The performance of African protected areas for lions and their prey, determinants of success and key conservation threats

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Abstract

Using surveys of experts associated with 186 sites across 24 countries, we assessed the effectiveness of African protected areas (PAs) at conserving lions and their prey, identified factors that influence conservation effectiveness, and identified patterns in the severity of various threats. Less than one third of sampled PAs conserve lions at ≥ 50% of their estimated carrying capacity (K), and less than half conserve lion prey species at ≥ 50% of K. Given adequate management, PAs could theoretically support up to 4x × the total extant population of wild African lions (~ 83,000), providing a measurable benchmark for future conservation efforts. The performance of PAs shows marked geographic variation, and in several countries there is a need for a significant elevation in conservation effort. Bushmeat poaching was identified as the most serious threat to both lions and to wildlife in general. The severity of threats to wildlife in PAs and the performance of prey populations were best predicted by geographic-socioeconomic variables related to the size of PAs, whether people were settled within PAs, human/livestock densities in neighbouring areas and national economic indicators. However, conservation outcomes for lions were best explained by management variables. PAs tended to be more effective for conserving lions and/or their prey where management budgets were higher, where photographic tourism was the primary land use, and, for prey, where fencing was present. Lions and prey fared less well relative to their estimated potential carrying capacities in poorer countries, where people were settled within PAs and where PAs were used for neither photographic tourism nor trophy hunting.

1.1

Introduction

Protected areas (PAs) are critical to the protection of biodiversity and habitat integrity (Geldmann et al., 2013). Approximately 209,000 PAs exist globally, covering ~ 15.4% of the world''s land and inland waters (Juffe-Bignoli et al., 2014). State-owned terrestrial PAs in Africa cover 14.7% of the continent''s land area, slightly less than the global average (Juffe-Bignoli et al., 2014), yet some African countries have set aside vast PA networks. For example, Botswana has gazetted 40% of its terrestrial area as PAs, Zambia 38% and Tanzania 32% (www.protectedplanet.net, accessed October 2016, Botswana Department of Wildlife and National Parks unpublished data). African countries are also home to some of the largest individual PAs. For example, Tanzania''s Selous Game Reserve and adjacent buffer zones cover ~ 90 000 km2, the Luengue-Luiana-Mavinga complex of parks in Angola encompass ~ 84,200 km2, and Kafue National Park complex in Zambia > 66 ,000 km2. Furthermore, several (mainly southern) African countries have established treaties to conserve even larger areas through the establishment of transfrontier conservation areas (TFCAs) (MacKinnon et al., 2015), such as the ~ 520,000 km2 Kavango-Zambezi TFCA.

PAs contain essential habitat for many of Africa’'s most iconic, threatened and endemic species (Bergl et al., 2007). Parks and reserves are a central component of sub-Saharan Africa’'s tourism industry, which creates millions of jobs and which has been valued at US$25 billion (WTTC, 2016). PAs are thus of key importance from ecological, economic and social perspectives, and through the provision and maintenance of ecological services (MacKinnon et al., 2015; Van Zyl, 2015). However, while frequently valuable on national levels, PAs rarely cover their costs at a site level (MacKinnon et al., 2015), and can impose significant costs on local people through human-wildlife conflict and foregone opportunities for using the land for alternatives (Brockington and Igoe, 2006). Such issues can undermine political support for government expenditure on PAs and local support for their existence.

The importance of PAs to conservation efforts will increase with time as human populations grow and habitat in unprotected lands is converted for agriculture and settlement or to compensate for decreased productivity on over utilised land (Caro, 2015). This is of particular significance in Africa, where the human population is projected to grow from 1.1 to 2.8 billion by 2060 (Canning et al., 2015). Even under current human population densities, the effectiveness of many PAs at conserving biodiversity is questionable, and many are under-performing (Craigie et al., 2010; Lindsey et al., 2014). This is particularly evident in West and Central Africa (Bouché et al., 2010; Henschel et al., 2014b; Henschel et al., 2015; Bauer et al., 2015a).

Human pressures on PAs take various forms, including poaching, encroachment by humans and livestock, mining and deforestation (Okello and Kiringe, 2004; Lindsey et al., 2014). These anthropogenic pressures on PAs are becoming more severe, yet resources available for management and protection are often far from adequate (James et al., 1999; Mansourian and Dudley, 2008; Lindsey et al., 2016; Henschel et al., 2016b) and there is little information on the impacts of these threats on conservation outcomes. In addition, the functionality of PAs is often undermined further by mismanagement and corruption (Smith et al., 2003).

1.1.1.1

Protected areas and African lion conservation

The African lion (Panthera leo) is an iconic and charismatic species that is highly valued by society (Macdonald et al., 2015). Lions play a key ecological role due to their status as apex predators (Ripple et al., 2014), and have significant economic value as drawcards for photographic tourism and trophy hunting (Lindsey et al., 2007; Lindsey et al., 2012a). The species has significant cultural value to some societies (in Africa and elsewhere), such as being symbols of royalty, acting as sports emblems, or being totems. Lions also confer value in some places through the illegal and legal trade in lion body parts (Williams et al., 2016).

Despite their social, ecological, and economic value, lions have undergone significant declines in numbers and geographic range in recent years. Lion numbers declined ~ 43% during 1993-–2014, with particularly marked declines in West and Central Africa (Bauer et al., 2015a). As few as 23,000 individuals persist in the wild and the species is listed as Vulnerable on the IUCN Red List (Henschel et al., 2015); in West Africa, they are considered Critically Endangered (Henschel et al., 2015; Bauer et al., 2015c). Approximately ~ 56% of lion range has protected area status; when well managed, these PAs can frequently support high lion densities (Riggio et al., 2012).

Key threats to lions include human-lion conflict, habitat destruction, depletion of prey populations, targeted poaching of lions for their body parts and poorly regulated trophy hunting (Bauer et al., 2015a). However, the relative importance of those threats in specific PAs is poorly understood. Threats to lions and other wildlife are often exacerbated by unfavourable policies, political and economic instability and institutional weakness on the part of state wildlife authorities and lack of adequate resources by protected area authorities to mitigate these threats (MacKinnon et al., 2015). There have been some attempts to understand the determinants of conservation success for lions in West Africa (Henschel et al., 2014b), and a narrow focus on the role of management interventions such as fencing in influencing conservation outcomes (Packer et al., 2013; Creel et al., 2013). However, little is known about the performance of individual PAs continent-wide, patterns in the threats facing them and the factors that influence their effectiveness (Geldmann et al., 2013).

Thus, we build upon previous work by looking more broadly at the role of PAs in conservation success, using the African lion as our focal species. We sought to understand, at a protected area level, (1) which PAs are currently sustaining lion populations at 50% or above estimated carrying capacity, (2) what factors are associated with positive conservation outcomes for lions and their prey, and (3) to understand patterns in severity of five main threats to African wildlife in PAs, namely: illegal hunting for bushmeat, encroachment by humans for settlement or agriculture, encroachment by livestock for grazing, human-wildlife conflict, and the poaching of wildlife for non-meat body parts (e.g. ivory, skins, scales, teeth or other products).

2.2 Methods

2.1.2.1 PAs in lion range

We assessed the number and area of PAs in lion range, and estimated the potential lion population that could be conserved on such an area. The potential carrying capacity for lions for each site was estimated using a model that predicts the variation in lion density based on soil type and rainfall (Loveridge, 2009). For the purposes of estimating the area of land under protection in lion range, and estimating potential lion numbers if those areas were managed optimally, we defined PAs as being state-owned land officially gazetted as a protected area, and where wildlife conservation/utilisation is considered to be the primary land use (excluding private land and community 'conservancies', which typically occur on land with customary tenure/ownership). We excluded wildlife areas on private and community land to provide a conservative estimate of the lion range that is protected because the legal protection status of such land is variable. However, we do acknowledge that private and community conservation areas are of high conservation value. Our definition included hunting areas and other local protected designations as well as national parks. We excluded PA complexes (individual PAs or groups of contiguous PAs) of < 1000 km2, except in South Africa, where fencing and intensive management allows for the maintenance of lion populations in smaller areas (Packer et al., 2013). Consequently, in South Africa, where PAs are fenced, our cut off for inclusion was 500 km2. A cut off of 500 km2 allowed for the inclusion of some South African reserves, while excluding very small reserves where management is likely to be so intensive as to preclude meaningful comparison with PAs in other parts of Africa.

