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More than $1 billion needed annually to secure Africa's protected areas with lions

Peter Lindsey[a,b,c,1,2], Jennifer R. B. Miller[a,d,1], Lisanne S. Petracca[a,e,1], Lauren Coad[f], Amy J. Dickman[g], Kathleen H. Fitzgerald[h], Michael V. Flyman[i], Paul J. Funston[a], Philipp Henschel[a], Samuel Kasiki[j], Kathryn Knights[k], Andrew J. Loveridge[g], David W. Macdonald[g], Roseline L. Mandisodza-Chikerema[l], Sean Nazerali[m], Andrew J. Plumptre[n,o], Riko Stevens[a], Hugo W. Van Zyl[p], Luke Hunter[a,q]

[a] Panthera, New York, NY 10018, United States
[b] Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[c] Environmental Futures Research Institute, Griffith University, Queensland, Australia
[d] Department of Environmental Science, Policy, and Management, University of California-Berkeley, Berkeley, CA 94720, United States
[e] State University of New York College of Environmental Science and Forestry, Syracuse, NY, United States
[f] Centre for International Forestry Research, Bogor, Indonesia
[g] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, United Kingdom
[h] African Wildlife Foundation, Ngong Road, Nairobi, Kenya
[i] Department of Wildlife and National Parks, Gaborone, Botswana
[j] Kenya Wildlife Service, Nairobi, Kenya
[k] School of BioSciences, University of Melbourne, Melbourne, Australia
[l] Zimbabwe Parks and Wildlife Management Authority, P. Bag CY140, Causeway, Harare, Zimbabwe
[m] Independent analyst/researcher, Maputo, Mozambique
[n] Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, United States
[o] Conservation Science Group, Zoology Department, Cambridge University, Cambridge, United Kingdom
[p] Independent Economic Researchers, Cape Town, 8001, South Africa
[q] School of Life Sciences, University of Kwazulu-Natal, Durban, 4000, South Africa

[1] Authors contributed equally to this work
[2] Corresponding author: Peter Lindsey, peter@wildnet.org, +1 (646) 786-0400, 8 West 40th Street, 18th Floor, New York, NY 20018, United States

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Abstract

Protected areas (PAs) play an important role in conserving biodiversity and providing ecosystem services, yet their effectiveness is increasingly undermined by funding shortfalls. Using lions (*Panthera leo*) as a proxy for PA health, we assessed available funding relative to budget requirements for PAs in Africa's savannahs. We compiled a novel dataset of 2015 funding for 282 state-owned PAs with lions. We applied three methods to estimate the minimum funding required for effective conservation of lions, and calculated deficits in PAs where available funding did not meet estimated need. We estimated minimum required funding as $978/km^2 per year based on the cost of effectively managing lions in nine reserves by the African Parks Network; $1,271/km^2 based on modelled costs of managing lions at ≥50% carrying capacity across diverse conditions in 115 PAs; and $2,030/km^2 based on Packer et al.'s cost of managing lions in 22 unfenced PAs. PAs with lions require a total of $1.2-2.4 billion annually, or ~$1,000-2,000/km^2, yet PAs received only $381 million annually, or a median of $200/km^2. Ninety-six percent of range countries had funding deficits in at least one PA, with 88-94% of PAs with lions funded insufficiently. In funding-deficit PAs, available funding satisfied just 10-20% of PA requirements on average and deficits total $0.9-2.1 billion. African governments and the international community need to increase the funding available for management by three to six times if PAs are to effectively conserve lions and other species and provide vital ecological and economic benefits to neighbouring communities.

Keywords: budget, conservation effectiveness, deficit, funding need, management, *Panthera leo*, protected area

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Significance Statement

Protected areas (PAs) are the cornerstone of conservation yet face funding inadequacies that undermine their effectiveness in safeguarding biodiversity and vital ecosystem services. Successfully funding PAs requires reliable estimates of management costs. Using the conservation needs of lions as a proxy for those of wildlife more generally, we compiled a novel dataset of funding in Africa's PAs with lions and estimated a minimum target for conserving the species and managing PAs effectively. PAs with lions require \$1.2-2.4 billion or \$1,000-2,000/km^2 annually, yet receive just \$381 million or \$200/km^2 (median) annually. Nearly all PAs with lions are inadequately funded, with deficits totalling \$0.9-2.1 billion. Governments and donors must urgently and significantly invest in PAs to prevent further declines of lions and other wildlife, and to foster the range of potential economic, social and environmental benefits that healthy PAs can confer.

Introduction

Protected areas (PAs) are the foundation of international efforts to secure biodiversity (1, 2). PAs play a critical role in conserving high-priority species, including the African lion (*Panthera leo*), one of the most iconic symbols of Africa and a proxy for ecological health (3, 4). At least 56% of lion range falls within PAs, and the species reaches its highest population densities in PAs with high prey densities and where lion populations are well-managed and protected from primary threats (3, 5). Shortfalls in funding, combined with mounting human pressures, have weakened the management capacity in most African PAs and contributed to rapid declines in numbers of lions, their prey and other species (6–9). Lion numbers have decreased by 43% in just two decades, to as few as 23,000-35,000 wild individuals (8, 10). If managed optimally, Africa's PAs could theoretically support three to four times more wild lions than the current continental total, which would secure the ecosystems that lions encompass and allow for conservation gains for many other species (3).

Investing more financial resources into Africa's PAs would not only strengthen the conservation of lions and their ecosystems, but also generate social and economic benefits for Africa and the world at large. Africa's PAs encompass species and areas of natural heritage that are of great symbolic and cultural significance both within Africa and elsewhere, perhaps most notably in the West (4, 11, 12). PAs also support and supply vital ecosystem services to African countries (13–15) and bolster and diversify rural and national economies via nature-based tourism (9, 16–18). Visitation to parks and reserves has been increasing in Africa to the extent that in Southern Africa, for instance, ecotourism generates as much as farming, forestry and fishing combined (19, 20).

However, Africa's PAs are often underfunded, and receive less international support than their global value merits or than is required to unlock their economic or ecological potential. While many African governments spend proportionally more on PA networks relative to their economic means than countries in other parts of the world (21), rapidly declining wildlife populations and the poaching crisis in Africa indicate that such expenditures are insufficient to protect wildlife (22). In addition, funding levels are widely divergent among African countries, with a handful of countries investing sufficiently, while the majority invests far less than is required for the effective functioning of PAs (23). Continent-wide funding of PAs is so low that most African countries risk losing the majority of their remaining wildlife resources before they have chance to benefit from them in economic terms (11). As PAs become depleted and ecologically degraded, benefits from tourism earnings decrease relative to those from conversion of the land to agriculture or development, making PAs increasingly difficult to justify in economic and political terms (24, 25). As a result, many PAs have already been downsized, downgraded or degazetted (9, 26).

Investment in PAs must clearly be increased, but by how much is unclear. Budgets are notoriously challenging to track due to some state wildlife authorities' unwillingness to make their budgets available publicly and given variations in accounting methodologies between countries (27). Reputable estimates for African PA budgets are valuable but are now 10-34 years out of date due to the rapidly increasing and diversifying anthropogenic pressures on PAs (23, 28–30). A reassessment of the costs of maintaining Africa's PAs amidst current threats is urgently needed.

Lions are a useful species for assessing funding requirements for PAs. The species is listed as 'Vulnerable' on the International Union for Conservation of Nature (IUCN) Red List and affected by a wide range of threats, including habitat loss, prey depletion, retaliatory killing by people and targeted poaching, which also drive declines in many other wildlife species (31). Hence, their conservation status is emblematic of the human pressures facing wildlife more generally in Africa (10). Because lions are a keystone and umbrella species, adequate investment to secure their future is likely to protect numerous other species, as well as preserve ecosystem function and safeguard the long-term viability of Africa's PAs (4, 32).

Here we report on the funding available for Africa's PAs with lions and use three different methods to estimate the minimum amount required for effective conservation of the species. We also explore associations between funding, management capacity and PA characteristics to identify the patterns and magnitude of financial shortfalls. This work provides a minimum financial target for conserving lions and more broadly securing prey populations and the ecological and economic services offered by PAs on which people and biodiversity depend.

Results

We collected funding data for 282 PAs covering 1.2 million km^2 in 23 of 27 African lion range countries (data available upon request, see methods). Africa's PAs with lions receive a minimum of $381 million in total funding annually (Table 1). Annual funding varied widely among individual PAs, from $6/km^2 to $17,449/km^2, with a median of $200/km^2. When PAs were aggregated at a national scale, PAs in Cameroon received the lowest investment (median of $21/km^2), while PAs in four other countries (Angola, Niger, South Sudan and Senegal) also received less than $50/km^2 in total funding (Table 1; Fig. 1). Even Tanzania, which supports ~40% of the global lion population, and most of the other countries that contain at least 1,000 lions (Zambia, Central African Republic, Mozambique, Botswana and Zimbabwe; 8), suffer from severe under-resourcing, with median budgets of less than $300/km^2 (Table 1). Some countries, like Tanzania, are characterised by relatively higher budgets for national parks, but lower budgets for other types of PA, which comprises the majority of the protected estate. At the other end of the spectrum, three countries showed budgets above $1,600/km^2 (Kenya, Rwanda and South Africa; Table 1). Funding was marginally higher in East Africa (median of $265/km^2) than Southern ($200/km^2) or West-Central Africa (262/km^2; *SI Table 1).*

Three independent methods estimated that an annual minimum funding requirement of ~$1,000-$2,000/km^2 is necessary 'on average' for PAs to effectively conserve lions. African Parks Network spent a mean of $978 ± $773/km^2 SD per year (range: $497-1,833/km^2). Our study model determined a higher threshold of $1,271/km^2 for 'effective' PAs (95% CI = $457-$2,423/km^2; *SI Table 2, SI Fig. 1*). Packer et al.'s inflation-adjusted estimate represented the highest requirement at $2,030/km^2.

These estimates predict that Africa's PAs with lions require a total of at least $1.2-2.4 billion annually to conserve lions effectively (Table 1). Among countries, total funding requirements generally varied with the number of PAs and PA area with lions, such as from as low as $1 million in Rwanda (number of PAs with lions: n = 1 PA) and $3 million in Niger (n = 2) and Chad (n = 1), to as high as $203 million in Botswana (n = 49) and $225 million in Tanzania (n = 37) based on the African Parks Network method (Table 1).

In comparing available to required funding for effective conservation, we estimated a total annual deficit ranging from $0.9-2.1 billion across all assessed PAs (*SI Table 3*). Funding deficits existed in 88% (African Parks Network) to 94% (Packer et al.) of PAs with lions (Fig. 2). Of 23 countries assessed, 22 countries (96%) had at least one PA with deficit, and PAs in only three countries were funded above minimum funding requirements on average (Kenya, South Africa and Rwanda, the last which was the only country without PA deficit, although n = 1 PA; Table 2; Fig. 1B, *SI Table 4*). As expected, the highest total deficits occurred in countries with the most and largest PAs with lions, in Botswana (n = 49 PAs), Zambia (n = 35), Tanzania (n = 37) and Mozambique (n = 21; Fig. 1A). In ranking countries by median deficit per km^2, the highest deficits occurred in the Central African Republic ($944-2,009/km^2; n = 4) and Angola ($944-1,996/km^2; n = 1), where only 1-2% and 2-3% of funding needs were met on average, respectively (Table 2; Fig. 1B).

