

The Trophy Hunting of African Lions: Scale, Current Management Practices and Factors Undermining Sustainability

Peter Andrew Lindsey^{1,2}*, Guy Andrew Balme^{1,3}, Paul Funston¹, Philipp Henschel¹, Luke Hunter¹, Hilary Madzikanda⁴, Neil Midlane³, Vincent Nyirenda⁵

1 Lion Program, Panthera, New York, United States of America, 2 Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, Gauteng, South Africa, 3 Department of Biological Sciences, University of Cape Town, Cape Town, Western Cape, South Africa, 4 Zimbabwe Parks and Wildlife Management Authority, Harare, Mashonaland East, Zimbabwe, 5 Zambia Wildlife Authority, Chilanga, Lusaka Province, Zambia

Abstract

The trophy hunting of lions Panthera leo is contentious due to uncertainty concerning conservation impacts and because of highly polarised opinions about the practice. African lions are hunted across at least ~558,000 km², which comprises 27-32% of the lion range in countries where trophy hunting of the species is permitted. Consequently, trophy hunting has potential to impart significant positive or negative impacts on lions. Several studies have demonstrated that excessive trophy harvests have driven lion population declines. There have been several attempts by protectionist non-governmental organisations to reduce or preclude trophy hunting via restrictions on the import and export of lion trophies. We document the management of lion hunting in Africa and highlight challenges which need addressing to achieve sustainability. Problems include: unscientific bases for quota setting; excessive quotas and off-takes in some countries; fixed quotas which encourage over-harvest; and lack of restrictions on the age of lions that can be hunted. Key interventions needed to make lion hunting more sustainable, include implementation of: enforced age restrictions; improved trophy monitoring; adaptive management of quotas and a minimum length of lion hunts of at least 21 days. Some range states have made important steps towards implementing such improved management and off-takes have fallen steeply in recent years. For example age restrictions have been introduced in Tanzania and in Niassa in Mozambique, and are being considered for Benin and Zimbabwe, several states have reduced quotas, and Zimbabwe is implementing trophy monitoring. However, further reforms are needed to ensure sustainability and reduce conservation problems associated with the practice while allowing retention of associated financial incentives for conservation.

Citation: Lindsey PA, Balme GA, Funston P, Henschel P, Hunter L, et al. (2013) The Trophy Hunting of African Lions: Scale, Current Management Practices and Factors Undermining Sustainability. PLoS ONE 8(9): e73808. doi:10.1371/journal.pone.0073808

Editor: Matt Hayward, Bangor University, United Kingdom

Received April 27, 2013; Accepted July 25, 2013; Published September 18, 2013

Copyright: © 2013 Lindsey et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and re credited.

Funding: This research was funded by Panthera. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

1

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: plindsey@Panthera.org

Introduction

Over the last century the distribution of lions Panthera leo in Africa has shrunk by as much as 82%, with the most severe contraction occurring in West Africa [1]. Although the historic size of the lion population is not known, heightened rates of decline in recent decades have left a remaining population of just 23,000-39,000 [2], [3], [4], [5], [6]. Most of the factors that contribute to this decline are now well understood [7], although evidence of the impacts of trophy hunting on lions has only emerged relatively recently. Trophy hunting has contributed to population declines outside (and inside some) protected areas in Tanzania, a country that holds between 30-50% of Africa's lions [8]. Excessive offtakes from trophy hunting also lowered population density of lions and altered sex-ratios of lions in Hwange National Park, Zimbabwe [9], [10], South Luangwa, Kafue and Lower Zambezi national parks in Zambia [11], and the Bénoué Complex in Cameroon [12]. Conversely, trophy hunting can create incentives for the conservation of lions and the retention of land under wildlife-based land uses [13]. Trophy hunting can also theoretically increase local tolerance of lions [14], and thus reduce persecution resulting from the threat that the species poses to livestock and human life [15], [16].