2.2.2.2 Surveys

We conducted an online questionnaire survey of individuals with expertise of PAs within lion range (Appendix 1). The survey was designed to obtain insights into the performance of populations of lions and their prey, to understand what the main threats to both are, and to provide insights into the determinants of conservation success. In order to obtain a larger sample, for the surveys, we expanded our definition of PAs for to include legally recognised conservancies occurring on private and community lands. 'Experts' were defined as those who are working in the PA in the context of management (n = 102) or research related to lions or their prey (n = 32). Respondents had a mean of 9.31 ± 1.1 years of experience in the area in question (range 1-–40 years) and were identified through professional networks and via 'snowballing' sampling technique (Atkinson and Flint, 2001). We managed to obtain responses from experts from 21 of the 25 known lion range countries (Bauer et al., 2015a). In addition, data were collected from experts in Ghana, where the presence of lions is questionable, and Rwanda, where lions have recently been reintroduced. In total, experts provided data for 186 PAs.

The effectiveness of PAs for conserving lions was calculated by using estimates of the population of lions relative to the estimated carrying capacity. Lion population estimates were derived from three sources: (1) The literature, where available (24.2% of PAs, accounting for ~ 61.6% of the total lion population for which we could find estimates) (Tumenta et al., 2010; Kiffner et al., 2012; Becker et al., 2012; Cozzi et al., 2013; Ferreira et al., 2013; Olléova and Dogringar, 2013; Midlane, 2014; Rosenblatt et al., 2014; Yirga et al., 2014; Omoya et al., 2014; Everatt et al., 2014a; Henschel et al., 2014a; Henschel et al., 2014b; Henschel et al., 2015; Bauer et al., 2015a; Bauer et al., 2015b; Bauer et al., 2015c; Bauer and Ryskay, 2016; Bauer et al., 2016). Of these, 56.3% used call-ups, 43.8% spoor counts, 25.0% individual recognition, 12.5% camera trapping, all of which are considered to be adequately scientific for our purposes (Henschel et al., 2014a; Midlane et al., 2015; Bauer et al., 2015c). (2) From estimates derived from on-going unpublished research provided by the management authority on site (45.0% of Pas accounting for 34.1% of the total lion population for which we could find estimates) (sources: African Parks, M. Becker, C. Begg, S. Bhalla, Borana Wildlife Conservancy, A. Cotterill, H. de Longh, K. Everatt, P. Funston, Groom, R., P. Henschel, Lewa Wildlife Conservancy, B. Kissui, R. Kokes, A. Loveridge, G. Maude, A. S., Miller, Snyman, S. Savini, I. Stevenson, K. Young); and (3) in the absence of results from recent surveys, from the estimates of the experts interviewed (32.7% of PAs, accounting for 4.3% of the lion population for which we could find estimates). Expert-based estimates of lion numbers were relied upon only where lion populations are known to be very small or absent. For statistical modelling, we considered PAs to be currently 'effective' for lion conservation if lions occurred above 50% of estimated K. We made two exceptions: for Akagera National Park in Rwanda and Majete Wildlife Reserve in Malawi, where lions have been reintroduced and are increasing in number (but are not yet at 50% of estimated K) following the establishment of effective management and injection of significant donor funding (African Parks, 2015).

The effectiveness of PAs for lion prey populations was based on responses to questionnaire surveys. Respondents were asked to estimate the abundance of medium to large ungulates (lion prey species) relative to the likely carrying capacity of the PA. To reduce scope for error, we converted these estimates to a binary variable, whereby PAs were considered to be 'effective' for prey where populations were > 50% of estimated K. Such a distinction required that respondents were simply able to indicate whether prey populations were substantially depleted or not, which respondents could comfortably do. In cases where the situation was considered borderline or where estimates looked questionable, we followed up with the respondents and sought secondary information sources to qualify those estimates. We found a large degree of congruence between respondents'' estimates and indications from aerial census data (Appendix 2) (in 87.0% of cases respondents'' impressions matched those from census data from a sample of 99 (56.6%) of the PAs). In the remaining 13% of PAs where the estimates from surveys and aerial census data did not correspond, the reason for the discrepancy may be due to changing circumstances on the ground (as the aerial censuses were conducted 1-–10 years ago). We made an exception for Gonarezhou National Park in Zimbabwe, which we considered to be effective, a PA that since 2008 has had significant elevation in management capacity and funding and where prey species have been reintroduced and are increasing following the effects of a devastating drought in 2002 and subsequent heavy poaching, but are not yet at 50% of K (Gandiwa et al., 2013).

The extent of the threat posed to wildlife by each anthropogenic pressure was estimated using survey respondents. Respondents were asked to rate 11 potential threats to wildlife in the PA on a 1-–5 scale (where 1 was no threat and 5 was a severe threat) (Appendix 3). These questions were congruent with current insights into conservation threats from the literature (Appendix 3). 'Total threat' scores were calculated from the sum of the scores allocated to each threat. A management capacity score was derived from questions related to various aspects of management capacity and resource availability scored on a 1-–5 scale of adequacy (Appendix 1).

2.3.2.3 Protected areas with survey data

We used ArcMap v.10.3.1 (ESRI, 2016) to compile geospatial data for 175 of the 186 PAs within lion range for which we had survey responses; boundary data for the remaining 11 protected areas were unavailable. Boundaries were derived from the World Database of Protected Areas (IUCN/UNEP WCMC, 2007). We computed various metrics for (1) individual PAs and (2) complexes of PAs, the latter of which were established by aggregating PAs separated by a maximum of 500 metres. This distance was chosen due to minor inaccuracies in the boundary data. Accounting for this error allowed adjacent PAs to be properly assigned to the same complex.

2.4.2.4 Data on management budgets

Data on management budgets for protected areas were derived from: a) from grey and published literature (MET, 2010; Cumming, 2012; Tanzania Government, 2013; Packer et al., 2013; Sichilongo et al., 2013; Namibia, 2014; Henschel et al., 2014a, 2014b; Nazeralis, 2015; Van Zyl, 2015; Zim Parks, 2015; Games, 2016); b) following direct requests for data from wildlife authorities (Botswana, Kenya, Zimbabwe); c) from Management Effectiveness and Tracking Tool assessments; c) through the surveys of experts affiliated with PAs. For instances where respondents were not clear on the extent of donor support for the PA, we contacted the donors/NGOs directly. Collecting data on management budgets was challenging because of: the reluctance of some wildlife authorities to provide data; perceived sensitivity of the information (Hanks and Attwell, 2003); because data on budgets are often not compiled at the PA level (e.g. they are allocated to regions); and because documenting all of the donor support, particularly where there are multiple small donors is difficult. However, we are confident that our estimates are of the correct order of magnitude and in many cases significantly more accurate, and that they constitute the most up to date and accurate compilation of such data in existence at present. Details and caveats on management budget data are provided in Appendix 4. All budget data were converted to 2015 USD.

2.5.2.5 Statistical analyses

We assessed how PA effectiveness (modelled separately for lions and prey) was associated with various characteristics of PAs and complexes. These variables included factors that are known to affect lions and their prey or would logically be expected to influence conservation outcomes (Appendix 5). These variables were categorised as: (a) ‘Geographic-socioeconomic’, which were considered characteristic of the PA’'s local environment and generally unmodifiable by management practices; (b) ‘Management variables’, which were considered modifiable by PA managers or governments; and, (c) ‘Threat variables’, which were considered modifiable by management practices but also strongly affected by the PA’'s local environment.

We used logistic regression to investigate hypothesized relationships between “effectiveness” of PAs (for lion, and then prey) and the variables listed in Appendix 5. We first standardized all variables according to (Schielzeth, 2010), such that 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 (ΔAICc of <=≤ 7) (Burnham and Anderson, 2004). Models were discarded if the candidate variable was correlated at | r |>= ≥ 0.70 with stronger predictors retained (as determined by AIC). We then built multivariate models with all possible combinations of this variable set, and model-averaged those models (as in (Grueber et al., 2011) with a ΔAICc of <=≤ 2.