In PAs with deficits, just 10-20% of funding requirements were available on average (*SI Table 4*). Funding shortfalls were widespread and extensive: 27-59% of countries in deficit showed shortages of > 90% of required funding on average (Fig. 3). The vast majority of countries (87%) reported a lower average available funding per km^2 across all PAs than even the lowest $978/km^2 amount estimated as necessary for effective conservation of lions (Table 1). Only three of all countries assessed (South Africa, Rwanda and Kenya) showed average funding levels higher than the minimum needed (Table 1), and even in these relatively well-funded countries a significant proportion of PAs showed deficits (2 of 13 PAs in South Africa and up to 17 of 20 PAs in Kenya; Fig. 1, Table 2).

State funding was twice as large as donor support (Table 1). State funding per unit area was more than three times as high in Southern Africa than other regions, whereas donor funding per unit area was higher in West-Central Africa than other regions (*SI Table 1*). Accordingly, several Southern (Botswana, Namibia) and East African countries (Kenya, Tanzania) were especially reliant on state support, while several West-Central (Democratic Republic of the Congo and Central African Republic) and Southern African countries (Angola, Malawi) were largely reliant on donor contributions (Fig. 4).

Higher funding per km^2 was associated with smaller-sized, fully fenced PAs that contained rhinos and supported active tourism, and that were part of a Transfrontier Conservation Area (TFCA), jointly managed by a non-profit organisation and located in a country with lower corruption (model fit $R^2 = 0.98$; *SI Table 5, SI Fig. 2*). Donor contributions were higher in smaller, fully fenced PAs of IUCN categories I or II that supported active tourism, were co-managed by a non-profit partner and located in countries with lower GDP ($R^2 = 0.91$; *SI Tables 6-7*). Greater state funding was associated with smaller PAs that contained rhinos and were part of a TFCA and IUCN categories I or II, that were located in East Africa and in countries with higher GDP, and that were not co-managed by a non-profit ($R^2 = 0.91$; *SI Table 8*).

Among PAs, higher funding per km^2 was associated with higher management capacity ($r = 0.54$, $P < 0.001$; Fig. 5A), lower threat to wildlife ($r = -0.28$, $P = 0.001$; Fig. 5B) and the availability of more staff and patrol vehicles ($r = 0.67$ and $r = 0.71$, respectively, both $p < 0.001$; Fig. 5C, Fig. 5D). In turn, greater management capacity was associated with a lower threat to wildlife ($r = -0.28$, $P = 0.003$) and more staff and vehicles ($r = 0.42$ and $r = 0.44$, respectively, both $p < 0.001$).

Discussion

Our findings reveal major deficits in the management funding of Africa's PAs with lions. For PAs to achieve baseline effective conservation of lions (which reflects effective management more generally), overall funding must be increased by three to six times to meet minimum need, i.e. adding $0.9-2.1 billion to supplement the $381 million of total annual funding already available. Existing funding is highly skewed, with a minority of PAs funded above minimum required levels, while the majority of PAs and countries receive a fraction of the funding needed to conserve lion populations and broader ecosystems effectively. In some countries (e.g. South Sudan, Zimbabwe), though moderate funding from the state is available, substantial proportions are tied up for salaries, leaving modest amounts for operations. Unless action is taken to increase resources for most PAs in African savannahs, lions and many other species are likely to suffer continued steep declines in number and distribution, with serious ecological and economic ramifications. Countries with some of the largest PA networks, such as Botswana, Tanzania and Zambia experience some of the largest deficits in spite of strong political commitments to conservation. This presents an opportunity for additional donor support for conservation efforts in these countries, given the impressive contribution of land for conservation, the difficulty associated with securing such vast areas and the significance of these areas for the conservation of a wide range of species valued worldwide.

Our results are consistent with prior studies in highlighting the importance of management budgets for effective conservation of African wildlife. Inadequate PA funding in part leads to the wildlife population declines observed in many of Africa's PAs, and helps explain the severity of declines in charismatic species such as rhinos, elephants and increasingly lions (3, 5, 10, 33–35). Our finding that lower funding was associated with greater threats to wildlife suggests that management funding does not scale with the degree of threat and that threats are exacerbated in the absence of adequate funding. Adequate budgets are required to develop and maintain infrastructure, to purchase and maintain vehicles and other equipment and to train, deploy and motivate staff (2, 36). In the absence of sufficient funding (and even with adequate funding in circumstances of weak PA governance and management), field staff can become ineffective. In the worst cases, poorly paid or unmotivated staff can actually contribute to wildlife declines due to the social and financial gains that can be derived from engaging in illegal activities such as poaching (37).

Efforts are drastically needed to raise the management budgets of PAs to \$1,000-2,000/km^2 to effectively conserve lions and their broader ecosystems. The African Parks Network method (\$978/km^2) represented the tried-and-true costs of managing stable and increasing lion populations in nine effective PAs with varying management conditions. African Parks have proven highly effective in the field and also at fundraising, due in part to their commitment to financial accountability. The African Parks Network method may yield the lowest estimates of budget requirements because their budgets are less likely to be affected by leakages to corruption or inefficiencies than those of some state wildlife authorities. Channelling an elevated proportion of funding to PAs through accountable NGO partners engaged in collaborative management partnerships represents one potential means of reducing loss of donor funding to corruption (38). Efforts to build the capacity of PA authorities to management finances transparently are also important. Our study method ($1,271/km^2) considered a broader spectrum of management conditions across 115 PAs with lions and identified the funding threshold that best predicted PAs maintaining lion populations at ≥ 50% of carrying capacity. Packer et al.'s method ($2,030/km^2) represented the high-end costs associated with managing unfenced, free-roaming lion populations. Collectively, these estimates represent a gradient of real-world management conditions and costs for effectively conserving lions. Although estimates are higher than prior (and now outdated) estimates of required funding, such as $174-424/km^2 for forest parks in Central Africa in 2004 (29) and $459/km^2 for parks Africa-wide in 1984 (28), our estimates approximate the $1,010/km^2 estimated need for managing tigers in Asia (39) (all figures in 2015 USD).

We emphasise that the two higher-end estimates ($1,271/km^2 and $2,030/km^2, or $1.2-2.4 billion total annually across all PAs with lions) are the minimum amounts necessary under current conditions to manage lion populations at half of the potential population size. However, 50% of carrying capacity is a low benchmark for conservation effectiveness, particularly for lions which have such great ecological and economic value. In addition, some of the PAs with lions at 50% of estimated carrying capacity are suffering ongoing declines (10), such that even larger budgets may be required to manage stable or growing populations of lions and their prey, and yield long-term security for the species.

Additional considerations. We caution that our study does not provide insights into the requirements for the management of individual PAs, which likely vary significantly with the extent of threat and the geographic location, habitat type and degree of remoteness. Large PAs are likely to benefit from economies of scale, as certain infrastructure developments are necessary regardless of the size of an area, and because larger areas will be more insulated from threats than smaller areas. Similarly, costs are likely to be higher in countries where corruption causes funding to be squandered (40). Additionally, in PAs where there is little or no infrastructure, such as the newly gazetted Luengue-Luiana and Mavinga National Parks in Angola, the required capital investment would be significantly greater than the operational costs used in our calculations. If PAs receive the increase in funding that we recommend, all wildlife species would benefit; that said, our estimates may not reflect the additional funding potentially needed to conserve rhinos (and to a lesser extent, elephants), due to the high prices obtained by illegal wildlife traders for their horns/tusks and the vigour with which poachers pursue them (41–43).

The costs of managing Africa's PAs and conserving species such as lions are likely to grow with time. Pressure on wildlife due to poaching for body parts for the illegal wildlife trade is severe, with an increasing range of species being affected (including lions), which makes PA management more difficult and expensive (3, 43). Africa's human population is growing faster than other parts of the world, which will increase pressure for land and natural resources contained within PAs (44, 45). Conversely, costs could be reduced by increasing the involvement of neighbouring communities in PA management and decision-making, thereby increasing their engagement and sense of ownership (12, 16, 46).

Funding protected areas for Africa's future. Greater investment in Africa's PAs is urgently needed, and is likely to yield significant social, economic and ecological benefits. PAs provide essential ecosystem services via the provisioning of clean water and other natural resources (13–15), which can reduce poverty, promote human health and improve the well-being of rural communities (47, 48). Wildlife-based tourism in PAs has significant potential to act as a vehicle for sustainable economic development and job creation in many African countries, particularly in rural areas with few alternatives (7). The ecotourism industry already generates $34 billion of revenue in sub-Saharan Africa, and the tourism industry more broadly creates nearly 6 million jobs (49, 50). Lions represent a key aspect of this success and are one of the most popular attractions to visitors of Africa's PAs (51). Tourism revenue represents a crucial means for African countries to diversify economies and reduce reliance on finite resources such as minerals, and on agriculture and livestock, which are vulnerable to climate change (52). The potential social and economic benefits associated with functioning PA networks build a strong case for the investment of general development aid funding to augment the traditional conservation-focused funding in PA management. An allocation of just 2% of the $51 billion allocated to development in Africa would likely cover the deficits facing PAs from a lion conservation perspective (53). Such investments to PAs should be normalised as part of the international development financial portfolio to support maturing tourism economies and protect the environmental services provided by PAs to people's health and general well-being. These benefits would increase if care was taken to maximise the extent to which benefits from tourism and PAs accrue to communities. Potential approaches include providing communities with part or complete ownership of concessions within PAs and, where funding permits, use of 'performance payments' (54, 55), while taking care to avoid elite capture. Similarly, developed countries could consider 'debt-for-nature' schemes, where debt alleviation is provided in return for PA investment by the host nation (56). Creative donor investment could assist many African countries to optimise the commercial viability of their PAs, especially in PAs with high deficits (Fig. 1) where state funding is in short supply (Fig. 4).

Over recent years, increasing effort has promoted community-based conservation areas outside of PAs, which are essential for maintaining landscape connectivity and intact ranges of far-roaming species such as lions. However, while such investments are essential, we urge the conservation and donor community to ensure that sufficient focus is given to the management and protection of PAs in order to maintain the 'backbone' of conserved landscapes. PAs should not be assumed to be adequately protected by virtue of their legal status. In addition to funding needs, improving the effectiveness with which existing funds are used is also essential. This means avoiding corruption and seeking options to provide long-term, drip-feed funding for PAs, rather than the large, non-recurrent funding packages commonly provided by multi-lateral funding agencies (11). To this end, collaborative management partnerships between NGOs and state wildlife authorities (such as those practiced by African Parks) are of potentially high value and should be a funding priority (38).

