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LETTER

Conserving large carnivores: dollars and fence

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Abstract

Conservationists often advocate for landscape approaches to wildlife management while others argue for physical separation between protected species and human communities, but direct empirical comparisons of these alternatives are scarce. We relate African lion population densities and population trends to contrasting management practices across 42 sites in 11 countries. Lion populations in fenced reserves are significantly closer to their estimated carrying capacities than unfenced populations. Whereas fenced reserves can maintain lions at 80% of their potential densities on annual management budgets of \$500 km^{-2}, unfenced populations require budgets in excess of \$2000 km^{-2} to attain half their potential densities. Lions in fenced reserves are primarily limited by density dependence, but lions in unfenced reserves are highly sensitive to human population densities in surrounding communities, and unfenced populations are frequently subjected to density-independent factors. Nearly half the unfenced lion populations may decline to near extinction over the next 20–40 years.

Keywords

Carnivores, carrying capacity, density dependence, exponential growth, landscape conservation, spatial separation.

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INTRODUCTION

Populations of large carnivores are declining around the globe, often with dramatic effects on lower trophic levels (Estes *et al.* 2011). These species typically range over such wide areas that it can be difficult to maintain viable populations without some individuals coming into close proximity to humans, posing serious threats to human safety and domestic livestock. Conservationists have therefore sought methods to promote human–carnivore co-existence outside the confines of national parks and wilderness areas (Woodroffe *et al.* 2005; Dickman *et al.* 2011). Given the potential conflicts with humans, however, separation of large carnivores from human communities may ultimately be preferable to a landscape-level conservation approach as has been demonstrated for forestry (Boscolo & Vincent 2003) and agriculture (Phalan *et al.* 2011).

Few species encapsulate these problems more dramatically than the African lion. Lion densities are directly dependent on prey biomass (Van Orsdol *et al.* 1985; Hayward *et al.* 2007), and annual range requirements for a single lion pride can exceed 1000 km^2 (Funston 2011). Habitat loss in the past 100 years has reduced the lion's range by 75% (Riggio *et al.* 2012), and human–lion conflicts have intensified because lions kill livestock (Woodroffe & Frank 2005; Kissui 2008) and people (Packer *et al.* 2005a, 2011a). In addition, poorly regulated sport hunting has resulted in over-harvesting in several countries (Packer *et al.* 2009, 2011b), the effects of which can extend into unhunted National Parks (Loveridge *et al.* 2007; Caro 2008; Kiffner *et al.* 2009). Finally, numerous lion populations are genetically isolated (Slotow & Hunter 2009), and inbreeding has caused measureable reductions in reproductive rates and disease resistance in several small populations (Kissui & Packer 2004; Trinkel *et al.* 2008, 2011; also see Johnson *et al.* 2010).

Yet, not all lion populations have declined. The Serengeti lions, for example, have steadily increased over the past half-century (Packer *et al.* 2005b), populations have remained stable in several large South African national parks (Ferreira & Funston 2010; Funston 2011), and numerous private reserves in South Africa and Zimbabwe have successfully restored lions to areas where they had previously been extirpated (Hunter *et al.* 2007; Lindsey *et al.* 2009a,b; Slotow & Hunter 2009). However, lions are considered so dangerous in South Africa that they can only be re-introduced after management authorities erect lion-proof fencing and agree to recapture or destroy any escaping lions (Hunter *et al.* 2007; Slotow & Hunter 2009).

Wildlife-proof fences effectively prevent most potential conflicts between lions and humans in southern Africa (Ferguson & Hanks 2010), yet this strategy runs counter to a long-standing conservation ethic of keeping protected areas unfenced and contrasts with the wildlife policies of many range states (Hayward & Kerley 2009; Licht *et al.* 2010; Slotow 2012). Depending on the size of the enclosed population, fencing often also necessitates routine genetic and demographic management of smaller populations via translocations of breeding-aged individuals (Trinkel *et al.* 2008; Johnson *et al.* 2010). Thus, many conservationists have instead sought to encourage human–wildlife co-existence through conflict-mitigation programmes, compensation schemes, insurance plans or payments for tolerance (e.g. Dickman *et al.* 2011). However, the costs of managing dangerous wildlife are formidable. For example, effective elephant and tiger conservation has been estimated to cost \$365–930 per km^2 per year (Leader-Williams & Albon 1988; Walston *et al.* 2010), and the overall costs of anti-poaching and compensation will only increase in range states with growing human populations (Wittemyer *et al.* 2008; Pfeifer *et al.* 2012), declining purchasing power of external funds (Garnett *et al.* 2011) or worsening corruption (Garnett *et al.* 2011).