To determine the relative contributions of geographic-socioeconomic and management variables in explaining PA effectiveness, the final models representing each category were ranked by AIC, with AIC weight equated to the degree of support for that model being the most explanatory model.

Lastly, we used a linear regression framework to investigate the relationship between the candidate variables and estimates of the severity of the most serious threats in PAs in lion range: bushmeat poaching, human encroachment for agriculture or settlement, livestock encroachment, human-wildlife conflict, and poaching for non-meat body parts (each modelled individually). Each global model was visually inspected for homogeneity of model residuals before the building of model subsets (Zuur et al., 2009). Model selection and model averaging were implemented as described above.

3.3 Results

3.1.3.1 Status of lions

There are 329 PAs of > 1000 km2 in lion range. Across all PAs for which data were available, lions were estimated to occur at ≥ 50% of their estimated carrying capacity in just 34.8% of PAs (n = 46, Fig. 1, Appendix 6). In Botswana, Kenya, Namibia and South Africa, lions occurred at ≥ 50% of estimated K and were stable or increasing in a high proportion of PAs (Fig. 2). Several countries/regions had no PAs where lions occurred > 50% of estimated K and in several, all lion populations were considered to be declining. Regionally, East Africa was estimated to have the highest proportion of PAs with lions at ≥ 50% of K (55.9% of PAs), followed by Southern (30.1%) and Central Africa (20.0%) (though data were missing for many Tanzanian PAs). West Africa had no PAs with lions > 50% of K. Lions were estimated to occur at < 25% of their potential in 50.7% (n = 76) of PAs. We estimate that if stocked to carrying capacity, the 329 state-owned PAs of > 1000 km2 in lion range could hold 83,212 lions (2.6-–4.2x × the current extant population, (Henschel et al., 2015)). Lions typically occurred at higher densities, (averaging 99.3% of K) in fenced reserves than in unfenced ones (37.4%). In 25.8% of fenced reserves, lions occurred above our estimates of K for the species, compared to in 9.8% of unfenced PAs.

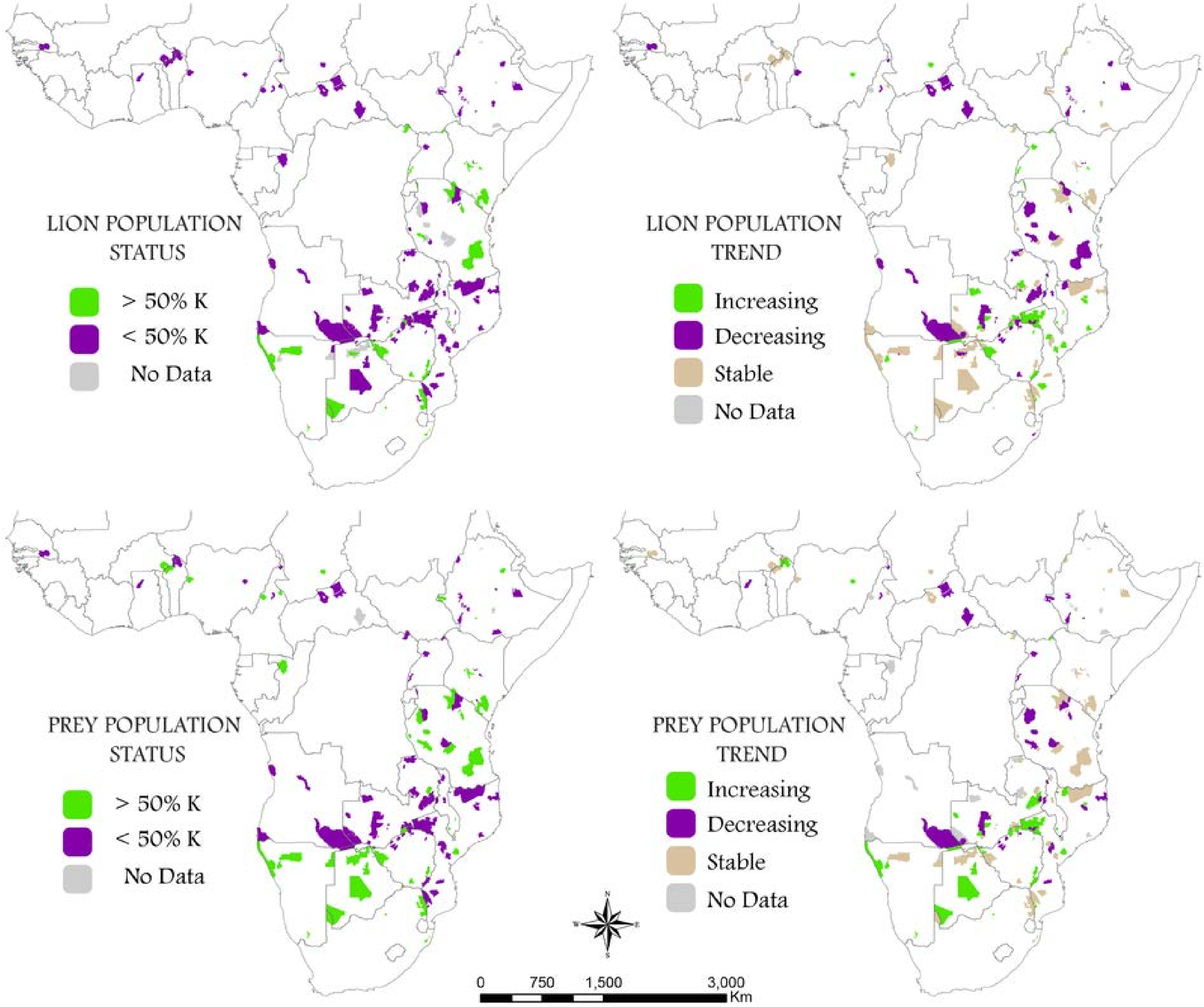

Fig. 1 Estimated status and trends of lion and prey populations.

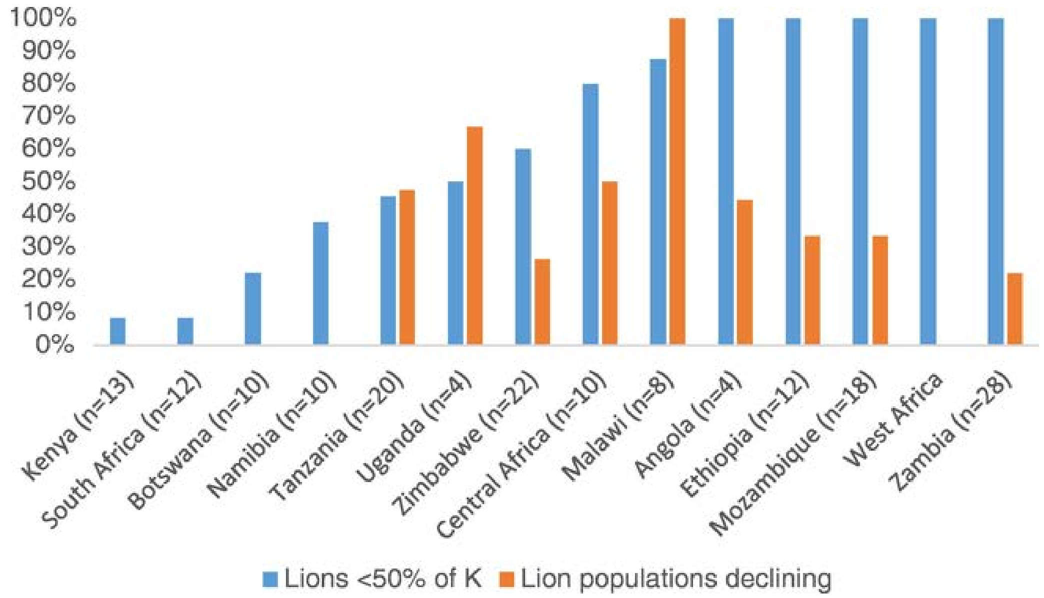

Fig. 2 The proportion of PAs in the survey in which PAs are not effective at conserving lions (i.e. occurring at < 50% of estimated carrying capacity) and the proportion of PAs where lion populations are declining.

