



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

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

<sup>a</sup>Panthera, New York, NY 10018; <sup>b</sup>Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa; <sup>c</sup>Environmental Futures Research Institute, Griffith University, Nathan, QLD 4222, Australia; <sup>d</sup>Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; <sup>e</sup>Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210; <sup>f</sup>Centre for International Forestry Research, Bogor 16115, Indonesia; <sup>g</sup>Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Reanati-Kaplan Centre, Tubney OX13 5QL, United Kingdom; <sup>h</sup>African Wildlife Foundation, Nairobi 00502, Kenya; <sup>i</sup>Department of Wildlife and National Parks, Gaborone, Botswana; <sup>j</sup>Kenya Wildlife Service, Nairobi 00100, Kenya; <sup>k</sup>School of BioSciences, University of Melbourne, Melbourne, VIC 3052, Australia; <sup>l</sup>Zimbabwe Parks and Wildlife Management Authority, Harare, Zimbabwe; <sup>m</sup>Independent analyst/researcher, Maputo 1100, Mozambique; <sup>n</sup>Wildlife Conservation Society, Bronx, NY 10460; <sup>o</sup>Conservation Science Group, Zoology Department, Cambridge University, Cambridge CB2 3EJ, United Kingdom; <sup>p</sup>Independent Economic Researchers, Cape Town 8001, South Africa; and <sup>q</sup>School of Life Sciences, University of Kwazulu-Natal, Durban 4000, South Africa

Edited by James A. Estes, University of California, Santa Cruz, CA, and approved September 11, 2018 (received for review March 22, 2018)

**Protected areas (PAs) play an important role in conserving biodiversity and providing ecosystem services, yet their effectiveness is 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 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. We estimated minimum required funding as \$978/km<sup>2</sup> per year based on the cost of effectively managing lions in nine reserves by the African Parks Network; \$1,271/km<sup>2</sup> based on modeled costs of managing lions at ≥50% carrying capacity across diverse conditions in 115 PAs; and \$2,030/km<sup>2</sup> based on Packer et al.'s [Packer et al. (2013) *Ecol Lett* 16:635–641] cost of managing lions in 22 unfenced PAs. PAs with lions require a total of \$1.2 to \$2.4 billion annually, or ~\$1,000 to 2,000/km<sup>2</sup>, yet received only \$381 million annually, or a median of \$200/km<sup>2</sup>. Ninety-six percent of range countries had funding deficits in at least one PA, with 88 to 94% of PAs with lions funded insufficiently. In funding-deficit PAs, available funding satisfied just 10 to 20% of PA requirements on average, and deficits total \$0.9 to \$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 neighboring communities.**

budget | comanagement | conservation effectiveness | deficit | funding need

**P**rotected 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 to 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 revenue 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

## Significance

**Protected areas (PAs) are the cornerstone of conservation yet face funding inadequacies that undermine their effectiveness. Using the conservation needs of lions as a proxy for those of wildlife more generally, we compiled a 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 to \$2.4 billion or \$1,000 to \$2,000/km<sup>2</sup> annually, yet receive just \$381 million or \$200/km<sup>2</sup> (median) annually. Nearly all PAs with lions are inadequately funded; deficits total \$0.9 to \$2.1 billion. Governments and donors must urgently and significantly invest in PAs to prevent further declines of lions and other wildlife and to capture the economic, social, and environmental benefits that healthy PAs can confer.**

Author contributions: P.A.L., J.R.B.M., and L.S.P. designed research; P.A.L., J.R.B.M., L.S.P., L.C., A.J.D., K.H.F., M.V.F., P.J.F., P.H., S.K., K.K., A.J.L., D.W.M., R.L.M.-C., S.N., A.J.P., H.W.V.Z., and L.T.B.H. performed research; P.A.L. and L.S.P. contributed new reagents/analytic tools; J.R.B.M., L.S.P., L.C., A.J.D., K.H.F., M.V.F., P.J.F., P.H., S.K., K.K., A.J.L., D.W.M., R.L.M.-C., S.N., A.J.P., R.S., H.W.V.Z., and L.T.B.H. analyzed data; P.A.L., J.R.B.M., L.S.P., L.C., A.J.D., K.H.F., M.V.F., P.J.F., P.H., S.K., K.K., A.J.L., D.W.M., R.L.M.-C., S.N., A.J.P., R.S., H.W.V.Z., and L.T.B.H. wrote the paper; and L.T.B.H. supervised the project.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

<sup>1</sup>P.A.L., J.R.B.M., and L.S.P. contributed equally to this work.