Conclusion

PAs in Africa are facing a funding shortfall of at least $0.9 billion and up to $2.1 billion for effective conservation of lions. Without significant increases in the amount of funding, PAs will not be able to fulfil the ecological, economic or social objectives for which they were established. The current budget deficit facing Africa's PAs is surmountable, but currently represents a great risk that lions and many other wildlife species will continue to decline in number and ultimately disappear from the majority of PAs in lion range (10). Such losses would mean that many African countries would lose their most iconic wildlife species before benefitting significantly from them.

Methods

Our methods comprised four main steps. First, we compiled a novel database of available funding in PAs with lions, which to our knowledge represents the most comprehensive and up-to-date database of its kind. Second, we applied three methods to estimate different thresholds of minimum funding required for effective conservation of lions. Third, we used required funding estimates to calculate deficits in PAs where available funding did not meet need. Fourth, we addressed the patterns and importance of funding for conservation by examining associations between funding and PA characteristics and management resources.

Available funding. We gathered data on the total funding available for management of PAs. Our study focused on state-owned PAs containing lions and located within lion range in Africa (*SI Appendix 1*). Total funding comprised 'state' (funding contributed by the PA country government) and 'donor' (funding contributed by non-state groups, including non-profit organisations, charitable foundations and bi- and multi-lateral agencies) funding. Management funding included costs related to staff, law enforcement, maintenance of infrastructure and roads, habitat management and engagement with adjacent communities. Sources broadly included (see *SI Appendix 2* for details): 1) expert surveys (see (3) for methods), 2) wildlife authorities, 3) 50 non-profit organisations involved in PA management, 4) private hunting companies and 5) major donors involved in PA management, such as foundations, non-profit organisations and multi-lateral government agencies. We obtained both state and donor funding data from 282 state-owned PAs with lions and in 23 countries, except for in Chad, where we were not able to obtain state data, and South Africa, where we could not comprehensively capture donor contributions (however, state budgets for PAs in South Africa are substantially higher than other countries and sufficient for effective lion management (3)). We emphasise the major challenges associated with obtaining budget data (*SI Appendix 3*) but are confident that our estimates are of the correct order of magnitude and constitute the most up-to-date and accurate data available.

From each source, we gathered information on the PA and the years over which funding was spent, tracking whether funds were channelled to other organisations to avoid double-counting resources. We primarily obtained budget data for the fiscal year spanning 2015-2016, but in rare cases where data was not otherwise available, we included data from several years before (no earlier than 2009) or after (2017). All financial data (and numbers reported in this paper) were converted to US$ at the average exchange rate from the year of origin (57) and scaled to USD in 2015 to account for inflation (58). To comply with requests for anonymity from our informants and reduce the vulnerability of poorly-funded PAs (exposure to funding levels could make them a target for threats such as poaching), we report results on individual PA data without mentioning PAs by name and present aggregated PA data at the country level. However, upon request, we will provide PA-level data to researchers or conservationists who demonstrate constructive ideas for further analysis. We calculated PA average funding (including funding requirements and deficits) using medians to prevent misrepresentation due to a minority of highly funded PAs. All statistical analyses were done using R (59).

Minimum funding requirements and deficits. We applied three methods to consider a range of cost estimates of the minimum funding required for effective lion conservation:

(1) African Parks Network method: We acquired data on management budgets for each PA managed by the African Parks Network, a non-profit organisation delegated management responsibility by state wildlife authorities for nine PAs as of 2015. Since both lions and prey species were stable or increasing in all nine PAs (3), we assumed that the levels of management investment were adequate for effective lion conservation. We calculated the minimum funding requirement as the amount that African Parks Network spent in 2015 on capital investments plus operating costs associated with management in each of their PAs. 'Capital investments' included: buildings, roads, airstrips, fencing, vehicles, aircraft, office equipment, furniture, tools, radio communications equipment and other fixed assets.

(2) Our study method: We used logistic regression to determine the minimum funding level that best predicted PA 'effectiveness' for 115 PAs for which we had funding and lion population data. We defined 'effective' PAs as PAs where lions occurred at $\geq$ 50% of estimated carrying capacity (3). Lion biomass is strongly correlated with prey biomass (60), which in turn is dictated primarily by rainfall and soil (61–63). We estimated the potential carrying capacity for lions in each PA based on the equation (64)

$$\text{lion density } (\#/100\text{ km}^2) = 0.0109 * ([\text{ungulate biomass}]^{0.8783}),$$

in which ungulate biomass was estimated based on local rainfall (calculated by cold cloud duration) and soil characteristics (cation exchange capacity). We acquired data on potential carrying capacity for lions at each PA (65) and paired these with data on lion population estimates from (3). Using effectiveness as a predictor variable and total funding ($/km^2) as a required response variable from a pool of 35 candidate variables (*SI Table 1*), we built a multivariate model to predict PA effectiveness. We then identified the funding threshold that best discriminated effective from non-effective PAs (see *SI Appendix 4* for details).

(2) Packer et al. method: We applied Packer et al.'s (5) finding based on 22 PAs that $2,000/km^2 of operational costs is required to maintain lions in unfenced PA at $\geq$ 50% carrying capacity, representing the high-end costs of managing free-roaming lions. Expert surveys indicated that most of the PAs in our dataset were unfenced (72%). We adjusted Packer et al.'s estimate to USD in the year 2015.

Using these estimates of required funding, we calculated funding needs and deficits for each PA and then aggregated PAs by country. PA funding need (in $) was calculated as the minimum funding requirement ($/km^2) multiplied by PA area (km^2). PA funding deficit ($) was calculated as the funding need ($) minus available funding ($; positive deficits indicate greater need than available funding and deficits were minimized at $0, since our approach aimed to assess baseline funding adequacy). PA funding deficit per area ($/km^2) was calculated as PA deficit ($) divided by PA area ($km^2$). Country totals for funding need and deficit ($) were calculated by summing PA need and deficit ($), respectively, for PAs in each country. When calculating budget deficits on a national and continental level, budget surpluses that occurred in a minority of PAs were not 'carried over' to other PAs to reduce overall estimated deficit, but were treated as zero deficit, reflecting the fact that such surpluses are generally not transferred to other PAs.

PA characteristics. We used a linear regression framework to assess what PA characteristics were associated with higher total, state and donor funding (see *SI Appendix 4* for details). For this analysis we used a subset of 128 PAs for which we had expert information from surveys. We assessed 36 variables (derived from a range of sources, including published papers, publicly available datasets and expert surveys) relating to governance, socioeconomic, management and ecological characteristics for each PA (*SI Table 9*).

Management factors. Expert surveys also collected information on how funding was associated with management resources and threats to wildlife. Experts were asked to provide information on (see (3) for details): 1) the number of vehicles and rangers available for management; 2) a rating of different aspects of management capacity on a scale of 1-5, which we summed to generate an overall 'management capacity score'; and 3) a rating of the severity of 11 specific threats to wildlife on a scale of 1-5, which we summed to generate an overall 'threat to wildlife score'. We calculated Pearson correlations to examine relationships among total funding, management resources (vehicles and staff), management capacity and threats to wildlife. As normality is a critical assumption in correlation analysis, total funding, vehicle and staff data were log-transformed to address the right skew in the data.

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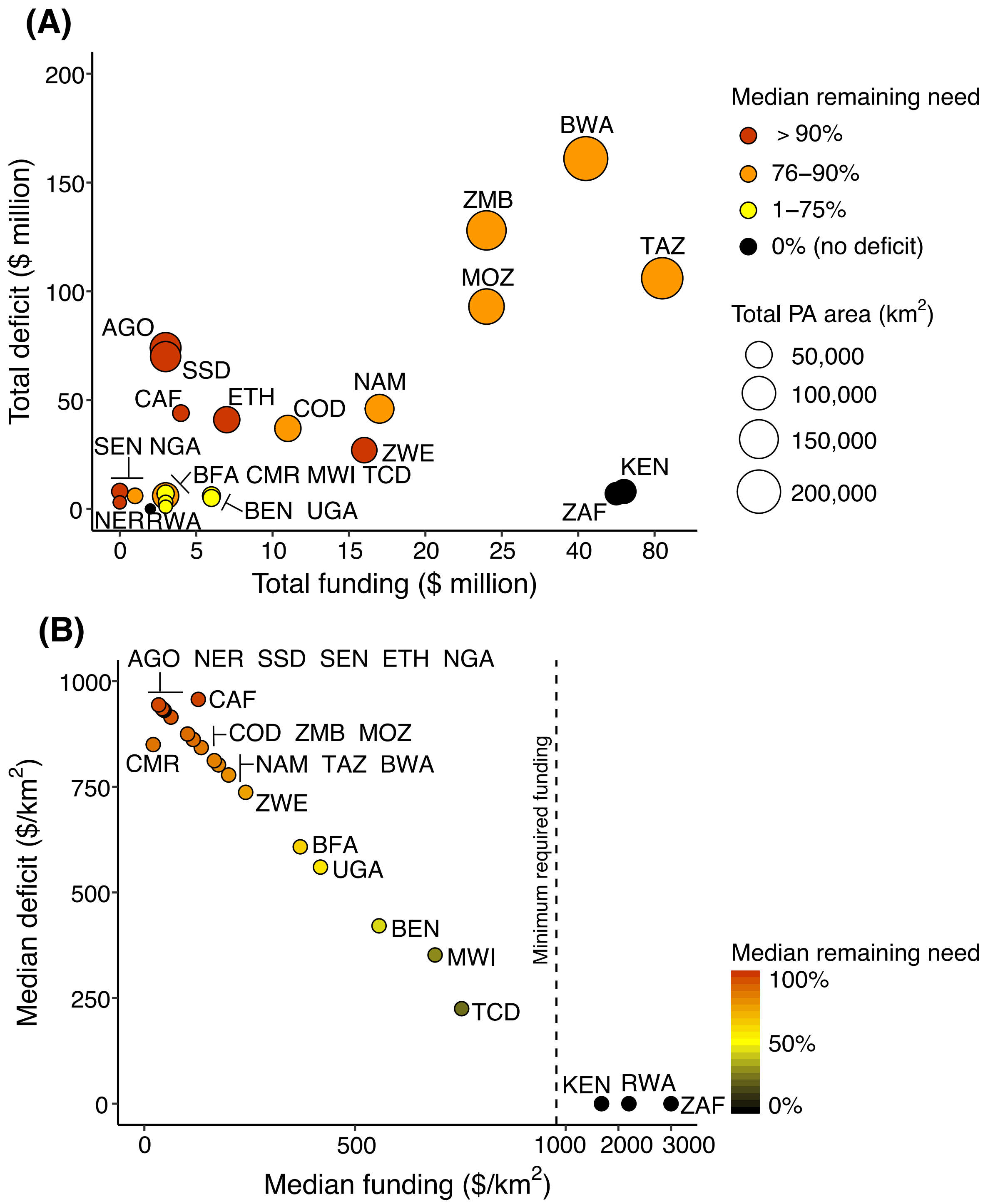

Fig 1. The most underfunded countries for lion conservation, in terms of (A) total and (B) median available funding and remaining shortfalls for effective conservation of Africa's protected areas (PAs) with lions. Median remaining need represents the average percentage of funding needed to meet the estimated required minimum. Minimum required funding and deficits represent lower-end estimates based on the African Parks Network method ($978/km^2). See Table 1 and 2 for the number of deficit PAs in each country, country rankings and ISO country code.