3.2.3.2 Factors determining whether PAs were successful at conserving lions

a) Geographic-socioeconomic variables:

PAs with lion populations ≥ 50% of estimated carrying capacity tended to be in countries with lower human infant mortality, higher GDP, in East Africa (notwithstanding a lack of data on lion populations for many Tanzanian PAs), and in PAs where human settlements did not occur within the boundaries (Table 1; see Appendix 7 for model selection tables).

b) Management variables:

Table 1 Standardized beta coefficients of final logistic regression models using geographic-socioeconomic covariates to predict conservation effectiveness of PAs for lions and their prey.

	Lion model		Prey model	
	β	SE	β	SE
Intercept			-– 0.3399	0.2087
Region--—South	-– 1.8813	0.4036		
Region--—Central/West	-– 1.3615	0.7377		
Region--—East	0.5364	0.4235		
Infant mortality	-– 0.8116	0.3275	-– 0.7427	0.2254

	Lion model		Prey model	
	β	SE	β	SE
GDP	0.9930	0.2759	0.8247	0.2825
Human settlement in PA	-− 0.9943	0.2938		
Percent of PA settled by humans			-− 0.7302	0.3348

Effectiveness of PAs for lions was associated with higher management budgets, where prey was more abundant, and where the PAs were completely fenced (Table 2). Lions performed best relative to their estimated carrying capacity in areas used for photo tourism, followed by areas with trophy hunting; they did not typically fare well relative to estimated carrying capacity in areas without these forms of use.

c) Threat variables:

Table 2 Standardized beta coefficients of final logistic regression models using management covariates to predict conservation effectiveness of PAs for lions and their prey. Estimates and standard errors with (*) are model-averaged coefficients from models with ΔAIC < 2; estimates and standard errors without (*) are for a single top model in which no other model was within 2 ΔAIC.

	Lion		Prey	
	β*	SE*	β	SE
Main Use—neither hunting nor tourism	-− 1.3074	0.6512	-− 1.2302	0.4030
Main Use-- —hunting	-− 1.1294	0.6997	-− 0.4478	0.3494
Main Use-- —tourism	-− 0.0851	0.3327	0.2471	0.2430
Management budget	3.4643	1.2402		
Estimated prey abundance	0.9141	0.2567		
PA is fully fenced	0.5071	0.2434		
PA is partially fenced			0.8559	0.2207

PAs were generally less effective for lions where the perceived threats from logging of commercially valuable timber, bushmeat poaching, legal hunting for meat, and human encroachment were higher (Table 3).

Table 3 Standardized beta coefficients of final logistic regression models using threat covariates to predict conservation effectiveness of PAs for lions and their prey.

	Lion		Prey	
	β	SE	β	SE
Intercept	-– 1.1809	0.2648	-– 0.3596	0.1740
Illegal logging score	-– 0.8632	0.3446		
Bushmeat poaching score	-– 0.7123	0.2372	-– 0.5987	0.1888
Legal hunting score	-– 0.5491	0.2760		
Human encroachment score	-– 0.5331	0.2615	-– 0.5126	0.1916

Of the three categories of variables, management variables were the most important determinants of conservation success for lions, with the top model for management having 97% of AIC weight compared to top models for geographic-socioeconomic and threat variables (Table 4).

Table 4 A comparison of top models containing geographic-socioeconomic, management, and threat variables in logistic regression predicting effectiveness of PAs for lions and their prey. K = number of parameters, ΔAICc is difference in AICc between that model and the top model, ω is AIC weight, and LL is log likelihood.

	K	AICc	ΔAICc	ω	LL
Lion					
Management	6	123.38	0	0.92	-– 55.4
Geographic-socioeconomic	6	128.21	4.83	0.08	-– 57.81
Threat	5	143.05	19.67	0	-– 66.32
Prey					
Geographic-socioeconomic	4	180.77	0	1	-– 86.26
Management	4	195.98	15.2	0	-– 93.86
Threat	3	201.91	21.13	0	-– 97.88

3.3.3.3 Status of lion prey

Prey populations were considered to occur at ≥ 50% of their potential carrying capacity in 44.5% of PAs surveyed (Figs. 1, 3). Prey populations were most frequently ≥ 50% of potential in Botswana, Namibia, South Africa, Tanzania and Kenya (Fig. 3). Prey populations were most commonly estimated by respondents to be stable or increasing in PAs in Uganda, Mozambique, South Africa, Botswana and Namibia (Fig. 3).

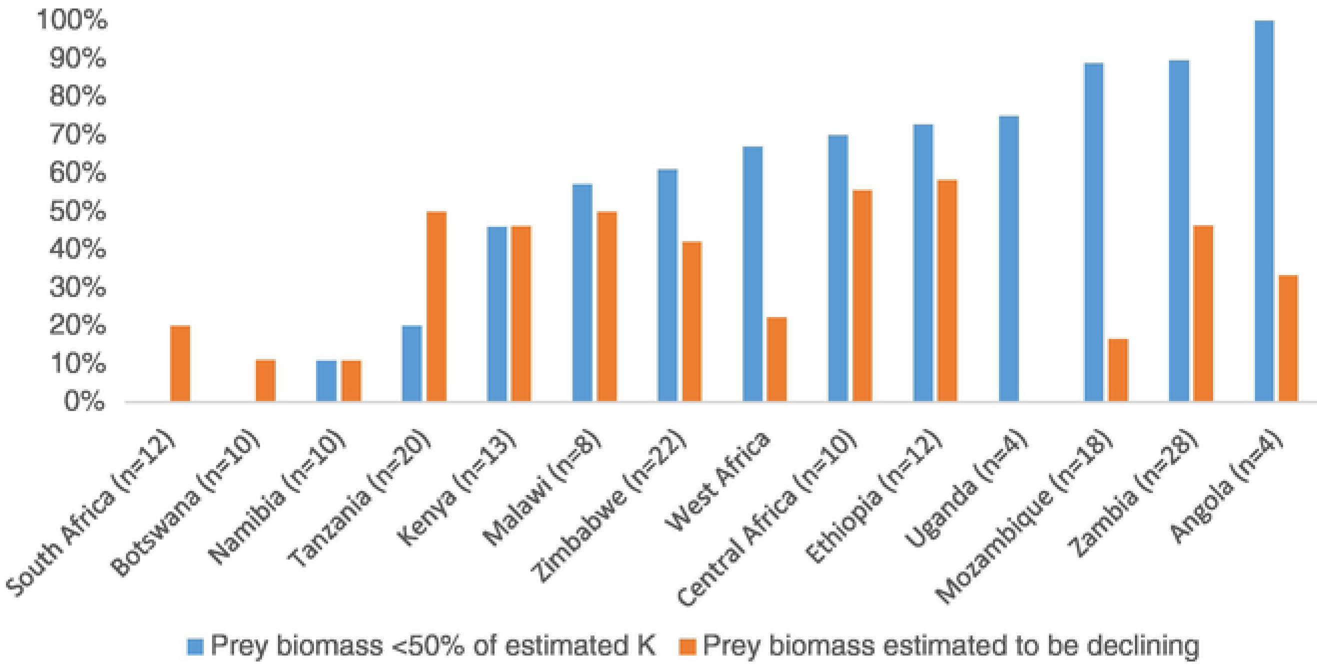

Fig. 3 Proportion PAs by country where prey populations are estimated to be < 50% of estimated carrying capacity (K) and the proportion of PAs where prey populations are considered to be declining.

3.4.3.4 Factors determining whether PAs were successful at conserving lion prey

a) Geographic-socioeconomic variables:

PAs with lion prey populations ≥ 50% of estimated carrying capacity tended to be in countries with lower human infant mortality and higher GDP, and in PAs where the proportion of land settled by humans was lower (Table 1; see Appendix 7 for model selection tables).

b) Management variables:

Prey populations fared poorly in PAs where neither photographic tourism nor trophy hunting was practiced. Prey populations fared better in PAs where there was at least partial fencing present (Table 2).

c) Threat variables:

Lion prey populations did not fare well in PAs where human encroachment and bushmeat hunting were perceived to be more severe (Table 3).