<sup>2</sup>To whom correspondence should be addressed. Email: peter@wildnet.org.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1805048115/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1805048115/-DCSupplemental).

Published online October 22, 2018.

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 the variations in accounting methodologies between countries (27). Reputable estimates for African PA budgets are valuable but are now 10 to 34 y 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 amid 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 (31) and is 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. 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 among 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, for 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 square kilometers in 23 of 27 African lion-range countries (see *Methods* for information on data availability). 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<sup>2</sup> to \$17,449/km<sup>2</sup>, with a median of \$200/km<sup>2</sup>. When PAs were aggregated at a national scale, PAs in Cameroon received the lowest investment (median of \$21/km<sup>2</sup>), while PAs in four other countries (Angola, Niger, South Sudan, and Senegal) also received less than \$50/km<sup>2</sup> in total funding (Fig. 1 and Table 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; ref. 8), suffer from severe under-resourcing, with median budgets of less than \$300/km<sup>2</sup> (Table 1). Some countries, like Tanzania, are characterized by relatively higher budgets for national parks but lower budgets for other types of PAs, which comprise the majority of the protected es-

tate. At the other end of the spectrum, three countries showed budgets above \$1,600/km<sup>2</sup> (Kenya, Rwanda, and South Africa; Table 1). Regional funding was marginally higher in East Africa (median of \$265/km<sup>2</sup>) than in Southern (\$200/km<sup>2</sup>) or West-Central Africa (262/km<sup>2</sup>; *SI Appendix, Table S1*).

Three independent methods estimated that an annual minimum funding requirement of ~\$1,000 to \$2,000/km<sup>2</sup> is necessary, on average, for PAs to effectively conserve lions. African Parks Network spent a mean of \$978/km<sup>2</sup> (SD, \$773/km<sup>2</sup>) per year (range, \$497 to 1,833/km<sup>2</sup>). Our study model determined a higher threshold of \$1,271/km<sup>2</sup> for effective PAs (95% CI, \$457 to \$2,423/km<sup>2</sup>) (*SI Appendix, Fig. S1 and Table S2*). Packer et al.'s (5) inflation-adjusted estimate represented the highest requirement at \$2,030/km<sup>2</sup>.

These estimates predict that Africa's PAs with lions require a total of at least \$1.2 to \$2.4 billion annually to conserve lions effectively (Table 1). Among countries, total funding requirements generally varied with the number of PAs and the number of PAs with lions; for example, from as low as \$1 million in Rwanda ( $n = 1$  PA with lions) and \$3 million in Niger ( $n = 2$ ) and Chad ( $n = 1$ ), to as high as \$173 million in Tanzania ( $n = 37$ ) and \$203 million in Botswana ( $n = 49$ ), based on the African Parks Network method (Table 1).

In comparing available funding with required funding for effective conservation, we estimated a total annual deficit ranging from \$0.9 to \$2.1 billion across all assessed PAs (*SI Appendix, Table S3*). Funding deficits existed in 88% (African Parks Network) to 94% [Packer et al. (5)] of PAs with lions (Fig. 2). Of 23 countries assessed, 22 (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 (Rwanda was the only country without PA deficit; however, as stated earlier, Rwanda has  $n = 1$  PA with lions) Fig. 1B, Table 2, and *SI Appendix, Table S4*]. As expected, the highest total deficits occurred in countries with the most and largest PAs with lions: in Botswana ( $n = 49$  PAs with lions), Zambia ( $n = 35$ ), Tanzania ( $n = 37$ ), and Mozambique ( $n = 21$ ) (Fig. 1A). In ranking countries by median deficit per square kilometer, the highest deficits occurred in the Central African Republic (\$944 to \$2,009/km<sup>2</sup>;  $n = 4$ ) and Angola (\$944 to \$1,996/km<sup>2</sup>;  $n = 1$ ), where only 1 to 2% and 2 to 3% of funding needs were met on average, respectively (Fig. 1B and Table 2).