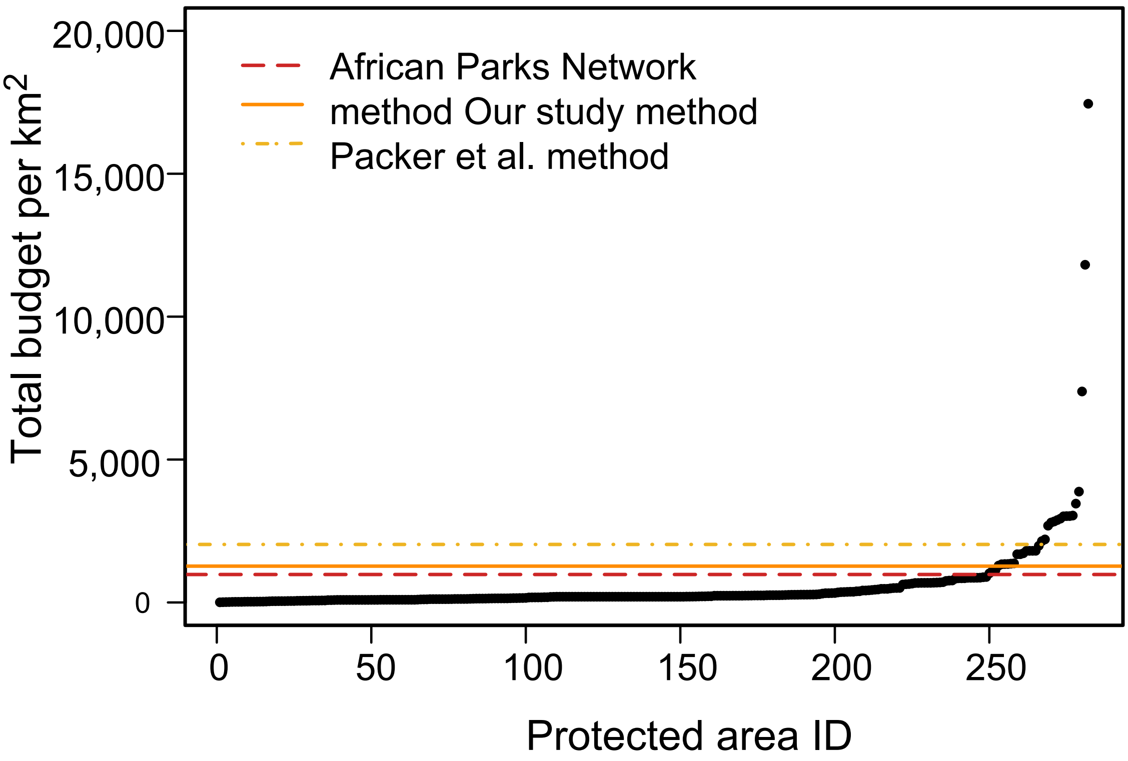

Fig. 2. Annual funding (\$/km^2) for 282 African PAs with lions (black circles) compared to minimum required need as estimated by the African Parks Network method (\$978/km^2), our study method (\$1,271/km^2) and the Packer et al. method (\$2,030/km^2). In total, 249 (88% of total), 252 (89%), and 266 (94%) of PAs failed to meet the minimum benchmarks of the African Parks Network, our study, and Packer et al. method, respectively.

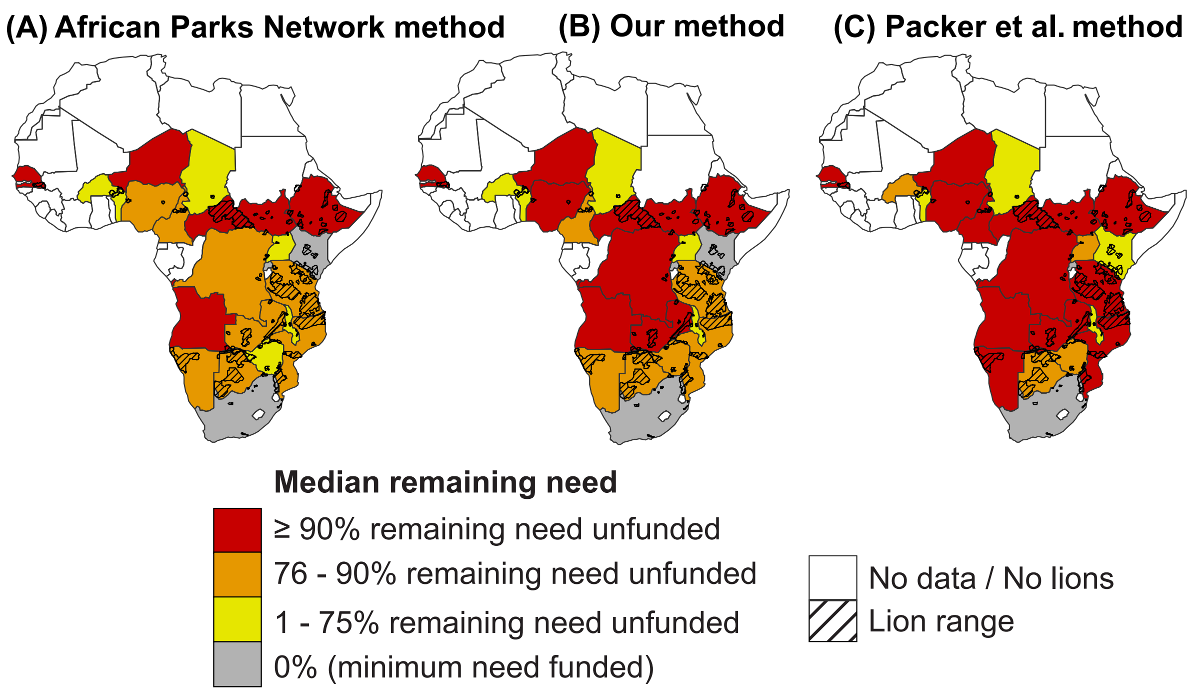

Fig. 3. Average funding shortfalls for lion conservation in protected areas (PAs) in 23 of 27 lion range countries. The 'median remaining need' represents the average (median) funding shortfall in PAs, calculated by comparing available funding for PA management to the required funding to effectively conserve lions. Minimum funding requirements were based on three estimation methods: (A) African Parks Network ($978/km^2 per year), (B) our study method ($1,271/km^2) and (C) Packer et al. method ($2,030/km^2). All assessed countries except Rwanda showed at least one PA with deficit. See Table 2 and *SI Table 4* for more detail on median deficit and the number of PAs with funding shortfalls in each country.

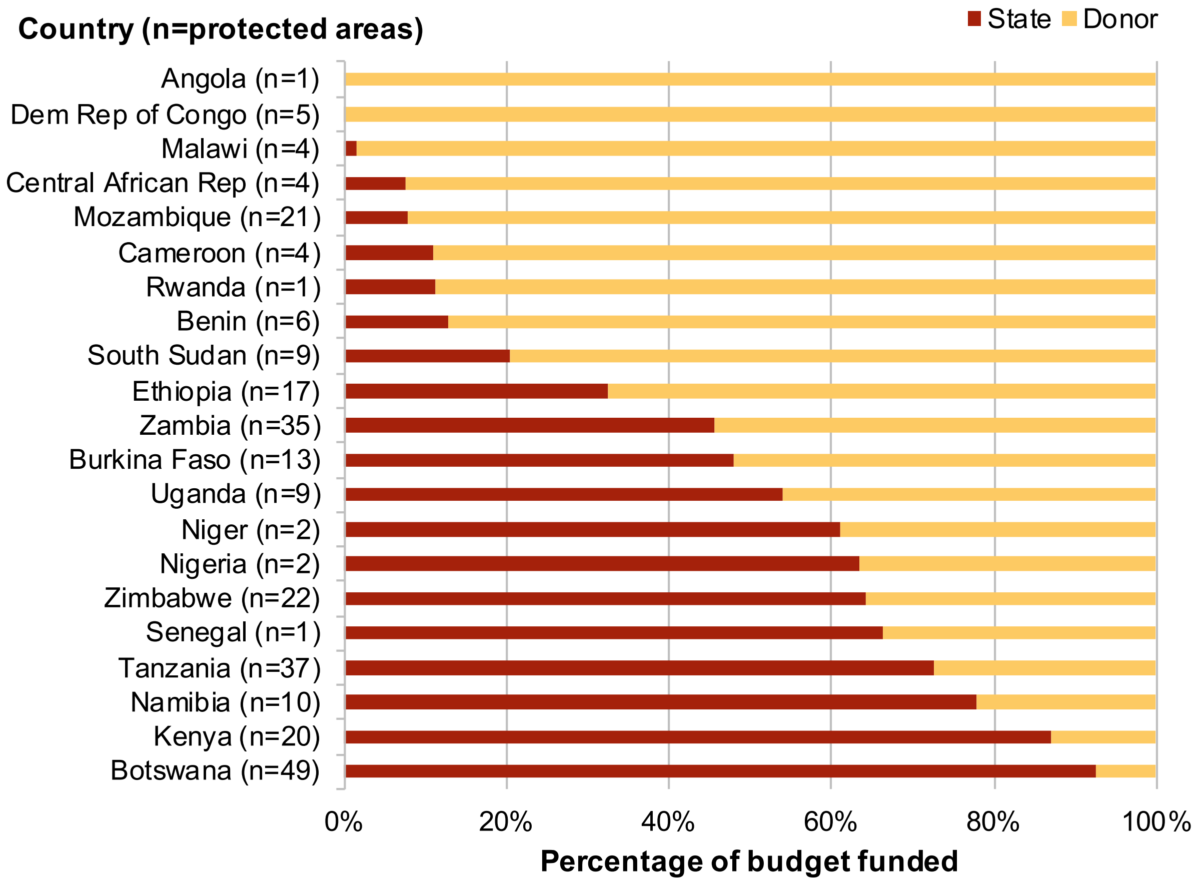

Fig. 4. Proportion of state versus donor contributions to management funding in 282 of Africa's protected areas (PAs) with lions. Data excludes South Africa and Chad, where data were not available on donor or state contributions, respectively.