African lions are among the most extensively studied carnivores in the world with population data available from a wide variety of protected areas in nearly a dozen different countries with divergent conservation practices. Several recently developed ecological models can accurately estimate lion carrying capacities across a wide range of ecological conditions (Hayward *et al.* 2007; Loveridge & Canney 2009), making it possible to estimate the effectiveness of lion conservation in a given reserve by measuring how closely the observed population density matches the expected density. The large number of long-term studies also provides measures of population trends across a wide variety of circumstances. Here, we explicitly test the effectiveness of fencing and management budgets on lion population size and growth rates, while including the impacts of human population density, governance, sport hunting, private management and protected area size.

MATERIALS AND METHODS

Data come from repeated surveys in 38 sites (median span = 12 years; range: 3–46 years) and single surveys in an additional four sites. Population growth rates were estimated from the exponents of exponential regressions of population size over the most recent 10 years for each time series, using nonlinear models in Program R (R Development Core Team 2011), function *nls*. Because many long-term study sites were surveyed irregularly, data were sometimes only available up to 1995–2004, and the median time span was 9 years (range: 3–14 years) (Table S1); Figure S1 shows time series as densities (lions/100 km^2) except for Mole Park, Ghana, where data were collected as number of 'contacts per 100 ranger patrols'.

In an analysis of historical data from 49 undisturbed sites, Loveridge & Canney (2009) found a tight correlation (r^2 = 0.9271) between contemporaneous population sizes of lions and large- to

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medium-sized ungulates; the resultant equation between lion and prey biomass was $Y = 0.0109x^{0.8782}$. Where ungulate surveys were not available, Loveridge & Canney found a close fit for ungulate biomass by modeling habitats according to NOAA's Africa Data Dissemination Service Rainfall Estimate (ADDS-RFE) and cation exchange capacities taken from the ISRIC-WISE soil profile data set (www.isric.org/data/isric-wise-international-soil-profile-dataset) separated into high-, medium- and low-nutrient levels. In the current analysis, 'expected' lion densities were calculated from known prey biomass where possible (34 sites); otherwise, herbivore densities were predicted from rainfall and soils (8 sites); the method used for estimating 'lion carrying capacity' did not significantly affect any of our results.

Each site is classified as managed by public or private agencies, subjected to sport hunting, separated from surrounding communities by wildlife-proof fencing, country/geographical region, and method of estimating carrying capacity (prey biomass vs. rainfall/soils); we also tested effects of reserve size. Human population data were taken from the AfriPop Project (www.afripop.org) (Linard *et al.* 2012; measuring human densities within one kilometre of protected area boundaries extracted from the World Database of Protected Areas (IUCN & UNEP 2009)(see Pfeifer *et al.* 2012). Governance was based on UNDP's six indicators (Voice/Accountability, Political Stability, Government Effectiveness, Regulatory Quality, Rule of Law and Control of Corruption) (UNDP 2010). Principal Components Analysis showed that 87% of variation between indicators was captured by a single component ('Governance') (Table S2). In the statistical analyses, management budgets are US\$ per km^2 per year while controlling for purchasing power and likely losses to corruption (Garnett *et al.* 2011). Budgets could not be partitioned according to anti-poaching, outreach, fence repairs, road maintenance, etc.

For 14 of 42 sites, wildlife surveys were restricted to the best-protected portion of each reserve, whereas budgets were only available for the entire reserve. Expenditures per km^2 were based on two alternative measures: first, total budget divided by the size of the overall protected area (a lower bound which assumes that management expenditures are spread evenly over the entire reserve); second, total budget divided by the size of the survey area (an upper bound which assumes that management expenditures are spent exclusively within the survey area). These alternative measures produced virtually identical results; statistical tests are based on the geometric mean of the two extremes.