In PAs with deficits, just 10 to 20% of funding requirements were available on average (*SI Appendix, Table S4*). Funding shortfalls were widespread and extensive: 27 to 59% of countries in deficit showed shortages of >90% of required funding on average (Fig. 3). The vast majority of countries (87%) reported lower average available funding per square kilometer across all PAs than even the lowest \$978/km<sup>2</sup> 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 and 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 in other regions, whereas donor funding per unit area was higher in West-Central Africa than in other regions (*SI Appendix, Table S1*). Accordingly, several countries in Southern Africa (Botswana and Namibia) and East Africa (Kenya and Tanzania) were especially reliant on state support, while several countries in West-Central Africa (Democratic Republic of the Congo and Central African Republic) and Southern Africa (Angola and Malawi) were largely reliant on donor contributions (Fig. 4).

Higher funding per square kilometer was associated with smaller-sized, fully fenced PAs that contained rhinos, supported

**Table 1. Management funding and estimated minimum need for effective lion conservation in PAs with lions, aggregated by country**

Rank	Country (ISO code)	Region	Total funding		State funding		Donor funding		Minimum required funding,* \$mil			Lion PA total area, km <sup>2</sup>	
			Median, \$/km <sup>2</sup>	Total, \$mil	Median, \$/km <sup>2</sup>	Total, \$mil	Median, \$/km <sup>2</sup>	Total, \$mil	African Parks Network	Our study	Packer et al. (5)		PAs with lions, <i>n</i>
1	South Africa (ZAF)	Southern	3,014 <sup>†</sup>	57.59 <sup>†</sup>	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 <sup>†</sup>	2.29 <sup>†</sup>	No data	No data	753	2.29	2.98	3.87	6.18	1	3,043
5	Malawi (MWI)	Southern	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)	Southern	241	16.06	235	10.32	1 or 272 <sup>‡</sup>	5.75	42.94	55.80	89.12	22	43,903
10	Botswana (BWA)	Southern	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)	Southern	166	17.07	0	13.29	35	3.78	63.34	82.31	131.47	10	64,763
13	Mozambique (MOZ)	Southern	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 <sup>§</sup>	116	11.19	47.70	61.99	99.01	5	48,771
16	Zambia (ZMB)	Southern	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)	Southern	34	2.66	~0 <sup>  </sup>	~0.00 <sup>  </sup>	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	380.72	104	257.21	55	123.50	1173.18	1524.65	2435.13	282	1,199,570

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. ISO, International Organization for Standardization; \$mil, million dollars.

\*Minimum funding requirement based on each method: African Parks Network, \$978/km<sup>2</sup>; our study, \$1,271/km<sup>2</sup>; and Packer et al. (5), \$2,030/km<sup>2</sup>.

<sup>†</sup>Represents an underestimation, as South Africa estimates did not include donor data and Chad did not include state data.

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

<sup>§</sup>State contributions for the Democratic Republic of the Congo totaled ~\$3,000.

<sup>||</sup>Data were not available, but experts indicated that state budgets were close to \$0/km<sup>2</sup>.

active tourism, were part of a Transfrontier Conservation Area (TFCA), were jointly managed by a nonprofit organization, and were located in a country with lower corruption (model fit  $R^2 = 0.98$ ; *SI Appendix*, Fig. S2 and Table S5). Donor contributions were higher in smaller, fully fenced PAs of IUCN category I or II that supported active tourism, were comanaged by a nonprofit partner, and were located in countries with lower gross domestic product (GDP) ( $R^2 = 0.91$ ; *SI Appendix*, Tables S6 and S7). Greater state funding was associated with smaller PAs that contained rhinos, were part of a TFCA and IUCN category I or II located in East Africa and in countries with higher GDP, and were not comanaged by a nonprofit ( $R^2 = 0.91$ ; *SI Appendix*, Table S8).