Of the three categories of variables, geographic-socioeconomic variables were the most important determinants of conservation success for prey, with the top model for geographic-socioeconomic variables having 100% AIC weight compared to top models for management and threat variables (Table 4).

3.5.3.5 Threats to lions

Respondents most frequently listed the following threats as the most serious for lions in the surveyed PAs: bushmeat poaching/snaring (26.7% of respondents); human-wildlife conflict (25.5%), encroachment with livestock (11.4%); human encroachment (6.3%) (Table 5, Figure. 4). Poaching of lions for body parts was not identified as a ubiquitous problem, but is clearly an emerging issue. Respondents reported evidence of targeted poaching of lions for body parts most frequently in West Africa (42.9% of PAs), Mozambique (35.3%), Central Africa (28.6%), Tanzania (22.2%), Zambia (17.4%) and Zimbabwe (10.5%), with no reports of occurrence from the surveys in other countries (though that is not to say that such incidents do not occur – e.g. limited incidences have been recorded in Botswana and South Africa (Botswana Department of Wildlife and National Parks, unpublished data, K. Marenwick pers. comm.).

Table 5 The percentage of PAs in which various threats were identified as being in the 'top three threats to lions' in various African countries.

	Bushmeat	HWC	Livestock incursion	Human incursion	Trophy hunting	Lion poaching	Deforestation	Small population issues	Disease	Isolation/ habitat destruction outside	Loss of prey not due to bushmeat	Poison - lions as a by product	Ceremonial killing	Mining
Angola, n = 4	100	50.0	25.0	25.0	0	0	0	0	0	0	0	0.0	0	0
Botswana n = 11	66.7	88.9	0	11.1	22.2	0	0	0	0	33.3	11.1	11.1	0	0
Central Africa, n = 9	88.0	100	50.0	10.0	10.0	10.0	30.0	0	20.0	10.0	10.0	0.0	0	10.0
Ethiopia, n = 12	8.3	25.0	50.0	41.7	0	8.3	25.0	0	8.3	8.3	23.1	0.0	0	8.3
Kenya, n = 12	28.6	71.4	42.9	14.3	0	0	14.3	14.3	14.3	7.1	21.4	0.0	14.3	0
Malawi, n = 9	100	33.3	0	33.3	0	0	33.3	33.3	0	0	0	0.0	0	0
Mozambique, n = 18	94.1	47.1	5.9	29.4	0	35.3	0	5.9	0	0	0	35.3	5.6	0

	Bush meat	HWC	Livestock incursion	Human incursion	Trophy hunting	Lion poaching	Deforestation	Small population issues	Disease	Isolation/ habitat destruction outside	Loss of prey not due to bush meat	Poison - lions as a by product	Ceremonial killing	Mining
Namibia, n = 12	21.4	92.9	0	0	0	0	0	0	14.3	14.3	0	7.1	0	0
South Africa, n = 13	27.3	27.3	0	0	0	9.1	0	45.5	18.2	0	0	0.0	0	0
Tanzania, n = 22	33.3	61.1	22.2	11.1	33.3	5.6	5.6	0	5.6	11.1	5.3	0.0	27.8	0
Uganda, n = 4	75.0	100	0	0	0	0	0	25.0	0.0	0	0	0	0	0
West Africa, n = 9	92.9	42.9	28.6	0	7.1	42.9	7.1	14.3	21.4	7.1	0	0	0	0
Zambia, n = 27	92.6	29.6	3.7	37.0	22.2	7.4	3.7	3.7	3.7	11.1	0	0	0	0
Zimbabwe, n = 22	57.1	57.1	0	4.3	42.9	0	0	0	4.8	4.3	4.3	14.3	0	0
Overall, n = 184	60.2	55.9	15.0	15.3	13.6	10.2	6.4	8.1	9.2	8.5	5.1	5.7	4.5	1.2%

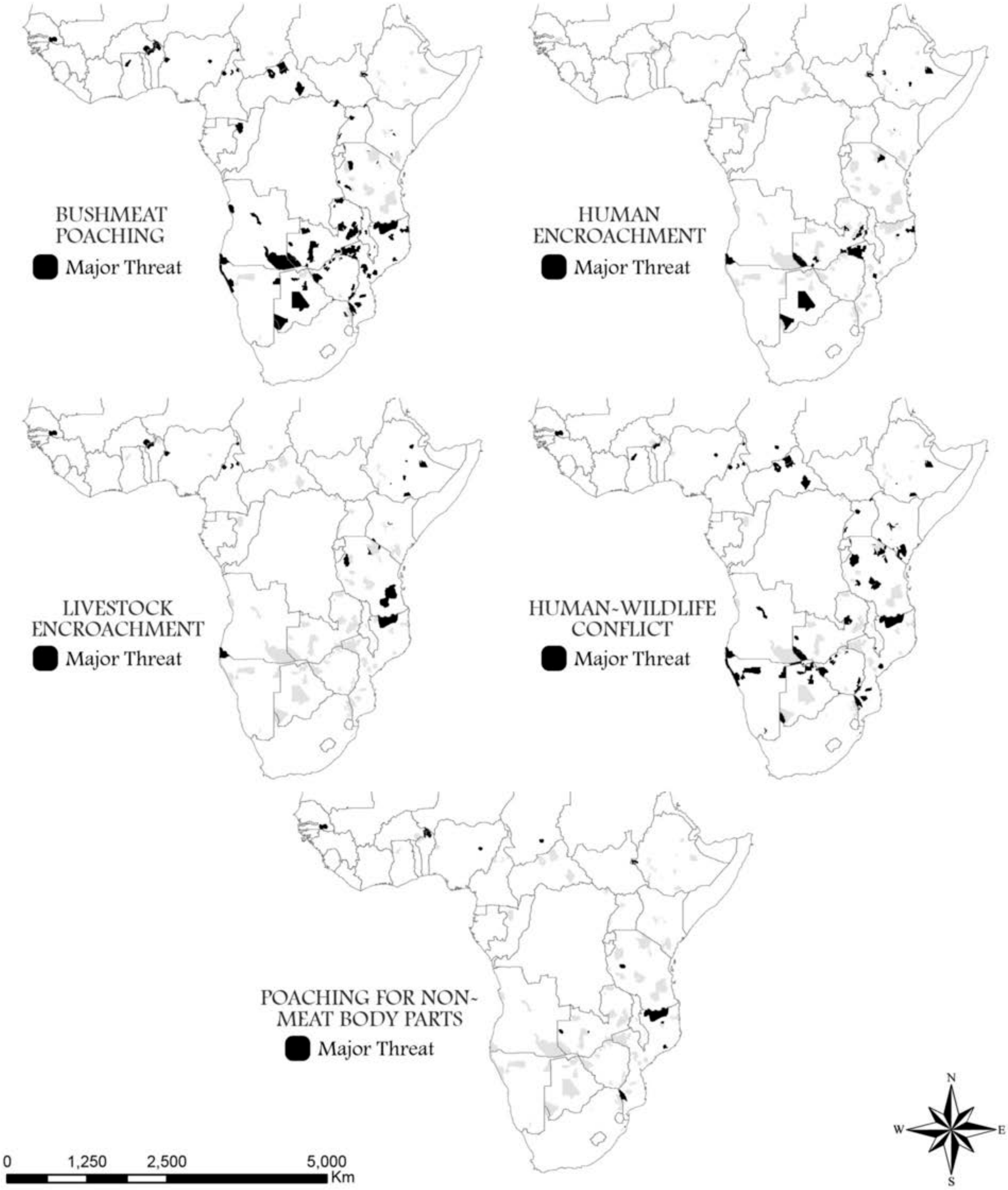

Fig. 4 PAs in which each of the five most serious threats to lions were identified as being in the top three threats to the species (binary scale).