Human population densities, protected area sizes, annual management budgets and the ratios of current-to-expected population size were all lognormal, so statistics on the two response variables (population growth rate and current-to-expected population density) were run on the log-transformed data. We used an information-theoretic approach (Burnham & Anderson 2002), with Akaike's Information Criterion (AIC) to calculate statistical models, using simple linear models in Program R, function *lm*. We determined the magnitude and direction of the coefficients for each independent variable using multi-model averaging across all models with ΔAIC less than 4.0 (Grueber *et al.* 2011). These outputs were examined to determine which predictors were statistically significant and to measure the relative importance of each variable (Tables 1–3). 'Relative importance' refers to the sum of the Akaike weights over all of the models containing the parameter of interest.

Given the nested nature of the geographical data, we evaluated a mixed-effects model with nested random intercepts for Region and Country. Log-likelihood ratio tests provided no support for including random effects: the fixed-effects model outperformed all random-effects models (testing Region only, as well as Country nested within

Table 1 Multi-model averages across all reserves for A. ratio of current-to-expected population densities ($n = 40$) and B. exponential growth rates over the past 10 years ($n = 33$). See Table S3 for the full list of models with ΔAIC less than 4.0

Variable	Estimate	SE	Adj. SE	z value	P-value	Relative importance
A. Multi-model averages for Current vs. Expected in all reserves:						
(Intercept)	−0.990	0.177	0.182	5.435	0.000***	1.00
Fence	0.478	0.112	0.115	4.153	0.000***	1.00
Management Budget	0.102	0.029	0.030	3.427	0.001***	1.00
Namibia + South Africa	0.212	0.138	0.142	1.493	0.136	0.50
Human Pop. Density	−0.109	0.068	0.071	1.548	0.122	0.46
Governance	0.003	0.040	0.041	0.077	0.939	0.16
Method	0.089	0.121	0.126	0.706	0.480	0.15
Size of PA	0.044	0.073	0.076	0.578	0.563	0.12
Hunted	0.040	0.117	0.121	0.328	0.743	0.08
State run	0.013	0.091	0.094	0.141	0.888	0.07
B. Multi-model averages for exponential growth rates in all reserves:						
(Intercept)	0.040	0.070	0.072	0.565	0.572	1.00
Fence	0.094	0.043	0.045	2.098	0.036*	0.78
State Run	−0.096	0.044	0.045	2.113	0.035*	0.69
Initial Pop. Size	−0.096	0.051	0.053	1.830	0.067	0.52
Namibia + South Africa	0.079	0.055	0.057	1.386	0.166	0.44
Size of PA	0.026	0.026	0.027	0.965	0.335	0.17
Method	0.058	0.061	0.064	0.901	0.368	0.15
Governance	0.006	0.014	0.015	0.385	0.700	0.14
Human Pop. Density	0.006	0.030	0.031	0.198	0.843	0.08
Hunted	0.010	0.048	0.050	0.201	0.841	0.07
Management Budget	0.001	0.012	0.013	0.086	0.932	0.07

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 2 Multi-model averages of the fenced reserves for A. ratio of current-to-expected population densities ($n = 17$) and B. exponential growth rates over the past 10 years ($n = 16$). See Table S4 for the full list of models with ΔAIC less than 4.0