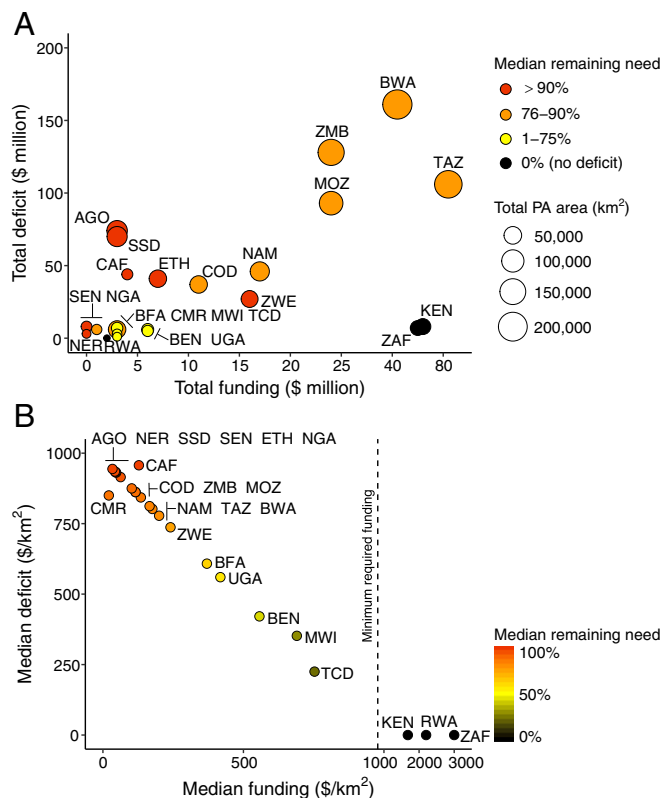
Among PAs, higher funding per square kilometer was associated with higher management capacity ( $r = 0.54$ ,  $P < 0.001$ ; Fig. 5A), lower threat to wildlife ( $r = -0.28$ ,  $P = 0.001$ ; Fig. 5B), and

the availability of more patrol vehicles and staff ( $r = 0.71$  and  $r = 0.67$ , respectively, both  $P < 0.001$ ; Fig. 5C and D). 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—that is, adding \$0.9 to \$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





**Fig. 1.** The most underfunded countries for lion conservation, in terms of total available (A) and median available (B) 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<sup>2</sup>). See Tables 1 and 2 for the number of deficit PAs in each country, country rankings, and International Organization for Standardization country codes.

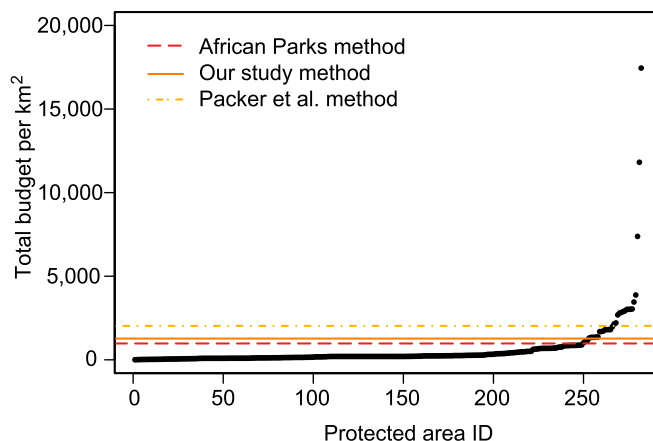
of PAs and countries receive a fraction of the funding needed to conserve lion populations and broader ecosystems effectively. In some countries (e.g., Zimbabwe), although moderate funding from the state is available, substantial proportions are tied up for salaries, leaving modest amounts for operations. 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 despite 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 re-

quired 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 to 2,000/km<sup>2</sup> to effectively conserve lions and their broader ecosystems. The African Parks Network method (\$978/km<sup>2</sup>) 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. Channeling an elevated proportion of funding to PAs through accountable nongovernmental organization (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 manage finances transparently are also important. Our study method (\$1,271/km<sup>2</sup>) 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  $\geq 50\%$  of carrying capacity. Packer et al.'s (5) method (\$2,030/km<sup>2</sup>) 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 to 424/km<sup>2</sup> for forest parks in Central Africa in 2004 (29) and \$459/km<sup>2</sup> for parks Africa-wide in 1984 (28), our estimates approximate the \$1,010/km<sup>2</sup> estimated need for managing tigers in Asia (39) [all figures in 2015 US dollars (USD)].

We emphasize that the two higher-end estimates (\$1,271/km<sup>2</sup> and \$2,030/km<sup>2</sup>, or \$1.2 to \$2.4 billion total annually across all



**Fig. 2.** Annual funding (\$/km<sup>2</sup>) for 282 African PAs with lions (black circles) compared with minimum required need as estimated by the African Parks Network method (\$978/km<sup>2</sup>), our study method (\$1,271/km<sup>2</sup>), and the Packer et al. (5) method (\$2,030/km<sup>2</sup>). Of the 282 PAs, 249 (88%), 252 (89%), and 266 (94%) failed to meet the minimum benchmarks of the African Parks Network, our study, and Packer et al. methods, respectively.

