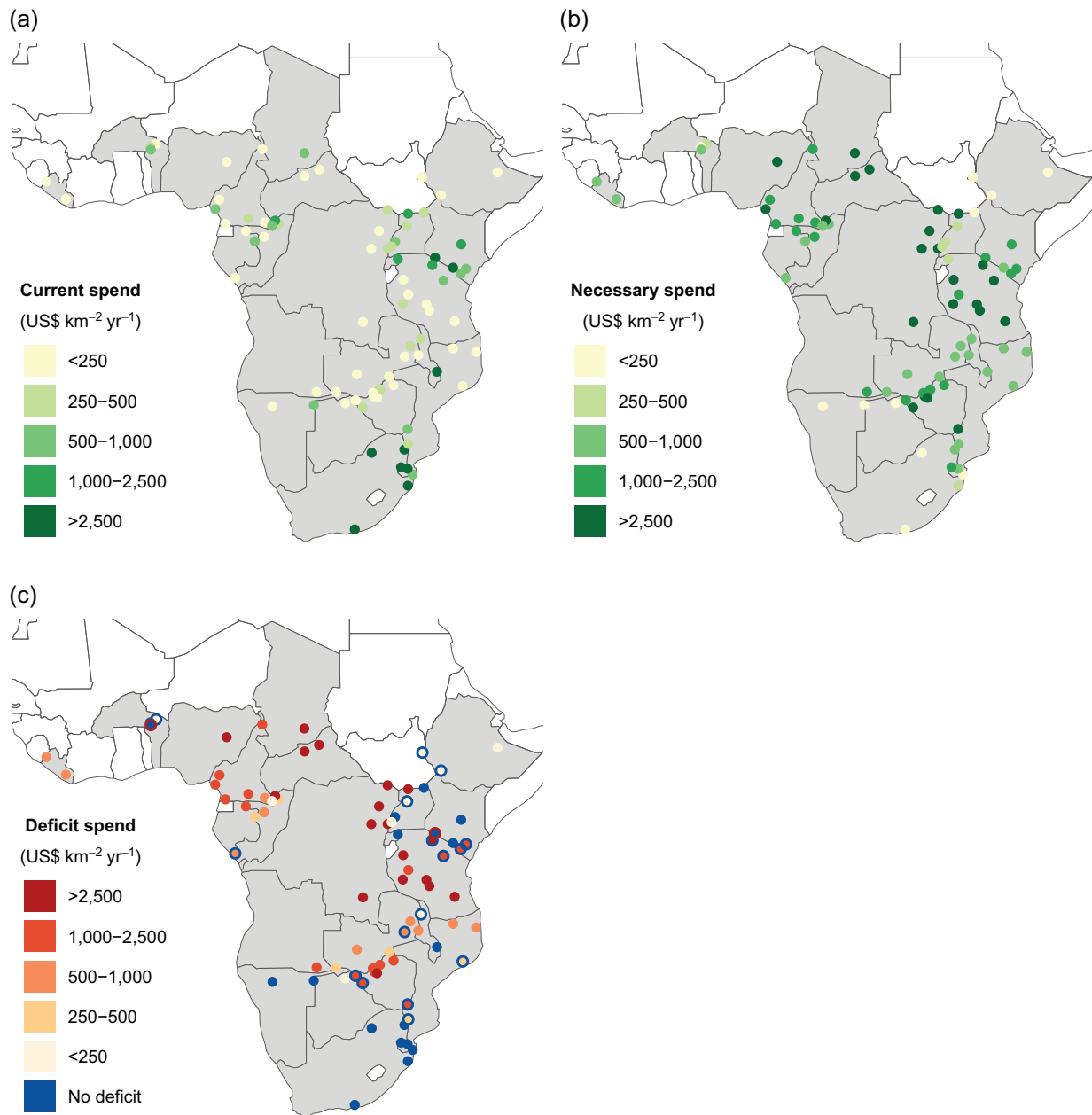


FIGURE 2 (a) Current annual spend, (b) estimated necessary annual spend to stabilize elephant populations (i.e., annual rate of change = 0%), (c) annual spend deficit. Blue outline indicates protected areas the model is estimated to require additional funding in order to stabilize their elephant populations, however based on actual census data, elephant populations in these protected areas were stable or increasing (Table S1). Red outline indicates protected areas the model is estimated to be sufficiently financed, however, based on actual census data, elephant populations in these protected areas were decreasing (Table S1). Gray indicates countries included in the analysis.

sevenfold from the current annual spend of US\$226 million to an estimated US\$1.75 billion yr^{-1} across the 80 sites to stabilize elephant populations. In addition, our study shows that existing funding is highly skewed, with only a minority of protected areas, predominantly in eastern and southern Africa, funded above the estimated required levels. The high levels of investments in eastern and southern Africa may reflect the likelihood that they can more easily benefit economically from conservation outcomes,

particularly in the form of tourism (Naidoo et al., 2016), thereby attracting greater financial support (Hickey & Pimm, 2011).