Variable	Estimate	SE	Adj. SE	*z* value	*P*-value	Relative importance
A. Multi-model averages for Current vs. Expected in fenced reserves:						
(Intercept)	0.297	0.411	0.421	0.706	0.480	1.00
Size of PA	−0.169	0.095	0.100	1.691	0.091	0.60
Namibia + South Africa	0.238	0.137	0.148	1.604	0.109	0.45
State Run	0.233	0.133	0.142	1.634	0.102	0.38
Governance	−0.036	0.030	0.032	1.132	0.258	0.38
Human Pop. Density	−0.008	0.106	0.109	0.073	0.942	0.15
Hunted	−0.089	0.314	0.325	0.274	0.784	0.14
Management Budget	−0.063	0.073	0.076	0.827	0.408	0.13
Method	0.005	0.145	0.159	0.034	0.973	0.02
B. Multi-model averages for exponential growth rates in fenced reserves:						
(Intercept)	0.225	0.081	0.084	2.688	0.007**	1.00
Initial Pop. Size	−0.108	0.037	0.040	2.706	0.007**	0.83
State Run	−0.091	0.041	0.044	2.063	0.039*	0.37
Size of PA	−0.039	0.018	0.020	1.924	0.054	0.37
Human Pop. Density	0.025	0.019	0.022	1.165	0.244	0.08
Management Budget	−0.013	0.012	0.014	0.985	0.325	0.06

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 3 Multi-model averages of the unfenced reserves for A. ratio of current-to-expected population densities ($n = 22$) and B. exponential growth rates over the past 10 years ($n = 17$). See Table S4 for the full list of models with ΔAIC less than 4.0

Variable	Estimate	SE	Adj. SE	*z* value	*P*-value	Relative importance
A. Multi-model averages for Current vs. Expected in unfenced reserves:						
(Intercept)	−1.186	0.332	0.344	3.443	0.001***	1.00
Management Budget	0.159	0.034	0.036	4.365	0.000***	1.00
Human Pop. Density	−0.326	0.127	0.136	2.405	0.016*	0.93
Hunted	−0.420	0.282	0.295	1.423	0.155	0.35
Namibia + South Africa	0.517	0.388	0.405	1.278	0.201	0.25
Size of PA	0.149	0.124	0.131	1.141	0.254	0.18
State Run	0.169	0.157	0.167	1.011	0.312	0.14
Method	0.078	0.150	0.161	0.486	0.627	0.06
Governance	−0.012	0.044	0.047	0.265	0.791	0.05
B. Multi-model averages for exponential growth rates in unfenced reserves:						
(Intercept)	−0.046	0.073	0.077	0.592	0.554	1.00
Namibia + South Africa	0.422	0.100	0.109	3.865	0.000***	1.00
Hunted	−0.258	0.085	0.094	2.752	0.006**	1.00
Method	0.113	0.082	0.091	1.239	0.215	0.16
State Run	0.069	0.062	0.069	1.006	0.314	0.11
Initial Pop. Size	−0.060	0.061	0.068	0.886	0.376	0.09
Governance	−0.015	0.016	0.017	0.836	0.403	0.09
Size of PA	0.026	0.033	0.036	0.717	0.474	0.08
Management Budget	0.004	0.012	0.013	0.313	0.755	0.06

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Region). However, South Africa and Namibia deviated most strikingly from other countries and geographical configurations, so we ran all AIC models using 'Namibia + South Africa vs. Other' as a fixed effect to minimise the number of coefficients. Note that because many of the fenced reserves were smaller than the overall average, 'fenced/non-fenced' showed a moderate degree of co-linearity with protected area size (Spearman rank-order correlation, $r_s = -0.516$); however, protected area size was not strongly correlated with either of the dependent outcome variables in a univariate analysis, and the effects of fencing remained robust in all AIC models that included protected area size. Finally, we extrapolated population sizes at 5-year intervals for 100 years into the future by combining current population size with the exponential growth rate over the past 10 years. Populations were considered likely to persist if their extrapolated population sizes exceed 10% of their potential carrying capacities at particular time points in the future.

RESULTS

Table 1 summarises the variables with the strongest effects on lion population status and population growth rates across Africa. Current population densities are highest compared to their expected values in reserves that (1) are fenced and (2) have the highest management budgets per km^2 (Fig. 1, Tables 1a and S3a). Over the past 10 yrs, population growth rates have been highest in (1) fenced reserves (Fig. 2) and (2) privately managed reserves (Tables 1b and S3b). Because fences have such a profound impact on lion management, we performed separate analyses for fenced and unfenced reserves. For fenced reserves, none of the tested variables had a significant effect on current population status (Tables 2a and S4a), whereas recent population growth has been highest in populations that had been farthest below their potential densities 10 years earlier (Fig. 2) with additional positive effects from private management (Tables 2b and S4b). For unfenced populations, current status is highest in reserves with the largest management budgets (Fig. 1) and lowest when surrounded by high human population densities (Tables 3a and S5a); growth rates were highest in Namibia + South Africa and in populations that were not subjected to trophy hunting (Tables 3b and S5b). Given current population sizes and recent trends, all of the fenced populations are expected to remain at or above their full potential for the next 100 years, whereas less than half of the unfenced reserves are likely to persist above 10% of their carrying capacities for the next 20–40 years (Fig. 3), including unfenced sites in Botswana, Kenya, Cameroon, Ghana, Tanzania and Uganda.