**Table 2. The most underfunded countries for protected area (PA) management and lion conservation**

Rank	Country (ISO code)	African Parks Network			Our study			Packer et al. (5)		
		Median deficit, \$/km <sup>2</sup>	Median remaining need,* %	PAs with deficit, <sup>†</sup> %	Median deficit, \$/km <sup>2</sup>	Median remaining need,* %	PAs with deficit, <sup>†</sup> %	Median deficit, \$/km <sup>2</sup>	Median remaining need,* %	PAs with deficit, <sup>†</sup> %
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

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<sup>2</sup>). 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 Appendix, Table S4*, which shows median deficits by country calculated using only PAs with deficits. ISO, International Organization for Standardization. \*Median percent of unmet minimum required funding relative to total available funding by PA.

<sup>†</sup>See Table 1 for total number of PAs with lions in each country.

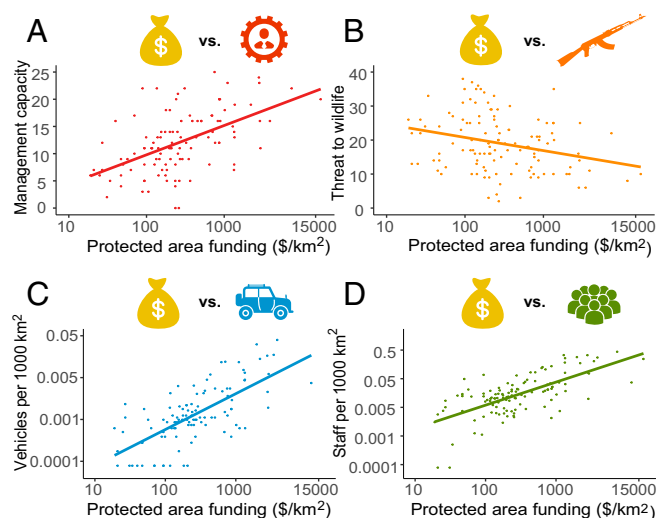
PAs with lions) are the minimum amounts necessary under current conditions to manage lion populations at half of the potential population size. However, 50% of carrying capacity is a low benchmark for conservation effectiveness, particularly for lions, which have such great ecological and economic value. 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 in which 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 were to receive the increase in funding that we recommend, all wildlife species would benefit; with that said, our estimates may not reflect the additional funding potentially needed to conserve rhinos due to the high prices obtained by illegal wildlife traders for their horns and the vigor 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). The human population is growing faster in Africa than in 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





**Fig. 5.** Associations between funding in 125 of Africa's PAs with lions and management capacity (A), threats to wildlife (B), vehicles available for patrols (C), and number of staff (D). 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 directionality of Pearson correlations.

PAs, rather than the large, nonrecurrent funding packages commonly provided by multilateral 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 fulfill 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 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 for which 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, Appendix 1*). Total funding comprised state funding (contributed by the PA country government) and donor funding (contributed by nonstate groups, including nonprofit organizations, charitable foundations, and bi- and multilateral agencies). Management funding included costs related to staff, law enforcement, maintenance of infrastructure and roads, habitat management, and engagement with adjacent communities. Sources (see *SI Appendix, Appendix 2* for details) broadly included (i) expert surveys (see ref. 3 for methods), (ii) wildlife authorities, (iii) 50 nonprofit organizations involved in PA management, (iv) private hunting companies, and (v) major donors in-

involved in PA management, such as foundations, nonprofit organizations, and multilateral government agencies. We obtained both state and donor funding data from 282 state-owned PAs with lions in 23 countries, except for Chad, for which we were not able to obtain state data, and South Africa, for which we could not comprehensively capture donor contributions [however, state budgets for PAs in South Africa are substantially higher than in other countries and sufficient for effective lion management (3)]. We emphasize the major challenges associated with obtaining budget data and that our estimates of donor support are likely underestimates (*SI Appendix, Appendix 3*). Nonetheless, we 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 channeled to other organizations to avoid double counting resources. We primarily obtained budget data for the fiscal year spanning 2015 to 2016, but in rare cases in which data were 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 USD 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 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:

- i) African Parks Network method: We acquired data on management budgets for each PA managed by the African Parks Network, a nonprofit organization 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.
- ii) 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 data 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 following equation (64):

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

where 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 (64) and paired these with data on lion population estimates from ref. 3. Using effectiveness as a predictor variable and total funding [USD per square kilometer ( $\$/\text{km}^2$ )] as a required response variable from a pool of 35 candidate variables (*SI Appendix, Table S1*), we built a multivariate model to predict PA effectiveness. We then identified the funding threshold that best discriminated effective from noneffective PAs (see *SI Appendix, Appendix 4* for details).