The median estimate of US\$1034 $\text{km}^{-2} \text{yr}^{-1}$ required to stabilize elephant populations is on the higher side of predictions made in previous studies looking at the costs of effective conservation in Africa (Table 3). Combined with the sevenfold financial shortfall in funding to protected areas, this does pose a very real challenge to elephant

TABLE 3 Comparison of estimated levels of spend (adjusted for inflation to 2015 US\$) required for the effective management of protected areas across Africa.

Study	Spend (US\$km ⁻² yr ⁻¹)	Year	Measure	Scope
Leader-Williams and Albon (1988)	657	1980	Achieve zero decline of elephants	Nine sub-Saharan African countries
Blom (2004)	283	2001	Effectively manage protected areas	Niger Delta and Congo Basin Forest region
Green et al. (2012)	918	2009	Achieve protected area objectives	29 protected area groups in the Eastern Arc Mountains of Tanzania
Packer et al. (2013)	>500	2010	Maintaining lions at 80% of potential density in fenced reserves	42 protected areas across 11 sub-Saharan countries
	>2000	2010	Maintaining lions at 80% of potential density in unfenced reserves	42 protected areas across 11 sub-Saharan countries
Lindsey et al. (2018)	1271	2015	Maintaining lions at ≥50% carrying capacity	115 protected areas across 23 sub-Saharan countries
	978	2015	Maintaining lions	Nine protected areas managed by African Parks network
This study	1034	2015	Achieve zero decline of elephants at all sites	80 protected areas across 25 sub-Saharan countries

conservation. We can see several reasons why managing elephants might be more expensive than previously estimated. First, elephant conservation requires considerable outlays due to the illegal wildlife trade (Leader-Williams & Albon, 1988) and most of our population trends were measured during an upsurge in elephant poaching between 2009 and 2011 (Hauenstein et al., 2019). Since management expenditure can be expected to scale with the degree of threat, the largest deficits occurred in countries that experienced high levels of poaching at the time of this study. Annual costs may decline if there is a reduction in poaching, as has been observed recently (Hauenstein et al., 2019).

Underresourcing of protected area management is the primary reason for poor performance in protected area effectiveness (Geldmann et al., 2018; Graham et al., 2021; Lindsey et al., 2017). However, increased investment is unlikely to succeed without action that tackles weak national governance (Hauenstein et al., 2019). Our model showed that indicators of better governance at a national level correlated positively with elephant population trends, supporting the finding elsewhere that weak governance can hamper conservation efforts (Eklund & Cabeza, 2017). The establishment of collaborative management partnerships between wildlife authorities and nonprofit organizations has the potential to develop successful conservation projects in countries with weak governance, particularly if they can link conservation outcomes with improved local governance and poverty alleviation (Baghai et al., 2018). More research is required to address the complex linkages

between national and local governance and conservation outcomes, as well as the socioeconomic dimensions associated with the establishment and maintenance of successful protected areas. For example, the high prevalence of armed conflict in and around protected areas and the resulting weakening of local institutions and disruption of livelihoods may explain why certain countries required an order of magnitude higher levels of spending (Daskin & Pringle, 2018).

Factors thought to be important determinants of elephant population trends, namely, protected area size, human population density, and gross domestic product, had less explanatory power in our models. We do not interpret this to mean these variables are unimportant since previous studies looking into factors that influence population trends found them to be significant (Barnes et al., 2016; Geldmann et al., 2018; Selier et al., 2016). Instead, the relative importance of these variables is likely reduced with the inclusion of site-level funding (Waldron et al., 2013). There are several ecological, socioeconomic factors that may also explain the lack of significant associations between elephant population changes and these variables. First, larger protected areas may benefit from economies of scale; our estimates of deficits for countries with exceptionally large protected areas may be overestimated relative to those with smaller average protected area sizes (Armsworth et al., 2011). However, annual population changes were greater and often negative in larger protected areas (Figure 1b), potentially suggesting that larger protected areas are also underfunded (Craigie & Pressey, 2022). Second, funding

for protected areas is likely to be higher where human population density is high and threats are greater as a result (Geldmann et al., 2019). Finally, while countries with greater gross domestic product invest more money in conservation (Balmford et al., 2003; Waldron et al., 2018), poorer countries in sub-Saharan Africa receive substantial financial support from nongovernmental organizations (NGOs) and donors (Brockington & Scholfield, 2010; Hickey & Pimm, 2011).