DISCUSSION

Negative conservation impacts of human land use can often be minimised by restricting conflicting activities to separate areas rather than by encouraging their co-existence. For example, concentrating crop production in areas of intensive agriculture and sparing land as nature reserves can improve species conservation and crop production more effectively than land-sharing strategies that integrate conservation and low-intensity agricultural production (Phalan *et al.* 2011). Establishing separate areas of intensive timber production while maintaining well-defined forest reserves is also preferable to low-intensity harvests over a greater proportion of forest (Boscolo & Vincent 2003). Similarly, physical separation is highly effective for conserving African lions: all of the fenced lion populations were close to their estimated carrying capacities (Fig. 1), growth rates of the fenced populations were density dependent (Fig. 2), and every

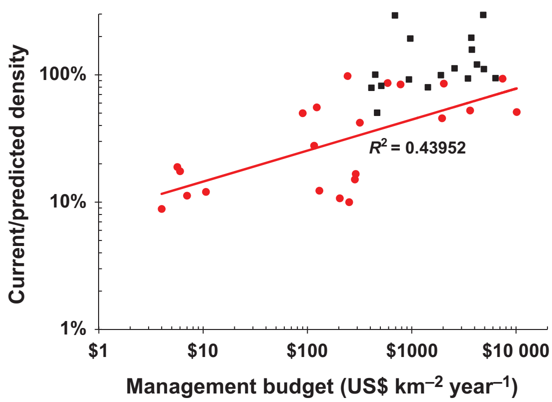

Figure 1 Percentage ratio of current population density to predicted carrying capacity of African lions in fenced (black squares) and unfenced (red circles) reserves according to management budget per square kilometre of lion survey area. The red regression line is for unfenced reserves; the effect of management budget in the fenced reserves is not statistically significant.

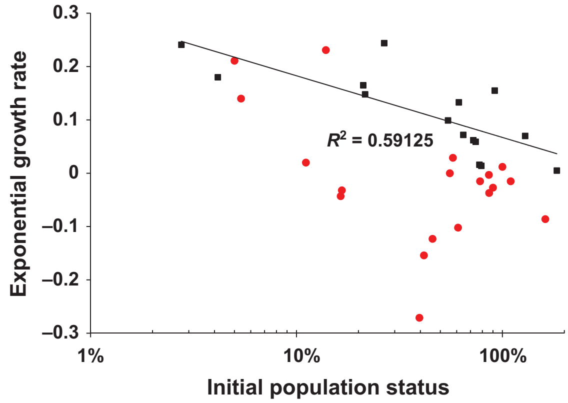

Figure 2 Effect of population density on population growth rate over the following 10 years for fenced (black) and unfenced (red) reserves. 'Initial population status' refers to the observed population density at the start of each time series compared to the expected density. The black regression line is for fenced reserves.

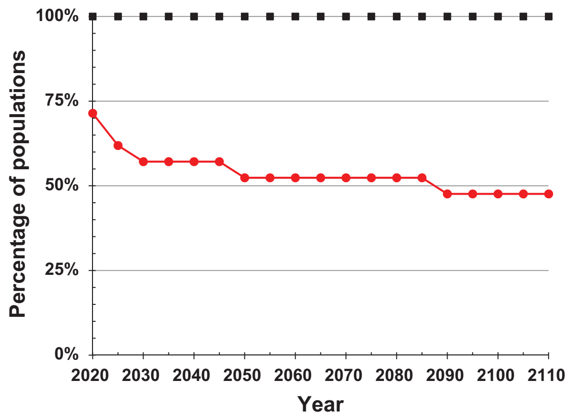

Figure 3 Percentage of populations expected to persist at densities > 10% of their potential in the future. Differences between fenced (black squares, n = 16) and unfenced (red circles, n = 21) reserves each year are all significant by Fisher test.