- i) Packer et al. (5) method: We applied Packer et al.'s finding based on 22 PAs that \$2,000/ $\text{km}^2$  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 (in USD) for each PA and then aggregated PAs by country. PA



funding need was calculated as the minimum funding requirement (\$/km<sup>2</sup>) multiplied by PA area (km<sup>2</sup>). 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<sup>2</sup>) was calculated as PA deficit divided by PA area. 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, 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 Appendix, Table S9*).

**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 (see ref. 3 for details) on (i) the number of vehicles and rangers available for management; (ii) a rating of different aspects of management capacity on a scale of 1 to 5, which we summed to generate an overall management capacity score; and (iii) a rating of the severity of 11 specific threats to wildlife on a scale of 1 to 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.

**ACKNOWLEDGMENTS.** We thank the staff at the state wildlife agencies and nonprofit and donor organizations who generously provided information. We thank Elizabeth Schultz, Timothy Hodgetts, Richard Davies, Craig Packer, Kelsey Farson, Justin Brashares, and members of the Brashares laboratory at University of California, Berkeley for providing feedback that improved the manuscript. Panthera provided funding to support the study. J.R.B.M. was supported in part by National Science Foundation Coupled Human and Natural Systems Grant 115057. L.C. was funded by the US Agency for International Development.