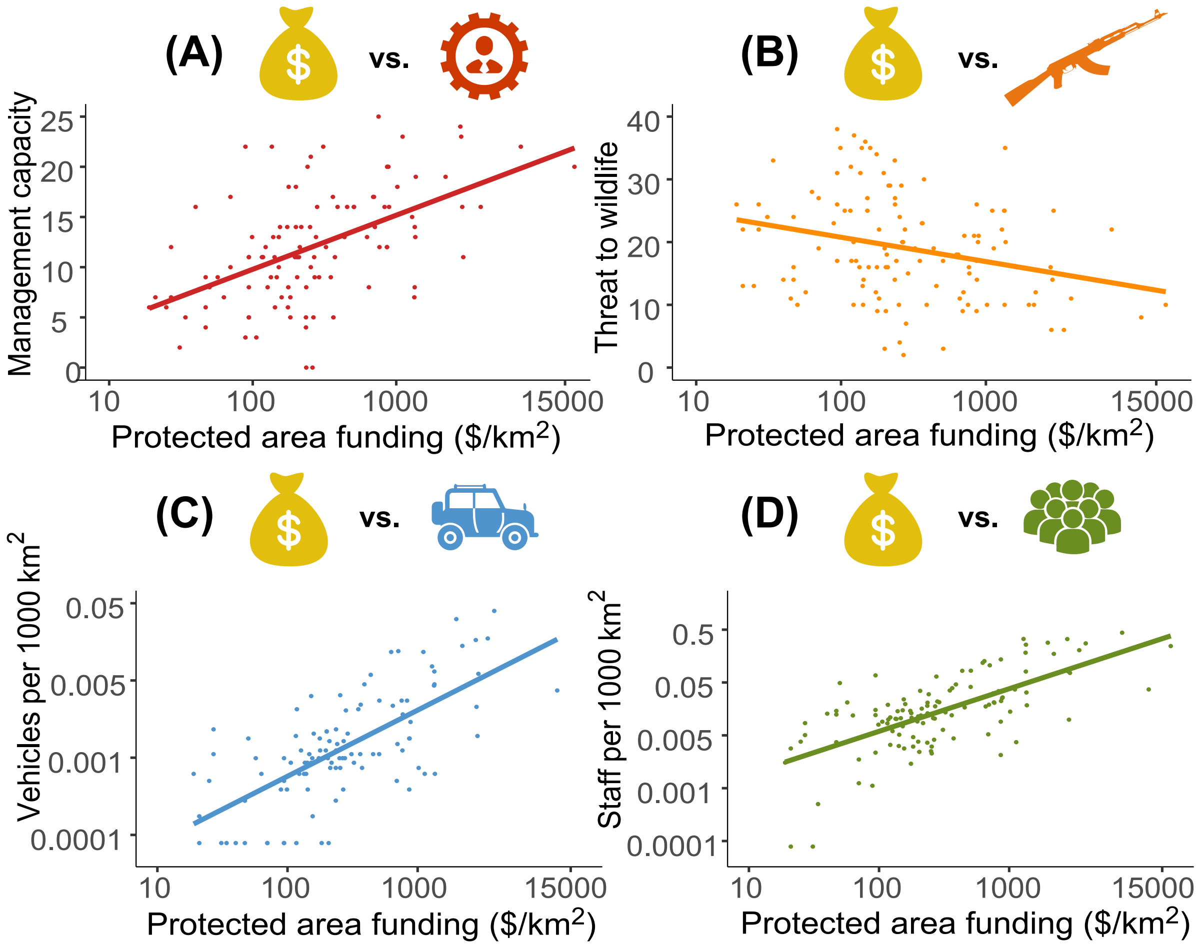

Fig. 5. Associations between funding in 125 Africa's protected areas with lions and (A) management capacity, (B) threats to wildlife, (C), vehicles available for patrols and (D) numbers of management staff (C). The 125 PAs are a subset of the 282 state-owned PAs for which both funding and the relevant data were available. Lines indicate the relationship directionality of Pearson correlations.

Table 1. Management funding and estimated minimum need for effective lion conservation in protected areas (PA) with lions, aggregated by country. Countries are ranked from highest to lowest average (median) total available funding among PAs. Minimum required funding was estimated using three different methods of calculating the minimum funding requirement for effective lion conservation (see footnote).

			Total funding		State funding		Donor funding		Minimum required funding* ($mil)				
Rank	Country (ISO code)	Region	Median ($/km^2)	Total ($mil)	Median ($/km^2)	Total ($mil)	Median ($/km^2)	Total ($mil)	African Parks Network	Our study	Packer et al.	PAs with lions	Lion PA total area (km^2)
1	South Africa (ZAF)	South	3,014¶	57.59¶	3,014	57.59	No data	No data	28.09	36.51	58.31	9	28,725
2	Rwanda (RWA)	East	2,206	2.25	245	0.25	1,960	2.00	1.00	1.30	2.07	1	1,020
3	Kenya (KEN)	East	1,688	59.61	1,435	51.95	82	7.66	35.39	46.00	73.47	20	36,190
4	Chad (TCD)	West-Central	753¶	2.29¶	No data	No data	753	2.29	2.98	3.87	6.18	1	3,043
5	Malawi (MWI)	South	690	2.79	6	0.04	681	2.75	4.44	5.77	9.22	4	4,540
6	Benin (BEN)	West-Central	557	6.27	54	0.80	498	5.46	12.54	16.30	26.03	6	12,822
7	Uganda (UGA)	East	418	5.50	332	2.96	85	2.54	9.66	12.56	20.05	9	9,879
8	Burkina Faso (BFA)	West-Central	370	3.37	207	1.62	164	1.75	10.46	13.60	21.72	13	10,700
9	Zimbabwe (ZWE)	South	241	16.06	235	10.32	1 or 272§	5.75	42.94	55.80	89.12	22	43,903
10	Botswana (BWA)	South	200	42.46	189	39.26	11	3.20	203.16	264.03	421.69	49	207,731
11	Tanzania (TAZ)	East	176	85.74	41	62.24	54	23.50	173.27	225.18	359.64	37	177,164
12	Namibia (NAM)	South	166	17.07	0	13.29	35	3.78	63.34	82.31	131.47	10	64,763
13	Mozambique (MOZ)	South	135	24.09	4	1.87	121	22.22	114.56	148.88	237.79	21	117,138
14	Central African Republic (CAF)	West-Central	128	3.66	29	0.27	84	3.39	8.80	11.44	18.27	4	8,999
15	Democratic Republic of the Congo (COD)	West-Central	116	11.19	0	0.00†	116	11.19	47.70	61.99	99.01	5	48,771
16	Zambia (ZMB)	South	116	23.88	70	10.88	46	13.00	151.94	197.46	315.38	35	155,361

17	Nigeria (NGA)	West-Central	103	0.58	58	0.37	45	0.21	6.47	8.41	13.42	2	6,613
18	Ethiopia (ETH)	East	63	6.80	45	2.21	35	4.59	47.78	62.09	99.17	17	48,852
19	Senegal (SEN)	West-Central	47	0.39	31	0.26	16	0.13	8.05	10.47	16.72	1	8,234
20	South Sudan (SSD)	East	45	2.94	9	0.60	4	2.34	73.35	95.32	152.24	9	74,996
21	Niger (NER)	West-Central	43	0.11	26	0.06	17	0.04	2.93	3.81	6.09	2	3,000
22	Angola (AGO)	South	34	2.66	~0‡	~0.00‡	34	2.66	76.76	99.75	159.32	1	78,484
23	Cameroon (CMR)	West-Central	21	3.42	12	0.38	9	3.04	47.57	61.82	98.74	4	48,642
	All countries		200	320.84	104	257.21	55	123.50	1173.18	1524.65	2435.13	282	1,199,570

* Minimum funding requirement based on each method: African Parks Network = $978/km^2; our study = $1,271/km^2; Packer et al. 2013 = $2,030/km^2.

† State contributions for the Democratic Republic of Congo totalled ~$3,000.

‡ Data were not available but experts indicated that state budgets were close to $0/km^2.

§ Median does not accurately represent the right-skewed distribution of donor funding in Zimbabwe, where 50% of 22 PAs received < $1/km^2 and 50% received a median of $272/km^2.

¶ Represents an underestimation, as South Africa estimates did not include donor data and Chad did not include state data.

Table 2. The most underfunded countries for protected area (PA) management and lion conservation. Countries are ranked from highest to lowest median deficit among PAs with lions, as estimated by the African Parks Network method, the approach with the lowest minimum funding requirement ($978/km^2). More detail on PA deficits in countries that contain very few PAs with deficits (e.g. Kenya and South Africa) can be found in *SI Table 4*, which shows median deficits by country calculated using only PAs with deficits.

		African Parks Network			Our Study			Packer et al.		
Rank	Country (ISO code)	Median deficit ($/km^2)	Median remaining need (%)*	PAs with deficit (%)†	Median deficit ($/km^2)	Median remaining need (%)*	PAs with deficit (%)†	Median deficit ($/km^2)	Median remaining need (%)*	PAs with deficit (%)†
1	Central African Republic (CAF)	957	98	100	1,250	98	75	2,009	99	100
2	Angola (AGO)	944	97	100	1,237	97	100	1,996	98	100
3	Niger (NER)	935	96	100	1,228	97	100	1,987	98	100
4	South Sudan (SSD)	933	95	100	1,226	96	100	1,985	98	100
5	Senegal (SEN)	931	95	100	1,224	96	100	1,983	98	100
6	Ethiopia (ETH)	915	94	94	1,208	95	94	1,967	97	100
7	Nigeria (NGA)	875	89	100	1,168	92	100	1,927	95	100
8	Zambia (ZMB)	862	88	100	1,155	91	100	1,914	94	100
9	Democratic Republic of the Congo (COD)	862	88	100	1,155	91	100	1,914	94	100
10	Cameroon (CMR)	850	87	75	1,143	90	100	1,902	94	100
11	Mozambique (MOZ)	843	86	86	1,136	89	90	1,895	93	95
12	Namibia (NAM)	812	83	100	1,105	87	100	1,864	92	100
13	Tanzania (TAZ)	802	82	92	1,095	86	95	1,854	91	95
14	Botswana (BWA)	778	80	100	1,071	84	100	1,830	90	100
15	Zimbabwe (ZWE)	737	75	100	1,030	81	100	1,789	88	100
16	Burkina Faso (BFA)	608	62	100	901	71	100	1,660	82	100
17	Uganda (UGA)	560	57	89	853	67	89	1,612	79	89
18	Benin (BEN)	421	43	100	714	56	100	1,473	73	100
19	Malawi (MWI)	352	29	50	581	46	75	1,340	66	75
20	Chad (TCD)	225	23	100	518	41	100	1,277	63	100
21	South Africa (ZAF)	0	0	22	0	0	22	0	0	22
22	Kenya (KEN)	0	0	30	0	0	30	343	17	85

No deficit	Rwanda (RWA)	0	0	0	0	0	0	0	0	0
	All countries	778	80	93	1,071	84	94	1,830	90	95

* Median percent of unmet minimum required funding relative to total available funding by PA.