Overall, our study highlights an important policy implication, which is the need to better understand if, how, and when conservation spending improves protected area performance, especially given that elephant populations can benefit from the presence of buffer areas and connectedness, as well as strict protection when populations are isolated (Huang et al., 2024). Furthermore, although we defined successful conservation performance as stabilizing of a site-level population, there are alternative definitions, such as maintaining species range by concentrating on smaller sites or increasing site-level populations. Alternative measures of conservation success will likely impact levels of required conservation finance. There are also several data limitations that need to be addressed if the funding–management relationship is to be fully measured in the future. First, the lack of uniformly applied guidelines for the collection and reporting of financial costs of protected area management (e.g., what costs are associated with law enforcement, community engagement, habitat management) restricts the ability of conservation practitioners to discern which actions are most beneficial and the context in which they are best applied (Iacona et al., 2018). Protected area budget information is notorious difficulty to obtain, collate, and attribute to management costs. This is due to the diversity of funding sources (e.g., governments, NGOs, multilateral agencies), their levels of reporting, and the temporal variation in funding allocation. For example, some government wildlife authorities were unwilling to share data or were only able to provide a breakdown of their total budget that is shared among multiple sites, and the NGO contributions may not be an exhaustive list. Consequently, although our finance data are in the right order of magnitude (Lindsey et al., 2018) and overlap temporally with the elephant population census data, the total budgets available for protected area management may be underestimated. Further details are provided in the Supporting Information. Second, despite being the most comprehensive database on the status of any single species of mammal in the wild, population data within the African Elephant Database are collected by a variety of sources, using a variety of different techniques and covering different areas. Consequently, for some protected areas, the population size may not be comparable between different time periods. Furthermore, few cross-border and ecosystem-wide

surveys are conducted, which may result in either under- or overcounting of populations. Third, the temporal disjunction between estimates of protected area management expenditure and population time series highlights a lack of coordination between the collection of data on protected area interventions and outcomes (Geldmann et al., 2019). Lastly, using population time series has shortcomings in its ability to assess protected area performance, because positive slopes are not a direct measure of conservation success but only of growing populations (Barnes et al., 2016), this is particularly important where populations are approaching carrying capacity; demographic data should also be used to determine conservation success and management (Hauenstein et al., 2022). Addressing these data limitations will require a concerted effort by the conservation community, and substantial financial support, to collect cost and population data in a more comprehensive, detailed, and systematic way across protected areas and over time to ensure comparability (Geldmann et al., 2019; Iacona et al., 2018).

Our results align with evidence-based calls for increased funding for the management of the existing protected area network in Africa, which would benefit biodiversity conservation as a whole, not just elephant populations (Balmford et al., 2003; Lindsey et al., 2018; McCarthy et al., 2012). If governments and the global community allocate sufficient financial resources to effectively manage protected areas, our results show that African elephants can be conserved effectively, and that it is this resourcing that is critical for their conservation.

AUTHOR CONTRIBUTIONS

R.J.C. and A.J.P. conceived the study. R. C., R.J.C., A.J.P., and C.M.B. collected the data. P.A.L. and J. G. contributed data. R.J.C., R. C., and C.M.B. analyzed the data. R. J. C., R.C., A.J.P., and C.M.B. were involved in data interpretation and drafting the paper. All authors were involved in revisions of the paper.

ACKNOWLEDGMENTS

We thank the Department of Zoology, in particular Andrew Balmford, at the University of Cambridge for supporting R.J.C. in undertaking this research. We thank the staff at the state wildlife agencies and nonprofit and donor organizations who generously provided information. R.C. and R.J.C. were supported by USFWS Grant Award F19AC00770 and J.G. was supported by The Danish Independent Research council (Grant Number 0165-00018B).


CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The African Elephant Database (<https://africanelephantdatabase.org/>) contains the latest elephant population data for each protected area. Data on spend at sites are sensitive and the authors relied on personal contacts to obtain this information for many of the protected areas. We can provide these data on request but cannot make them widely available.

ORCID

Roberto J. Correa  <https://orcid.org/0000-0003-1660-2826>

Rob Critchlow  <https://orcid.org/0000-0003-4524-1417>

Colin M. Beale  <https://orcid.org/0000-0002-2960-5666>

Jonas Geldmann  <https://orcid.org/0000-0002-1191-7610>

Andrew J. Plumptre  <https://orcid.org/0000-0002-9333-4047>

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SUPPORTING INFORMATION

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How to cite this article: Correa, R. J., Lindsey, P. A., Critchlow, R., Beale, C. M., Geldmann, J., & Plumptre, A. J. (2024). Performance of protected areas in conserving African elephants. *Conservation Letters*, *17*, e13041. <https://doi.org/10.1111/conl.13041>