3.6.3.6 Threats to wildlife in general

Total threat scores for wildlife in PAs were relatively high in Angola (32 ± 3.0), Zambia (23.7 ± 1.9), Malawi (20.4 ± 3.5) and Tanzania (20.8 ± 2.0) and low in South Africa (8.5 ± 1.0), Botswana (10.1 ± 1.2), Namibia (12.5 ± 1.6) and Kenya (12.6 ± 3.6). The major threats to wildlife were considered to be: bushmeat poaching (Fig. 5, mean score ± S.E. - 3.0 ± 0.13 across all PAs); poaching of wildlife for non-meat body parts (Fig. 5, 2.79 ± 0.12); human-wildlife conflict (Fig. 5, 2.43 ± 0.10), encroachment with livestock (Fig. 5, 2.31 ± 0.14) and human encroachment for settlement and agriculture (Fig. 5, 2.03 ± 0.13). Legal hunting for meat (0.87 ± 0.11), trophy hunting (0.89 ± 0.11), mining (1.13 ± 0.11) and disease (1.42 ± 0.10) were considered markedly less severe. Experts'' insights into the geographic distribution of threats were congruent with insights from the literature (Appendix 3).

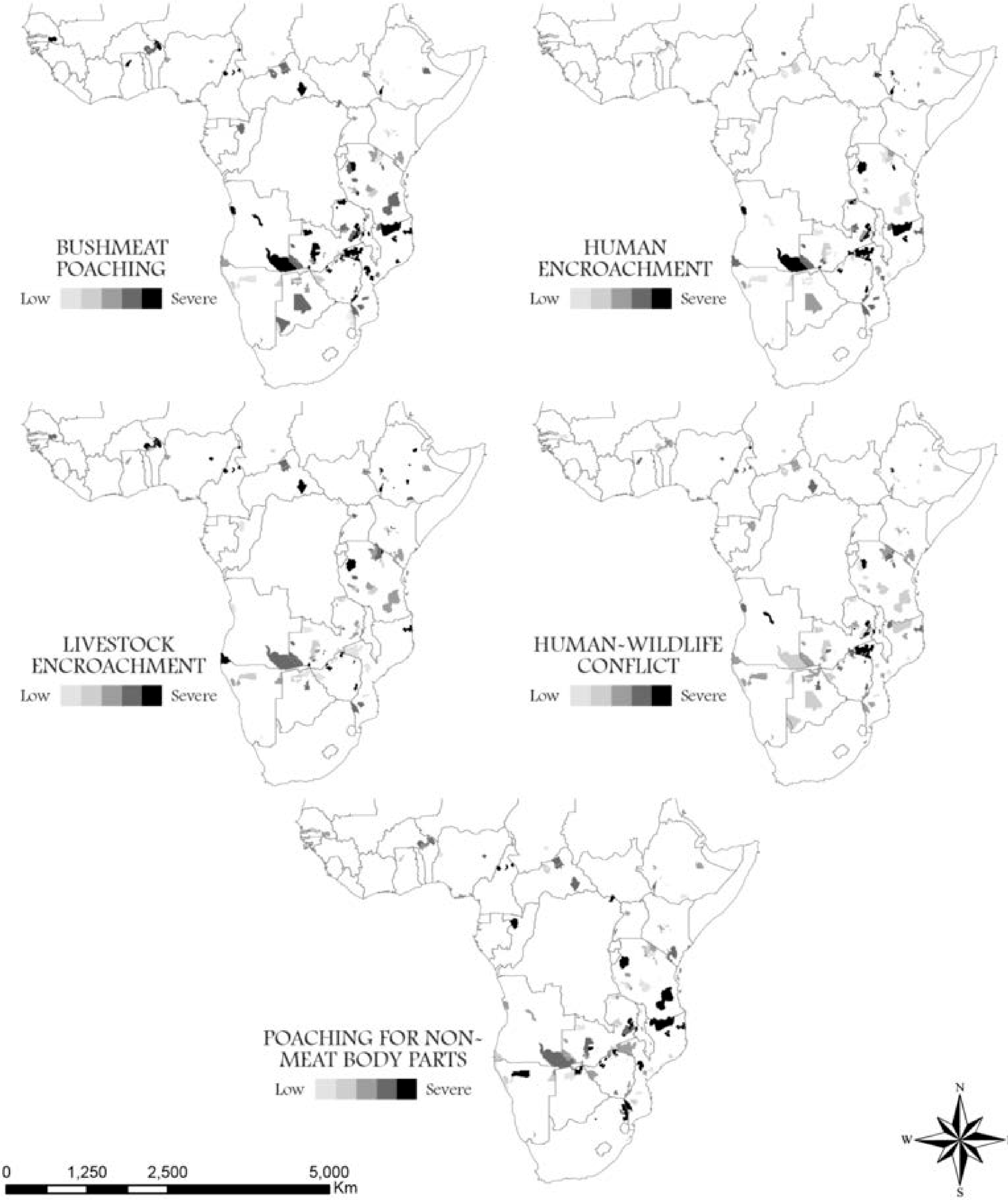

Fig. 5 The five top-ranked threats to wildlife in general in PAs, and the PAs in which each was considered to be a 'major threat' (categorised as such when respondent gave a score of 4-–5 on a 1-–5 scale when asked how serious the threat is).

3.7.3.7 Conditions under which each threat emerged

a) Geographic-socioeconomic:

Central/West Africa was associated with highest scores for bushmeat hunting, livestock encroachment, human-wildlife conflict, and poaching for non-meat body parts, while East Africa was associated with lowest scores for bushmeat hunting and poaching of wildlife for non-meat body parts. The presence of human settlement within PAs was positively associated with bushmeat hunting, human encroachment, and human-wildlife conflict, while the percentage of land occupied by humans within PAs was associated with perceived severity of livestock encroachment (Table 6; see Appendix 7 for model selection tables). Bushmeat hunting was perceived to be more severe in larger PAs, in poorer countries, and where livestock densities in the 20 km around the PA were lower. To the contrary, livestock encroachment was more severe in areas with higher densities of livestock in the areas adjacent to PAs. Human encroachment and poaching for non-meat body parts were worse in smaller PA complexes. For all threats except human-wildlife conflict, geographic-socioeconomic variables were better predictors of severity than management variables (Table 7).

b) Management:

Table 6 Standardized beta coefficients of final linear regression model using geographic-socioeconomic covariates to predict the emergence of key threats to wildlife in PAs. Estimates and standard errors with (*) are model-averaged coefficients from models with ΔAIC < 2; estimates and standard errors without (*) are for a single top model in which no other model was within 2 ΔAIC.

	Bushmeat		Livestock encroachment		Human encroachment		Human-wildlife conflict		Poaching for non-meat body parts	
	β*	SE*	β	SE	β	SE	β	SE	β	SE
Region-- — South	3.3593	0.1528	1.8080	0.1646	2.2596	0.1487	2.4127	0.1371	3.0532	0.1573
Region-- — Central/West	3.9964	0.3204	3.8346	0.3524	1.8244	0.3350	2.8261	0.3145	3.3394	0.3546
Region-- — East	2.4639	0.2353	2.9551	0.2517	2.0290	0.2127	2.5860	0.1958	2.2042	0.2251
GDP	-– 0.5859	0.1184								
Human settlement in	0.2816	0.1102			1.0056	0.1122	0.2683	0.1061		

	Bushmeat		Livestock encroachment		Human encroachment		Human-wildlife conflict		Poaching for non-meat body parts	
	β*	SE*	β	SE	β	SE	β	SE	β	SE
PA										
Area of PA (km2)	0.3188	0.1111								
Cattle Density 20 km from PA	-– 0.2384	0.1249	0.3820	0.1443						
Percent of PA settled by humans			0.4506	0.1192						
Area of PA Complex (km2)					-– 0.3854	0.1207			-– 0.2987	0.1270

Table 7 A comparison of top models containing geographic-socioeconomic versus management in linear regression models predicting the emergence of key threats to wildlife. K = number of parameters, ΔAICc is difference in AICc between that model and the top model, ω is AIC weight, and LL is log likelihood.