† See Table 1 for total number of PAs with lions in each country.

Supplementary Information

More than $1 billion needed annually to secure Africa's protected areas with lions

Peter Lindsey[1], Jennifer R. B. Miller[1], Lisanne S. Petracca[1], Lauren Coad, Amy J. Dickman, Kathleen H. Fitzgerald, Michael V. Flyman, Paul J. Funston, Philipp Henschel, Samuel Kasiki, Kathryn Knights, Andrew J. Loveridge, David W. Macdonald, Roseline L. Mandisodza-Chikerema, Sean Nazerali, Andrew J. Plumptre, Riko Stevens, Hugo W. Van Zyl, Luke Hunter

[1] Authors contributed equally to this work

Table 1. Regional differences in available funding, minimum required funding and deficits.

Region	Median deficit ($/km2)			Total need ($ million)			Median funding ($/km2)		
	African Parks Network	Our study	Packer et al.	African Parks Network	Our study	Packer et al.	Total	Donor	State
West-Central	716.09	1009.09	1724.24	1.76	2.28	3.65	261.5	164	51
East	712.74	1005.74	1764.74	1.54	2.01	3.20	265	82	52
Southern	777.59	1070.59	1810.56	1.96	2.55	4.08	200	24	189

Table 2. Coefficients for top model (adjusted $R^2 = 0.98$) from linear regression identifying the covariates associated with higher *total* PA budget in 115 state-owned African PAs with lions. All other model subsets had delta AICc > 2. Covariates in the final model were MainUse (main uses of 2, 1, and 0 were mainly photographic tourism, mainly trophy hunting and neither tourism nor hunting, respectively), Area (PA area), TFCA (PA is part of transfrontier conservation area), Rhino (rhino presence), Comgmt (PA is co-managed by a non-profit organization), Fenced (PA is completely fenced), and CorruptionControl (corruption control).

Covariate	Estimate	Std. Error	p-value
MainUse0 (No main use)	4.8625	0.1597	< 2e-16
MainUse1 (Hunting as main use)	5.0975	0.1617	< 2e-16
MainUse2 (Tourism as main use)	5.9185	0.1116	< 2e-16
Area	-0.5522	0.0799	< 2e-5
TFCA	0.2987	0.0783	0.0002
Rhino	0.2984	0.0849	0.0006
Comgmt	0.2838	0.0790	0.0005
Fenced	0.2675	0.0847	0.0020
CorruptionControl	0.2352	0.0811	0.0044

Table 3. Total estimated deficit by country.

Rank	Country	Total deficit ($ million)		
		African Parks Network	Our study method	Packer et al.
1	Botswana	160.70	221.56	379.23
2	Zambia	128.06	173.59	291.50
3	Tanzania	105.93	155.23	283.13
4	Mozambique	92.68	125.30	213.78
5	Angola	74.10	97.10	156.67
6	South Sudan	70.40	92.38	149.30
7	Namibia	46.27	65.24	114.40
8	Central African Republic	44.16	58.41	95.33
9	Ethiopia	41.16	55.33	92.37
10	Democratic Republic of Congo	36.51	50.79	87.81
11	Zimbabwe	26.87	39.74	73.06
12	Senegal	7.67	10.08	16.33
13	Kenya	7.63	15.25	37.23
14	Burkina Faso	7.09	10.23	18.35
15	South Africa	7.04	9.94	17.44
16	Benin	6.27	10.03	19.76
17	Cameroon	5.95	7.96	14.61
18	Nigeria	5.88	7.82	12.84
19	Uganda	4.59	7.38	14.60
20	Niger	2.83	3.71	5.98
21	Malawi	2.61	3.70	6.79
22	Chad	0.69	1.58	3.89
	All countries	885.09	1,222.33	2,104.40

Table 4. Average funding shortfalls in protected areas (PAs) with deficit within each country. Deficits are estimated by the African Parks Network method, the approach with the lowest minimum funding requirement. This table complements Table 2 by showing more information about deficit PAs in countries that contain very few PAs with deficits (e.g. Kenya and South Africa). Medians were calculated on PAs with deficits only; PAs with total funding per area exceeding estimated minimum funding requirements were omitted.

	African Parks Network			Our study			Packer et al.		
Country (ISO code)	Median deficit ($/km^2)	Median remaining need (%)*	PAs with deficit (%)†	Median deficit ($/km^2)	Median remaining need (%)*	PAs with deficit (%)†	Median deficit ($/km^2)	Median remaining need (%)*	PAs with deficit (%)†
Angola (AGO)	944	97	100	1,237	97	100	1,996	98	100
Benin (BEN)	421	43	100	714	56	100	1,473	73	100
Botswana (BWA)	778	80	100	1,071	84	100	1,830	90	100
Burkina Faso (BFA)	608	62	100	901	71	100	1,660	82	100
Cameroon (CMR)	957	98	75	1,250	98	100	2,009	99	100
Central African Republic (CAF)	861	88	100	1,154	91	75	1,902	94	100
Chad (TCD)	225	23	100	518	41	100	1,277	63	100
Democratic Republic of the Congo (COD)	862	88	100	1,155	91	100	1,914	94	100
Ethiopia (ETH)	918	94	94	1,211	95	94	1,967	97	100
Kenya (KEN)	502	51	30	795	63	30	684	34	85
Malawi (MWI)	768	79	50	998	79	75	1,757	87	75
Mozambique (MOZ)	853	87	86	1,144	90	90	1,899	94	95
Namibia (NAM)	812	83	100	1,105	87	100	1,864	92	100
Niger (NER)	935	96	100	1,228	97	100	1,987	98	100
Nigeria (NGA)	875	89	100	1,168	92	100	1,927	95	100
Senegal (SEN)	931	95	100	1,224	96	100	1,983	98	100
South Africa (ZAF)	532	54	22	825	65	22	1,584	78	22
South Sudan (SSD)	933	95	100	1,226	96	100	1,985	98	100
Tanzania (TAZ)	835	85	92	1,128	89	95	1,887	93	95
Uganda (UGA)	560	57	89	853	67	89	1,612	79	89
Zambia (ZMB)	862	88	100	1,155	91	100	1,914	94	100

	African Parks Network			Our study			Packer et al.		
Country (ISO code)	Median deficit ($\$/km^2$)	Median remaining need (%)*	PAs with deficit (%)†	Median deficit ($\$/km^2$)	Median remaining need (%)*	PAs with deficit (%)†	Median deficit ($\$/km^2$)	Median remaining need (%)*	PAs with deficit (%)†
Zimbabwe (ZWE)	737	75	100	1,030	81	100	1,789	88	100
Rwanda (RWA)	No deficit			No deficit			No deficit		
All countries	778	80	88	1,071	90	89	1,830	100	94

* Median percent of unmet minimum required funding relative to total available funding by PA.
† See Table 1 for total number of PAs in each country.

Table 5. Coefficients for top model from logistic regression identifying the threshold of *total* PA budget that best discriminated "effective" from "non-effective" PAs in 115 African PAs with lions. All other model subsets had delta AICc >2. "Effective" PAs are defined as maintaining lion populations >50% of carrying capacity. An ROC cut-off of 0.3129 was used to obtain the total budget threshold, leading to sensitivity and sensitivity values of 0.91 and 0.88, respectively. Covariates in the final model were TotalBudget (total PA budget), PercSettle (percentage of PA with human settlement), Rainfall (annual rainfall), and Rhino (rhino presence).

	Estimate	Std. Error	p-value
(Intercept)	-3.010	0.941	0.001384
TotalBudget	1.899	0.530	0.000343
PercSettle	-4.170	1.938	0.031438
Rainfall	-0.969	0.370	0.008802
Rhino	0.847	0.350	0.015448

Table 6. Results of linear regression identifying the covariates associated with higher *donor* PA budget in 115 African PAs with lions, showing multivariate models with delta AICc < 2. Covariates in the final model were MainUse (main uses of 2, 1, and 0 were mainly photographic tourism, mainly trophy hunting and neither tourism nor hunting, respectively), Comgmt (PA is co-managed by a non-profit organization), Area (PA area), IUCN_12 (PA is of IUCN category I or II), Fenced (PA is completely fenced), and GDP (Gross Domestic Product at national level).

	df	logLik	AICc	delta	weight	MainUse		Comgmt	Area	IUCN_12	Fenced	GDP
DonorBudget ~ MainUse + Comgmt + Area + IUCN_12 + Fenced + GDP	9	-214.58	448.7	0	0.384	MainUse0 MainUse1 MainUse2	3.56637 4.35671 4.60287	0.585	-0.3569	0.3693	0.2314	-0.2556
DonorBudget ~ MainUse + Comgmt + Area + IUCN_12 + GDP	8	-216.15	449.6	0.82	0.255	MainUse0 MainUse1 MainUse2	3.54123 4.28759 4.65000	0.6015	-0.3376	0.3835		-0.2354
DonorBudget ~ MainUse + Comgmt + Area + IUCN_12 + Fenced	8	-216.44	450.1	1.39	0.192	MainUse0 MainUse1 MainUse2	3.61052 4.44637 4.53596	0.6363	-0.4	0.3743	0.2099	
DonorBudget ~ MainUse + Comgmt + Area + IUCN_12	7	-217.71	450.4	1.64	0.169	MainUse0 MainUse1 MainUse2	3.58438 4.37677 4.58384	0.6477	-0.3794	0.3869		

Table 7. Coefficients for model-averaged top model (adjusted $R^2 = 0.91$) from results of linear regression identifying the covariates associated with higher *donor* PA budget in 115 African PAs with lions. Covariates in the final model were MainUse (main uses of 2, 1, and 0 were mainly photographic tourism, mainly trophy hunting and neither tourism nor hunting, respectively), Comgmt (PA is co-managed by a non-profit organization), Area (PA area), IUCN_12 (PA is of IUCN category I or II), Fenced (PA is completely fenced), and GDP (Gross Domestic Product at national level).

	Estimate	Std. Error
MainUse0 (No main use)	3.572	0.261
MainUse1 (Hunting as main use)	4.360	0.332
MainUse2 (Tourism as main use)	4.599	0.219
Comgmt	0.610	0.136
IUCN_12	0.377	0.177
Area	-0.364	0.134
GDP	-0.248	0.138
Fenced	0.224	0.136

Table 8. Coefficients for top model (adjusted $R^2 = 0.91$) from results of linear regression identifying the covariates associated with higher *state* PA budget in 115 African PAs with lions. All other model subsets had delta AICc >2. Covariates in the final model were Region (South, Central/West, East), GDP (Gross Domestic Product at national level), Area (PA area), TFCA (PA is part of transfrontier conservation area), Comgmt (PA is co-managed by a non-profit organization), IUCN_12 (PA is of IUCN category I or II), and Rhino (rhino presence).