fenced population is expected to remain close to its carrying capacity for the next century. Indeed, managers in many of the smaller fenced reserves currently remove 'excess' lions in attempts to stabilise ungulate numbers (see Fig. S1). Fenced lion populations were less sensitive to human densities in adjacent areas than were unfenced populations, presumably because fences reduce poaching, minimise habitat loss, curtail illegal grazing and prevent direct human–lion conflict (Kiffner *et al.* 2012). Such density-independent 'edge effects' likely prevented recovery of numerous unfenced lion populations that had fallen substantially below their respective carrying capacities 10 years earlier.

Conservationists have long recognised that large carnivores should be kept apart from humans. However, fencing has so far only been widely employed in a few African countries because of aesthetic objections, financial costs and the impracticality of enclosing large-scale migratory ungulate populations. Thus, recent conservation efforts have increasingly promoted human–wildlife co-existence, either by initiating conflict-mitigation projects in buffer zones or by providing economic incentives for local people to tolerate the costs of living with wildlife (Woodroffe *et al.* 2005; Dickman *et al.* 2011). However, our analysis suggests that human–lion co-existence should only be considered in areas where large-scale megafaunal (and pastoralist) migration precludes any form of fencing. In some cases, human-occupied zones within larger wildlife-dominated ecosystems may even need to be fenced as enclaves (e.g. 30,000 people live in 40 villages inside Mozambique's Niassa National Reserve), as has been recommended for reducing conflicts between wolves and ranchers in livestock-production areas around Yellowstone National Park (Stone *et al.* 2008).

Whether or not more lion populations are eventually fenced, large-scale lion conservation will be expensive. Currently, many of the best-financed reserves are too small to sustain long-term ecosystem processes without frequent and costly management interventions (e.g. Hunter *et al.* 2007), and a 10- to 100-fold increase in management budget will be required to sustain many of the reserves that are not yet fenced (Fig. 1). Although fenced reserves can typically achieve considerable management success on annual budgets as low as \$500 km^{-2} (Fig. 1), fences cost ca. \$3000 per km to install (Vercauteren *et al.* 2006). Long-term costs of successfully managing unfenced lion populations are even higher: \$2000 per km^2 per year is only sufficient to maintain an unfenced lion population at 50% of its potential density (Fig. 1). By comparison, the 2010 management budget in Yellowstone was \$4100 per km^2 – enough to maintain an average unfenced lion population at about two-thirds of its potential. Under current financial practices in Africa, only a small proportion of tourism revenues are directly available to park managers (Bushell & Eagles 2007) and trophy hunting rarely raises more than \$1000 per km^2 (Lindsey *et al.* 2012).

Although our focus on a single species may seem narrow, top predators can only flourish in healthy ecosystems: many components of lower trophic levels must also thrive for lion populations to remain close to their potential limits, thus the price of successful lion management provides an important gauge for the true costs of sustaining *intact* savannah ecosystems. Finding financial solutions to long-term conservation of Africa's largest remaining intact ecosystems such as Niassa, Okavango, Selous, Serengeti and the W-Arly-Pendjari Complex will present an enormous challenge to African governments and conservationists.

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CP, AL, GB, TC, AS, HBa, CMB, KSB, SB, CB, TB, HBr, AB, ACB, BC, SD, AD, TD, SMD, DD, LF, PF, NG, RG, CH, LH, HHdeI, CJJ, SMK, BK, WK, BL, PAL, SDM, JWMcN, SMM, SN, PN, CN, KN, JOO, EOO, BDP, AP, JS, EAS, KJS, CW and HW performed field research. SC and AL developed the ecological model. CP, SC, AL, STG, DMacN, MP, AS and KKZ analysed data. CP, TC, AS, STG and SP wrote the manuscript. All authors discussed the results and commented on the manuscript.

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