	K	AICc	ΔAICc	ω	LL
Bushmeat					
Geographic-socioeconomic	8	592.2	0	0.88	-– 287.65
Management	6	596.14	3.94	0.12	-– 291.81
Livestock encroachment					
Geographic-socioeconomic	6	626.03	0	1	-– 306.75
Management	6	667.21	41.18	0	-– 327.34
Human encroachment					
Geographic-socioeconomic	6	606.77	0	1	-– 297.12

	K	AICc	ΔAICc	ω	LL
Management	4	654.74	47.97	0	-– 323.25
Human-wildlife conflict					
Management	3	581.43	0	0.98	-– 287.64
Geographic-socioeconomic	5	589	7.57	0.02	-– 289.32
Poaching for non-meat					
Geographic-socioeconomic	5	625.01	0	0.56	-– 307.32
Management	5	625.53	0.52	0.44	-– 307.58

Lower reported prey abundance was associated with increased severity of bushmeat poaching, human encroachment, and human-wildlife conflict; lower management budget was also associated with more severe bushmeat hunting (Table 8). Land use played a role in the severity of bushmeat poaching, in that problems were more severe when the land was used for neither hunting nor tourism or for hunting only. The presence of perimeter fencing was associated with reduced livestock and human encroachment. Livestock encroachment in PAs was more severe with lower management capacity scores. Lastly, there was a positive but weak relationship between more severe threats of poaching for non-meat body parts and the presence of legal trophy hunting within those PAs.

c) Threat:

Table 8 Standardized beta coefficients of final linear regression model using management covariates to predict the emergence of key threats to wildlife in PAs. Estimates and standard errors with (*) are model-averaged coefficients from models with ΔAIC < 2; estimates and standard errors without (*) are for a single top model in which no other model was within 2 ΔAIC.

	Bushmeat		Livestock encroachment		Human encroachment		Human-wildlife conflict		Poaching for non-meat body parts	
	β	SE	β	SE	β	SE	β	SE	β*	SE*
Intercept					2.1431	0.1290	2.5100	0.1041		
Main use—neither hunting nor	3.6509	0.2212	2.5365	0.2950					2.8818	0.3846

	Bushmeat		Livestock encroachment		Human encroachment		Human-wildlife conflict		Poaching for non-meat body parts	
	β	SE	β	SE	β	SE	β	SE	β*	SE*
tourism										
Main use-- — hunting	3.5127	0.2178	1.8745	0.2682					2.6251	0.9706
Main use-- — tourism	2.7478	0.1598	2.5380	0.2028					2.9229	0.3607
Estimated prey abundance	-– 0.3897	0.1169			-– 0.4781	0.1384	-– 0.3540	0.1044		
Management budget	-– 0.3317	0.1155								
PA is partially fenced			-– 0.4440	0.1438	-– 0.3682	0.1384				
Total management score			-– 0.3424	0.1661						
Trophy hunting present in PA									0.8499	0.4843

The presence of individual threats tended to be strongly associated with others (Table 9). The severity of bushmeat hunting was positively associated with that of poaching of wildlife for non-meat body parts, illegal logging, and human encroachment. Encroachment with livestock was associated with human-wildlife conflict, human encroachment, tree cutting for charcoal and higher perceived severity of wildlife diseases. Human encroachment was associated with higher threat from tree cutting for charcoal, livestock encroachment, human-wildlife conflict, illegal logging, and bushmeat poaching. Human-wildlife conflict was associated with higher perceived threats from livestock and human encroachment, poaching of wildlife for non-meat body parts, tree cutting for charcoal, and legal meat hunting. Poaching for non-meat body parts was associated with elevated threat from bushmeat poaching, wildlife diseases, legal meat hunting and excessive trophy quotas.

Table 9 Standardized beta coefficients of final linear regression model using perceived severities of threat to predict the emergence of other key threats to wildlife in PAs. Estimates and standard errors with (*) are model-averaged coefficients from models with ΔAIC < 2; estimates and standard errors without (*) are for a single top model in which no other model was within 2 ΔAIC.

	Bushmeat		Livestock encroachment		Human encroachment		Human-wildlife conflict		Poaching for non-meat body parts	
	β	SE	β	SE	β*	SE*	β*	SE*	β	SE
Intercept	3.1702	0.1034	2.3717	0.1194	2.1431	0.1044	2.5100	0.0905	2.8379	0.1072
Human encroachment score	0.3829	0.1197	0.3344	0.1500			0.2463	0.1218		
Poaching for non-meat score	0.4766	0.1055					0.2412	0.0968		
Illegal logging score	0.4317	0.1188			0.3189	0.1377				
Human-wildlife conflict score			0.4771	0.1334	0.2253	0.1223				
Tree cutting for charcoal score			0.3159	0.1466	0.4627	0.1422	0.2493	0.1188		
Disease score			0.3467	0.1218					0.2393	0.1088
Bushmeat poaching score					0.3040	0.1217			0.5133	0.1110
Livestock encroachment score					0.3558	0.1237	0.4024	0.1030		
Legal hunting score							0.2416	0.0985	0.2505	0.1214
Mining score					0.2490	0.1144				
Excessive quota score									0.2619	0.1205

4.4 Discussion

4.1.4.1 The state of Africa's PAs

A significant proportion of PAs in African savannahs currently appear to be underperforming in ecological, and subsequently, in economic terms (Lindsey et al., 2011; Lindsey et al., 2014; Van Zyl, 2015). Populations of both lions and their prey are reported to occur substantially below their likely carrying capacity in the majority of PAs in several countries. Furthermore, the situation may be worse than our analyses reveal because our sample is biased towards PAs where NGOs are engaged (particularly in West and Central Africa). Populations of both lions and their prey are declining in a high proportion of PAs and on-going population declines and range contractions will not be restricted to unprotected lands.

However, some PAs are performing well, and many are far from what could be described as ‘paper parks’ (Bruner et al., 2001). The pattern of performance of lions and their prey is more nuanced than depictions of regionally positive trends in Southern Africa and negative trends elsewhere (Craigie et al., 2010; Bauer et al., 2015a). For example, both lions and their prey appear to be faring relatively well in PAs in Botswana, South Africa and Namibia, but also in Kenya (in contrast to the situation in unprotected rangelands, where wildlife populations appear to be declining precipitously in some areas (Ogutu et al., 2015). Both lion and prey populations are widely regarded as being depressed in many PAs in Central and West Africa, Angola, Ethiopia, Malawi, Mozambique, and Zambia, whereas the picture appears more varied in Uganda, Tanzania and Zimbabwe. In Mozambique, wildlife and lion populations (while still depressed and excluding elephants) appear to be recovering in some PAs following the impacts of the civil war and impacts of the bushmeat trade thereafter (Lindsey et al., 2013). Drawing conclusions about lion population trends in Tanzania is especially difficult due to the lack of data on lion numbers there (Bauer et al., 2015c). While wildlife in savannah parks in West and Central African PAs are generally under severe pressure, in keeping with forest parks in those regions (Tranquilli et al., 2014), there is room for optimism regarding the prospects for some areas, such as Zakouma National Park in Chad, which has received significant technical and financial support from NGO partners and donors and which appears to be performing well.

4.2.4.2 Determinants of success

Across Africa, variables related to PA management were the most important determinants of effectiveness for the conservation of lions, in keeping with previous findings (Henschel et al., 2014a, 2014b; Bauer et al., 2015a; Henschel et al., 2016a; Henschel et al., 2016b) and with patterns observed for elephants and rhinos (Leader-Williams et al., 1990). This suggests that where resources and capacity are adequate, lions can be conserved effectively in a wide range of circumstances. Adequate management budgets are particularly important (Henschel et al., 2016b), and low budgets were associated with the emergence of threats.

African PAs are grossly under-funded in several countries, which undermines the ability of wildlife authorities to tackle human pressures (James et al., 1999; Mansourian and Dudley, 2008; Lindsey et al., 2016). Resourcing of PAs varies from relatively sufficient in Kenya and South Africa (and to a lesser extent Botswana and Namibia) to extremely low in countries such as Ethiopia, Central African Republic, Angola, Mozambique (James et al., 1999; Mansourian and Dudley, 2008). Funding alone is not sufficient, however, and management capacity has a significant additive effect on controlling threats.