	Estimate	Std. Error	p-value
Region: South	3.7644	0.1752	< 2e-16
Region: C/W	3.4681	0.3667	< 2e-5
Region: East	5.3733	0.2429	< 2e-16
GDP	0.7730	0.1436	< 2e-5
Area	-0.6375	0.1278	< 2e-5
TFCA	0.5937	0.1343	< 2e-5
Comgmt	-0.4633	0.1278	0.0004
IUCN_12	0.3530	0.1348	0.0100
Rhino	0.3481	0.1303	0.0086

Table 9. Data used in modelling the factors associated with PA budgets.

Category	Variable	Direction of hypothesised relationship with PA budgets	Source
Governance	Governance (national level); a combined metric of government effectiveness, corruption control, rule of law, and political stability. These indices were combined by calculating Z-scores for each and then summing the value of the Z-scores.	Positive: higher budgets with better governance because donors likely more willing to invest in more politically stable areas with better governance	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators, accessed August 2016.
	Government effectiveness	Positive: higher budgets with better governance	See above
	Corruption control	Positive: higher budgets with better governance	See above
	Rule of law	Positive: higher budgets with better governance	See above
	Political stability	Positive: higher budgets with better governance	See above
Socio-economic	Human infant mortality (national level)	Negative: higher budgets where human well-being is higher and poverty reduced	http://data.worldbank.org/indicator, accessed March 2016
	Proportion of PA occupied by human settlements and associated buildings or agricultural fields	Positive: higher budgets predicted where people are present in PAs, as the presence of people is often associated with illegal activities	Questionnaire surveys
	Presence of human settlement within the PA (1/0)	Higher budgets predicted where people are present in PAs, as the presence of people is often associated with illegal activities	Questionnaire surveys
	Mean human population density within 5, 10 and 20 km outside of the PA and PA complex (calculated separately; #/km^2)	Positive: higher budgetary requirements with higher densities of people, as more illegal activity and ranger patrolling would likely be necessary in the presence of more people	LandScan 2014™; ArcGIS
	Mean cattle density within 5, 10 and 20 km outside of the PA and PA complex (calculated separately; #/km^2)	Positive: higher livestock densities are likely to be associated with higher levels of threats such as incursions into PAs and human-wildlife conflict.	(31); ArcGIS

Management	PA completely fenced (1/0)	Budgets for managing lions are expected to be lower in fenced PAs (10)	Questionnaire surveys
	PA partly fenced (1/0)	Budgets for managing lions are expected to be lower in PAs with some fencing (10)	Questionnaire surveys
	Trophy hunting permitted within PA (1/0)	Negative: lower donor and state investments are expected in protected areas that permit hunting since hunting financially supports conservation	Questionnaire surveys
	Area of PA complex (km^2)	Negative: larger PA complexes likely to be associated with lower threats due to greater distances from human settlement.	(2); ArcGIS
	Whether PA is within a Transfrontier Conservation Area (TFCA)	Positive: PAs that are part of a larger PA network will have greater investment	Peace Parks Foundation (www.peaceparks.org); (2)
	Distance to nearest PA complex (km)	Positive: proximity to other PAs likely to be associated with better conservation outcomes greater tourism and higher budget	(2); ArcGIS
	Use of the reserve (no use, primarily trophy hunting, primarily photographic tourism)	Improved conservation outcomes and higher budgets expected in areas with tourism or trophy hunting due to revenue generated and greater management presence (32)	Questionnaire surveys
	Percentage of total PA management budget that comes from donors	Unknown	Study data (see methods)
	Percentage of total PA management budget that comes from the state	Unknown	Study data (see methods)
	Whether PA was under a long-term joint (or delegated) management arrangement whereby an NGO or private sector either shares or has the entire management responsibility (1/0)	Positive: Similarly, donor funding is considered more likely to succeed in the context of long-term projects where accountability is shared with a non-profit partner (33).	(2), questionnaire surveys

	IUCN PA category; whether the PA was category 1 or 2 versus other categories	Better conservation outcomes and therefore higher budgets in more strictly protected areas require higher budgets	(2), https://www.protectedplanet.net/
	Area of PA complex (km^2)	Unknown	(2); ArcGIS
Ecological	Rainfall	Unknown	WorldClim v 2.0 (34)
	Region (South, East, and Central/West)	Higher budgets in southern and East than West and Central Africa (35)	http://www.naturalearthdata.com/, accessed August 2016
	Rhinos are present within PA (1/0)	Positive: rhino presence will justify require higher PA budget	Questionnaire surveys

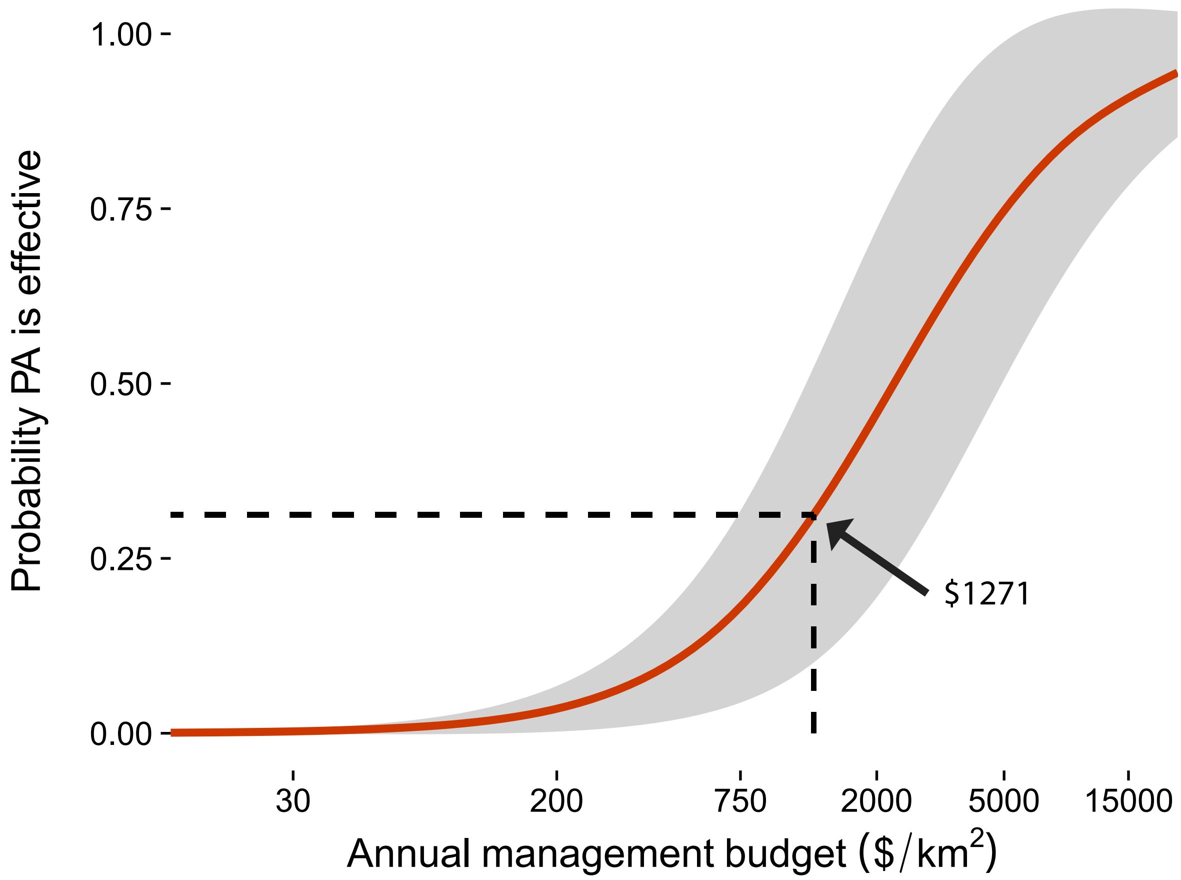

Figure 1. Minimum funding requirement estimated by our study method, which modelled the threshold of funding required annually in 115 protected areas (PAs) with lions to achieve effective conservation (lion populations at ≥ 50% carrying capacity).

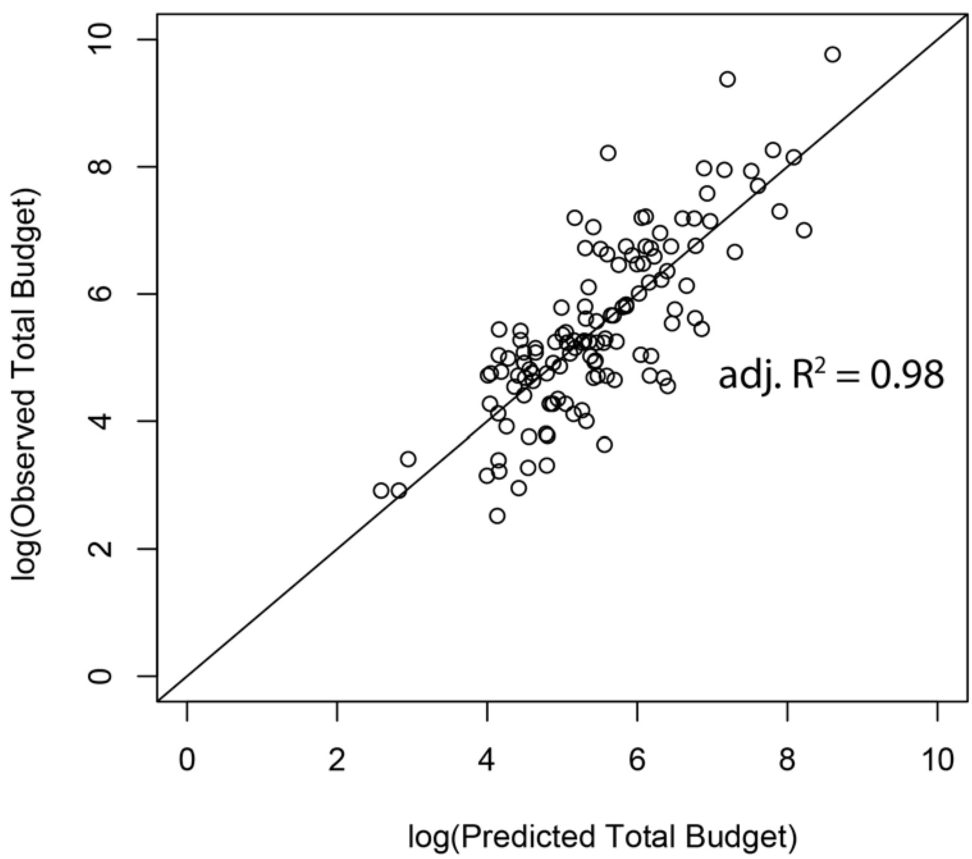

Figure 2. Observed and predicted values for the top regression model (adjusted $R^2 = 0.98$) identifying the covariates associated with higher total PA budget in 115 state-owned African PAs with lions. Covariates in the final model were MainUse (main uses of 2, 1, and 0 were mainly photographic tourism, mainly trophy hunting and neither tourism nor hunting, respectively), Area (PA area), TFCA (PA is part of transfrontier conservation area), Rhino (rhino presence), Comgmt (PA is co-managed by a non-profit organization), Fenced (PA is completely fenced), and CorruptionControl (corruption control).