- Bruner AG, Gullison RE, Rice RE, da Fonseca GAB (2001) Effectiveness of parks in protecting tropical biodiversity. *Science* 291:125–128.
- Hilborn R, et al. (2006) Effective enforcement in a conservation area. *Science* 314:1266.
- Lindsey PA, et al. (2017) The performance of African protected areas for lions and their prey. *Biol Conserv* 209:137–149.
- Macdonald EA, et al. (2015) Conservation inequality and the charismatic cat: *Felis feliscis*. *Glob Ecol Conserv* 3:851–866.
- Packer C, et al. (2013) Conserving large carnivores: Dollars and fence. *Ecol Lett* 16:635–641.
- Craigie ID, et al. (2010) Large mammal population declines in Africa's protected areas. *Biol Conserv* 143:2221–2228.
- Lindsey PA, et al. (2014) Underperformance of African protected area networks and the case for new conservation models: Insights from Zambia. *PLoS One* 9:e94109.
- Riggio J, et al. (2013) The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodivers Conserv* 22:17–35.
- Watson JE, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. *Nature* 515:67–73.
- Bauer H, et al. (2015) Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc Natl Acad Sci USA* 112:14894–14899.
- Lindsey PA, Balme GA, Funston PJ, Henschel PH, Hunter LTB (2016) Life after Cecil: Channelling global outrage into funding for conservation in Africa. *Conserv Lett* 9:296–301.
- Infield M (2001) Cultural values: A forgotten strategy for building community support for protected areas in Africa. *Conserv Biol* 15:800–802.
- Van Zyl H (2015) The economic value and potential of protected areas in Ethiopia. Report for the Ethiopian Wildlife Conservation Authority under the Sustainable Development of the Protected Areas System of Ethiopia Programme (Independent Economic Researchers, Cape Town, South Africa).
- Egoh B, Reyers B, Rouget M, Bode M, Richardson DM (2009) Spatial congruence between biodiversity and ecosystem services in South Africa. *Biol Conserv* 142:553–562.
- Van Jaarsveld AS, et al. (2005) Measuring conditions and trends in ecosystem services at multiple scales: The Southern African Millennium Ecosystem Assessment (SAfMA) experience. *Philos Trans R Soc Lond B Biol Sci* 360:425–441.
- Rylance A, Spenceley A (2017) Reducing economic leakages from tourism: A value chain assessment of the tourism industry in Kasane, Botswana. *Dev South Afr* 34:295–313.
- Gössling S (1999) Ecotourism: A means to safeguard biodiversity and ecosystem functions? *Ecol Econ* 29:303–320.
- Snyman SL (2012) The role of tourism employment in poverty reduction and community perceptions of conservation and tourism in southern Africa. *J Sustain Tour* 20:395–416.
- Balmford A, et al. (2009) A global perspective on trends in nature-based tourism. *PLoS Biol* 7:e1000144.
- Scholes RJ, Biggs R (2004) *Ecosystem Services in Southern Africa: A Regional Assessment* (Council for Scientific and Industrial Research, Pretoria, South Africa).
- Lindsey PA, et al. (2017) Relative efforts of countries to conserve world's megafauna. *Glob Ecol Conserv* 10:243–252.
- Pringle RM (2017) Upgrading protected areas to conserve wild biodiversity. *Nature* 546:91–99.
- Mansourian S, Dudley N (2008) Public funds to protected areas (WWF International, Gland, Switzerland).
- Kideghesho J, Rija A, Mwamende K, Selemani I (2013) Emerging issues and challenges in conservation of biodiversity in the rangelands of Tanzania. *Nat Conserv* 6:1–29.
- Norton-Griffiths M, Southey C (1995) The opportunity costs of biodiversity conservation in Kenya. *Ecol Econ* 12:125–139.
- Mascia MB, et al. (2014) Protected area downgrading, downsizing, and degazettement (PADDD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. *Biol Conserv* 169:355–361.
- Wilkie D, Carpenter JF, Zhang Q (2001) The under-financing of protected areas in the Congo Basin: So many parks and so little willingness-to-pay. *Biodivers Conserv* 10:691–709.
- Bell RHV, Clarke JE (1984) Funding and financial control. *Conservation and Wildlife Management in Africa*, eds Bell R, McShane-Caluzi E (U.S. Peace Corps, Washington, DC), pp 545–555.
- Blom A (2004) An estimate of the costs of an effective system of protected areas in the Niger Delta–Congo Basin forest region. *Biodivers Conserv* 13:2661–2678.
- James AN, Green MJBB, Paine JR (1999) A global review of protected area budgets and staff (World Conservation, Cambridge, UK). Available at <https://www.cbd.int/financial/expenditure/g-spendingglobal-wcmc.pdf>. Accessed January 3, 2018.
- Bauer H, Packer C, Funston PJ, Henschel PH, Nowell K (2016) *Panthera leo*. *The IUCN Red List of Threatened Species 2016*, e.T15951A115130419. Available at <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en>. Accessed January 3, 2018.
- Ripple WJ, et al. (2014) Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- Henschel PH, et al. (2016) Determinants of distribution patterns and management needs in a critically endangered lion *Panthera leo* population. *Front Ecol Evol* 4:110.
- Leader-Williams N, Albon SD, Berry P (1990) Illegal exploitation of black rhinoceros and elephant populations: Patterns of decline, law enforcement and patrol effort in Luangwa Valley, Zambia. *J Appl Ecol* 27:1055–1087.
- Geldmann J, et al. (2018) A global analysis of management capacity and ecological outcomes in terrestrial protected areas. *Conserv Lett* 11:e12434.
- Jachmann H (2008) Monitoring law-enforcement performance in nine protected areas in Ghana. *Biol Conserv* 141:89–99.
- Lindsey PA, et al. (2011) Dynamics and underlying causes of illegal bushmeat trade in Zimbabwe. *Oryx* 45:84–95.
- Baghai M, et al. (2018) Models for the collaborative management of Africa's protected areas. *Biol Conserv* 218:73–82.
- Walston J, et al. (2010) Bringing the tiger back from the brink—the six percent solution. *PLoS Biol* 8:1–4.
- MacKinnon J, Aveling C, Olivier R, Murray M, Carlo P (2015) Larger than elephants: Inputs for the design of an EU strategic approach to wildlife conservation in Africa (Publications Office of the European Union, Brussels). Available at [https://ec.europa.eu/europeaid/sites/devco/files/eu-wildlife-strategy-africa-synthesis-2015\\_en\\_0.pdf](https://ec.europa.eu/europeaid/sites/devco/files/eu-wildlife-strategy-africa-synthesis-2015_en_0.pdf). Accessed January 3, 2018.
- Wasser SK, et al. (2015) Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science* 349:84–87.
- Biggs D, Courchamp F, Martin R, Possingham HP (2013) Legal trade of Africa's Rhinoceros horns. *Science* 339:1038–1039.
- Williams VL, Loveridge AJ, Newton DJ, Macdonald DW (2017) Questionnaire survey of the pan-African trade in lion body parts. *PLoS One* 12:e0187060.
- Bradshaw CJA, Brook BW (2014) Human population reduction is not a quick fix for environmental problems. *Proc Natl Acad Sci USA* 111:16610–16615.
- Gerland P, et al. (2014) World population stabilization unlikely this century. *Science* 346:234–237.
- Naughton-Treves L, Holland MB, Brandon K (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annu Rev Environ Resour* 30:219–252.
- Naughton-Treves L, Alix-García J, Chapman CA (2011) Lessons about parks and poverty from a decade of forest loss and economic growth around Kibale National Park, Uganda. *Proc Natl Acad Sci USA* 108:13919–13924.
- Ferraro PJ, Hanauer MM, Sims KRE (2011) Conditions associated with protected area success in conservation and poverty reduction. *Proc Natl Acad Sci USA* 108:13913–13918.