The significance of fencing for lion conservation is debated (Packer et al., 2013; Creel et al., 2013). Our findings suggest that full and partial fencing had a strong positive effect on conservation outcomes for lions and prey, respectively, and that it is an effective tool for controlling encroachment by humans and livestock. As human pressures increase and land neighbouring PAs becomes more fragmented and densely populated, the case for partial or total fencing of some PAs will likely grow (Lindsey et al., 2012b).

Lions and their prey tended to fare most poorly relative to estimates of their potential carrying capacity in PAs where there was no economic utilisation of wildlife, and those with no tourism or trophy hunting were more affected by bushmeat poaching, likely due to the reduced presence of guards and PA staff, reduced management budgets within such PAs and potentially due to reduced motivation on the part of wildlife authorities to protect such areas if they do not generate income. Similarly, (Bauer et al., 2015a) hypothesized that lion population declines were steepest in reserves with no population monitoring, which reflects lack of conservation effort. Photographic tourism was associated with the best conservation outcomes for lions and prey, in keeping with the findings of (Tranquilli et al., 2014) for wildlife generally. Tourism is generally only viable in the areas with the highest densities of wildlife (Lindsey et al., 2006).

The effect of trophy hunting as the primary use of a PA on the status of lions and prey could not be determined due to the high standard errors in our models (Table 2). However, PAs used primarily for hunting were associated with elevated bushmeat poaching relative to PAs used primarily for tourism. To a lesser extent, the presence of trophy hunting within a PA was associated with increased severity of poaching of wildlife for non-meat body parts (Table 9). The causes of this relationship are not clear, but could conceivably be due to there being inadequate anti-poaching in some areas used for hunting or conversely due to there being greater vigilance and better information on illegal activities where hunters are present (Lindsey et al., 2016).

Large PAs were no better at conserving lion populations relative to their estimated carrying capacities than smaller PAs and were associated with higher perceived pressure from bushmeat poaching. On the other hand, human encroachment and poaching of wildlife for non-meat body parts was perceived as most severe in smaller PA complexes. Large PAs are particularly challenging to protect and manage due to scale and cost, and size does not confer immunity to illegal hunting (Kiffner et al., 2012; Midlane, 2014; MacKinnon et al., 2015). Notably, donors appear to be avoiding investing in the largest PAs, which arguably represents a missed opportunity for making significant gains for lion conservation.

Human settlement inside PAs had a negative impact on the conservation of lions and prey and was strongly associated with bushmeat poaching, livestock and human encroachment, and human-wildlife conflict, in keeping with (Everatt et al., 2014b). High human densities in lands adjacent to PAs, however, did not have a particularly strong effect on conservation outcomes – suggesting that so long as encroachment is prevented within PAs, conservation outcomes need not always be greatly impacted by human population growth. Poverty on a national level was associated with poor conservation outcomes for lions and their prey, and was associated with the emergence of key threats, as is the case for elephants (Blanc, 2013). Consequently, if African countries can achieve sustained economic growth and reduced poverty, the prospects for conservation may improve assuming other factors discussed in this paper are in place such as adequate PA budgets.

4.3.4.3 Threats to lions and their prey

We acknowledge that subjective comparisons of the relative severity of threats has potential to be affected by biases as some may be more obvious than others. However, insights into the distribution and severity of the various threats are congruent with knowledge presented in the literature (Appendix 2). Bushmeat poaching was identified as the most serious threat for lions and their prey in PAs, reinforcing the finding of Okello and Kiringe (2004), (Kiringe et al., 2007) and (Tranquilli et al., 2014). The belief among respondents that bushmeat is the top threat affirms the suggestion that PAs are more effective at securing wild lands against human encroachment than against illegal hunting (Bruner et al., 2001; Geldmann et al., 2013), though encroachment remains a serious threat. Lions are affected both by direct mortalities in snares and also through reductions in their prey base (Lindsey et al., 2013). Bushmeat poaching tends to occur in tandem with legal logging (Poulsen et al., 2009) (and as our data suggest, illegal logging), human encroachment and poaching for non-meat body parts. Human encroachment of PAs represents a severe threat where it occurs, is strongly associated with the emergence of a wide array of other threats (in keeping with the findings of (Tranquilli et al., 2014), is likely to be difficult to control and near impossible to reverse.

4.4.4.4 Necessary steps

If African governments and the global community allocate sufficient resources and human capacity, lions can be effectively conserved in a wide range of circumstances. There is an urgent need for elevated funding and more focused conservation effort directed towards PAs in many countries (Henschel et al., 2016b). Current levels of support from African governments and the donor community are not adequate in many countries (MacKinnon et al., 2015). Without such steps, an increasing number of PAs will fail to fulfil the objectives for which they were gazetted. Similar conclusions were reached for tiger conservation in Asia (Walston et al., 2010). We also acknowledge the importance of investing in conservation initiatives on communal and private lands (Ogutu et al., 2015), particularly those adjacent to PAs. Such investment can both increase the effective size of PAs and also reduce the costs of managing PAs by increasing local support for conservation.

On a continental level, funding for PAs needs to increase 3-–6 fold (Lindsey et al., 2016), and in some countries, by a much greater extent (James et al., 1999). Inadequate financial and human resources undermines the effectiveness of PA management throughout much of the tropics (Balmford and Whitten, 2003; Watson et al., 2014), but nowhere more so than Africa (James et al., 1999). There is a strong case for greater support from the international community for African PAs. Africa''s wildlife is a global resource that confers existence values for people around the world (Sylven et al., 2012), but one that imposes costs on the people that live with it. The illegal trade in wildlife products is being driven by growing international demand (Biggs et al., 2013; Williams, 2015). Developed nations pledged to assist the conservation efforts of developing nations by providing approximately USD2 billion per year at the Rio Earth Summit in 1992, but have never fulfilled those promises (Miller, 2014). Investing in PAs is a way that developed countries can promote sustainable economic growth through stimulation of tourism industries. For the same reason, African governments should consider allocating larger budgets for PA management to protect the wildlife resources and ecosystem services on which tourism industries, the African population and economic growth depend (Lindsey et al., 2014). In the few African countries where PAs are well funded, there are large and valuable tourism industries. The many countries that do not invest adequately in their PAs, however, risk losing their lions and other wildlife before ever having the chance to benefit from them (Lindsey et al., 2016). In addition, African countries and people benefit significantly from the ecosystem services delivered by PAs (Van Zyl, 2015). Most Africans are rural and directly dependent on natural resources for daily survival and as much of a quarter of wealth of low income countries is derived from ‘natural capital’ versus just 2% in developed nations (Fitzgerald, 2015).

Promoting the development of appropriate tourism in individual PAs is likely to yield long-term benefits, both by increasing the social and political sustainability of those areas and by helping to reduce threats to wildlife. Management capacity has a significant positive impact on conservation outcomes, and so fostering capacity-building and long-term partnerships among donor agencies, NGOs, the private sector and wildlife authorities is key (Nyirenda and Nkhata, 2013). Such partnerships should then focus on addressing specific threats to wildlife in PAs and building long-term sustainable management structures. The inter-linked nature of threats means that steps to address one issue will yield wider collateral benefits. This is particularly true of human encroachment of PAs, and there is a need for governments to resist political pressure to allow human settlement or livestock grazing in PAs (e.g. http://www.standardmedia.co.ke/article/2000197917/ps-against-bill-allowing-grazing-in-parks, accessed May 2016), so as to limit collateral conservation challenges.

5.5 Conclusions

PAs within lion range have potential to host a cumulative population size that is up to four times larger than the current total free-ranging lion population. African PAs present the world with the opportunity to effectively secure the future of lions and many other iconic wildlife species. However, the window for achieving those gains is closing and without urgent and significant investment, Africa''s PA networks will continue to deteriorate. As human populations increase, there is likely to be political and social pressure for the conversion of PAs for alternative land uses. This is particularly likely for depleted PAs that confer few economic or social benefits. Indeed, a significant number of African PAs have already been degazetted, downgraded in status and downsized (http://www.padddtracker.org/, accessed April 2016). Africa''s vast PA network can thus not be taken for granted, nor can it be assumed that wildlife in PAs is safe by virtue of the legally protected status of those areas.

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