Appendix 1. Definition of study protected areas.

We defined PAs following (1) as state-owned land officially gazetted as protected and where wildlife conservation and/or utilisation is considered to be the primary land use. Our definition included hunting areas and other local protected designations, as well as national parks, but excluded forest reserves, private land and community 'conservancies,' which typically occur on land with customary tenure/ownership. We excluded these areas to provide a conservative estimate of the lion range that is protected because the legal protection status of private and community land is variable, though we acknowledge that these areas are of high conservation value and serve as key sites in lion conservation. Because of this, our estimates of the cost to maintain extant populations of lions does not reflect the total funding needs for the management of wildlife areas in African lion range. PA boundaries were derived from the World Database of Protected Areas (2) and corrected by local experts. Lion range boundary was obtained from the IUCN Red List (3).

Appendix 2. Data sources and assumptions. 'Protected area' is abbreviated as 'PA'.

Country	Data source(s)	Notes
Angola	Expert surveys, direct contact with donors	Data were not available on state budgets, but respondents indicated that state budgets were close to zero on a per km^2 scale.
Benin	(4), direct contact with donors	
Botswana		The Department of Wildlife and National Parks availed data on their total, national-level management budgets. We assumed that 60% of this funding was used for PA management (the median proportion from a sample of 5 African countries). Management funding excluded compensation payments because in Botswana such payments are made by central government. Additional support for PA management is provided in Botswana by the Botswana Defence Force (BDF). The BDF had a budget of 2.04 billion Pula/year for the period 2014-5. Of this, a law enforcement expert working in northern Botswana estimated that 15% spent on anti-poaching per year.
Burkina Faso	(4), direct contact with donors	
Cameroon	Expert surveys, direct contact with donors	
CAR	Expert surveys, direct contact with donors	
Chad	Expert surveys, direct contact with donors	
DRC	Expert surveys, direct contact with donors	Data were not available on state budgets, but respondents indicated that state budgets were close to zero.
Ethiopia	(5)	(5) provided a detailed PA-by-PA assessment of the budgets of the wildlife authority and of donors.
Kenya	Expert surveys, Kenya Wildlife Service	Management funding excluded compensation payments because in Kenya such payments are made by the state.
Malawi	Surveys, direct contact with donors	
Mozambique	(6), expert surveys, direct contact with donors	(6) provided a comprehensive PA-by-PA assessment of the budgets provided by both the state and donors.

Country	Data source(s)	Notes
Namibia	(7), (8), (9), direct contact with donors, expert surveys	According to (7), 44% of the budget of the Ministry of Environment and Tourism was used for PA-management. (8) presented figures on the relative management budgets in different regions of Namibia (though estimates excluded salaries). We used the information on the proportional allocation of budgets to each PA presented in (8) to estimate PA specific budgets using the 2016 budget (9). In two PAs we used PA-specific budget data from expert surveys.
Niger	(4)	
Nigeria	Surveys, direct contact with donors	
Rwanda	Surveys, direct contact with donors	
Senegal	(4)	
South Africa	(10–15)	For PAs where data were lacking (6.6% of the area of PAs in lion range), we used the median PA budget from the areas for which did have data. Budgets for the management of state PAs are adequate for lion conservation, but are declining (anonymous SANParks respondent, June 2018). We were unable to comprehensively source data on donor support for South African PAs and consequentially omitted this category from analysis.
South Sudan	Expert surveys	
Tanzania	(10, 16), expert survey data, direct contact with donors	From the Tanzania National Parks Authority and Tanzania Wildlife Authority (TAWA) we obtained estimates of the total projected expenditure and total income in 2017 from Republic of Tanzania (2017). These estimates were adjusted to reflect the median expenditure on PA management (60% of total budget) from a sample of five countries where such data were available*.
Uganda	Expert surveys; direct contact with donors; (17)	Data are from 2009-2010 and were inflated to 2015 values, with the exception of one PA, for which 2015 data were obtained.
Zambia	(18)	National level estimate provided for the amount spent on PA management, which we divided by the total PA area.
Zimbabwe	Zimbabwe Parks and Wildlife Management Authority (ZPWMA)	The finance department of ZPWMA provide an estimate of the expenditure on PAs on a national level, which was divided by the area of the PAs in the country to yield an overall budget/km^2.

* We were able to source data on the proportion of wildlife authority budget allocated to PA management and associated salaries for: Ethiopia, [60%, (5)], Kenya [60%, Kenya Wildlife Service]), Mozambique [60%, (6)], Namibia [44%, (7)], and Zimbabwe [55%, Zimbabwe Parks and Wildlife Management Authority]).

Additional data sources:

Multi-lateral government agencies: We received data from the Austrian Development Cooperation, Banco Comercial de Investimentos, European Union, French Development Agency, German Corporation for International Development, German Development Bank, Global Environment Facility, Japanese International Cooperation Agency, United Nations Development Programme and Environment Programme, U.S. Agency for International Development, U.S. Fish and Wildlife Service and World Bank. Our sources for information on bilateral funding included Germany, France and the U.S., which provide 53% of total global bilateral conservation funding (19). Because bilateral funding is commonly spent through sub-contracts to non-profit organisations, a significant proportion of the remaining bi-lateral funding is likely to have been recorded via data collected from our contact with organisations and site-level surveys.

Non-profit organisations: We received data from 50 non-profit organizations, which included African Parks Network, African Wildlife Foundation, African World Heritage Fund, Born Free Foundation, Conservation International, Frankfurt Zoological Society, Nature and Biodiversity Conservation Union, Peace Parks Foundation, The Nature Conservancy, Wildlife Conservation Society and World Wildlife Fund for Nature.

Appendix 3. Data limitations.

Numerous researchers have recognised the notorious difficulty in obtaining budget data (e.g. (20). Our ambitious attempt to systematically track funding at a continental spatial scale offered several challenges that require consideration. These limitations simultaneously reveal systemic opacity and financial-management and accountability problems that likely contribute to the ineffectiveness of some protected areas (PAs). In several cases, country wildlife authorities were unwilling to share budget data (a challenge similarly experienced by Hanks and Attwell (21). In some cases, wildlife authorities were not *able* to calculate budgets for individual PAs, in one case because budgets are allocated to 'regions' rather than to individual PAs, and in another case due to apparent lack of adequate record keeping. For Botswana, Tanzania, Zambia, and Zimbabwe we lacked data on state wildlife budgets on a PA by PA basis but had information on the total budget of the state wildlife authorities (from which we derived budget data as explained in Appendix 1). Our degree of confidence in budget estimates varies among the countries presented. However in all cases, we are confident that our estimates fall within the right order of magnitude because we validated our numbers using PA-level survey estimates in several PAs in each country and cross-checking with published estimates where available.

Estimating levels of donor support is similarly challenging, and our estimates of donor contributions are underestimates for three reasons. Firstly, we were not able to obtain information on the investment in management provided by hunting operators who in some cases provide significant contributions to the management of PAs through support for law enforcement. However, given that the gross earnings from trophy hunting in most countries are <$400/km^2, resources available for management are likely to be modest in most cases once the operational costs (and profits) have been deducted (except in the cases where industry efforts are supported by philanthropists) (22). Secondly, we were not able to document expenditures by the entire multitude of low-budget non-profit organisations that support PA management in some parts of the continent. However, again, we are confident that these contributions would not substantially influence our conclusions because investments by such organisations are likely to be small relative to funding needs. Lastly, we lacked information from some bilateral donors. However, this omission is unlikely to substantially affect the general conclusions, firstly because such donors provide only ~$165 million of conservation aid globally (19), a small portion of which is likely to accrue to African PAs, and secondly because we are likely to have captured some of the support provided by such donors in our data on non-profit organisational support. Additionally, we were able to account for the funding provided by the US, Germany and France, which together are estimated to provide 53% of the world's bilateral donor funding (19). That said, in some instances donor funding estimates may include once-off Capex investments, which may inflate ongoing levels of donor support for operational expenditures.

Our estimates of funding requirements are meant to apply 'on average'. In many cases, the costs will be higher (such as where threats are particularly acute, and where PAs are remote and the terrain is difficult to patrol). Conversely, in some cases, costs may be lower (such as in PAs in areas bordered by other wildlife areas with low human densities and few threats). Large PAs are likely to benefit from economies of scale and for this reason, it is possible that our estimates of deficits for countries with exceptionally large PAs (such as Botswana, Tanzania and Zambia) may be over-estimated relative to those with smaller average PA sizes.

The primary threats facing lions are depletion of prey and direct mortality of lions in snares set by bushmeat hunters and retaliation following human-lion conflict (1, 23). Controlling these challenges is likely to be less expensive than tackling elephant and rhinoceros poaching, which is driven by poachers motivated by the high value of ivory and rhino horn (24, 25). African Parks Network has generally succeeded in controlling elephant poaching in the PAs in which they operate, suggesting that their budgets are adequate for controlling the threat. Our model of the costs of effectively managing lions is lower than funding requirements estimated by African Parks Network method because poaching of lions is not widespread. However, the targeted poaching of lions for their body parts is emerging as a serious issue, and if poaching becomes a widespread threat for lion population viability, the costs of conserving lions could increase dramatically (26).

Appendix 4. Modelling methods for our study method of estimating minimum funding requirements using logistic regression.

We standardised all variables according to (27) so the magnitude of the slope coefficients could be compared within and among models. We started with univariate models of all covariates and retained all models with some empirical support (ΔAIC_c of ≤ 7;(28). Univariate models were discarded if the candidate variable was correlated at $|r| \geq 0.60$ with another variable and the latter was a stronger predictor as determined by AIC_c. We then built multivariate models with all possible combinations of this variable set, and model-averaged those models with a ΔAIC_c of ≤ 2 (29). Each global model was assessed for homogeneity of model residuals via the Studentized Breusch-Pagan test prior to building model subsets.

We used the R package *ROCR* (30) to determine the Receiving Operator Curve (ROC) value that achieved best model predictive performance, namely the maximisation of both sensitivity (correctly identifying a PA as 'effective,' i.e. whether lions were present at $\geq 50\%$ of their carrying capacity) and specificity (correctly identifying a PA that is 'not effective'). In other words, the ROC value was equivalent to the predicted y value that best separated 'effective' from 'not effective' PAs. By setting this threshold as our predicted y value, and holding all other covariates at their mean, we were able to identify the minimum total budget per km^2 associated with 'effective' PAs.

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