49. UNWTO (2014) Towards measuring the economic value of wildlife watching tourism in Africa (World Tourism Organization, Madrid). Available at [sdt.unwto.org/content/unwto-briefing-wildlife-watching-tourism-africa](http://sdt.unwto.org/content/unwto-briefing-wildlife-watching-tourism-africa). Accessed January 3, 2018.
50. WTTC (2015) Travel and tourism, the economic impact: Sub-Saharan Africa 2015 (World Travel & Tourism Council, London). Available at <https://www.wttc.org/-/media/files/reports/economic%20impact%20research/regional%202015/subsaharanafrica2015.pdf>. Accessed January 3, 2018.
51. Lindsey PA, Alexander R, Mills MGL, Romañach S, Woodroffe R (2007) Wildlife viewing preferences of visitors to protected areas in South Africa: Implications for the role of ecotourism in conservation. *J Ecotour* 6:19–33.
52. Trade and Development Board (2017) Economic development in Africa Report 2017: Tourism for transformative and inclusive growth (United Nations, New York). Available at [unctad.org/en/PublicationsLibrary/aldcafrica2017\\_en.pdf](http://unctad.org/en/PublicationsLibrary/aldcafrica2017_en.pdf). Accessed January 3, 2018.
53. OECD (2017) Development aid at a glance: Statistics by region. 2. Africa. (Organisation for Economic Co-Operation and Development, Paris). Available at [www.oecd.org/dac/stats/documentupload/Africa-Development-Aid-at-a-Glance.pdf](http://www.oecd.org/dac/stats/documentupload/Africa-Development-Aid-at-a-Glance.pdf). Accessed January 3, 2018.
54. Ferraro PJ, Kiss A (2002) Direct payments to conserve biodiversity. *Science* 298:1718–1719.
55. Lapeyre R, Laurans Y (2017) Contractual arrangements for financing and managing African protected areas: Insights from three case studies. *Parks* 23:75–88.
56. Thapa B (1998) Debt-for-nature swaps: An overview. *Int J Sustain Dev World Ecol* 5:249–262.
57. OANDA (2017) Average exchange rates. Available at <https://www.oanda.com/fx-for-business/historical-rates>. Accessed July 1, 2017.
58. US Bureau of Labor Statistics (2017) CPI inflation calculator (US Bureau of Labor Statistics, Washington, DC). Available at [https://www.bls.gov/data/inflation\\_calculator.htm](https://www.bls.gov/data/inflation_calculator.htm). Accessed July 1, 2017.
59. R Core Team (2017) R: A Language and environment for statistical computing, v.3.5.1 (The R Foundation for Statistical Computing, Vienna). Available at [www.r-project.org](http://www.r-project.org). Accessed January 3, 2018.
60. Hayward MW, O'Brien J, Kerley GIH (2007) Carrying capacity of large African predators: Predictions and tests. *Biol Conserv* 139:219–229.
61. Coe MJ, Cumming DH, Phillipson J (1976) Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341–354.
62. East R (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr J Ecol* 22:245–270.
63. Fritz H, Duncan P (1994) On the carrying capacity for large ungulates of African savanna ecosystems. *Proc Biol Sci* 256:77–82.
64. Loveridge AJ, Canney S (2009) Report on the lion distribution and conservation modelling project: Final report (Born Free Foundation, Horsham, UK), p 58.