There have been several attempts to curtail trade in lion trophies to alleviate hunting pressure. For example, in 2004 Kenya submitted a proposal that lions be listed on CITES Appendix I at the 13th conference of the parties [2]. In 2011 a consortium of US-based non-governmental organizations (primarily animal rights/welfare groups) petitioned the United States government to list lions as endangered under its Endangered Species Act (ESA). Concurrent efforts are underway by Western protectionist NGOs to encourage the European Union to ban lion trophy imports. Recent pressure for trade bans have coincided with increasing evidence of negative ecological impacts associated with lion hunting. However, complicating the picture is the fact that the NGOs pushing for trade bans are strongly opposed to trophy hunting in principle. Consequently, their assessment of the pros and cons

Table 1. Rules and processes relating to the allocation of hunting blocks and management of lion hunting in southern Africa and Tanzania (derived from surveys with senior officials).

	Mozambique	Namibia	Tanzania	Zambia	Zimbabwe
Concession allocation process	Coutadas: closed tender. Game ranches: long term lease	State concessions – public auction; game ranches - privately owned; community conservancies – tender process	Closed tender, fixed fee (depending on status of wildlife in blocks)	GMAs: closed tender process. Game ranches: long term lease	State safari areas - public auction; Forestry areas - internally allocated; CAMPFIRE areas - closed tender; game ranches - long term lease (following land seizures)
Lease period	Coutadas/state owned blocks: ≥10 years (mean -27.4 years [13]	State concessions – 3 years; communal conservancies - 5 years	5 years	GMAs: 10–15 years (depending on status). Game ranches: long term lease	State safari areas: 5 years (with a 5 year performance based extension). CAMPFIRI areas: 3–10 years
Community benefits from hunting in areas occupied by people	Variable: tender bids partially assessed on basis of commitments to provide benefits to communities. In reality, benefit streams are limited in most cases.	Communal conservancies, user rights owned by communities, benefits stream directly to communities who have formed a conservancy	In WMAs, communities accrue 60–65% of total hunting income; in Game Controlled and Open areas benefits limited to mandatory contributions from operators to community projects (F. Nelson, pers. comm.)	In GMAs, communities accrue 50% of trophy fees and 20% of concession fees [48]	Benefits accrue to rural district councils, a proportion then remitted to communities. In an increasing number of cases communities receive direct payments [49], C. Jonga pers. comm.
Basis for establishing lion quotas	Quotas are set annually, based on a combination of the following (depending on availability): data from surveys; research reports; reports on human-lion conflict; historical surveys; opinions of govt representatives and operators	In small state concessions, data are usually available on lions numbers to guide quota allocation. In community conservancies, data on human-lion conflict are used to guide lion quotas as well as extensive research on lion populations	Based on various source of info: operators provide recommendations; officers working for the Wildlife Division provide opinion regarding whether the previous quota was too big or too small; info from surveys or reports where available	A set % of estimates of lion populations, but modulated by local communities and operators recommendations	Assessment of the extent to which historical quotas were utilized, extent of reports o problem lions, data from lion surveys (available for NW Matabeleland and conservancies)
Mandatory quota payments required from operators ('Fixed quota')	None – only pay for hunted animals	100% of quota – concession rights based on sale of quota rather than lease of land	40% of total quota regardless of off-take	60% of total quota regardless of off-take (Prime hunting blocks – 5 'classic' & 7 'mini' safaris; Secondary hunting blocks –3 classic and 5 mini safaris)	30% of total quota regardless of off-take
Monitoring	Coutadas: official observer; hunt return form; detailed monitoring in Niassa	State concessions and communal conservancies: sometimes official observers; hunt return form	Official observer, hunt return form	Official observer; completion of a hunt return form and submission of photos of the trophy required as a pre-requisite for obtaining export permits	State safari, forestry and CAMPFIRE areas – official observer; completion of hunt return form and submission of trophy photos is mandatory
Season	1 May-30 Nov	1 Feb-30 Nov	1 Jul–31 Mar	1 May-31 Dec	No set season
Time	No restriction (no artificial light)	30 min before sunrise- 30 min after sunset (no artificial light)	Sunrise – Sunset (no artificial light)	Sunrise – Sunset (no artificial light)	State: 30 min before sunrise-30 min after sunset CAMPFIRE/private: no restriction
Minimum stipulated length of lion hunts (in days)	None	None	21	No stipulation	None
Sex of lions hunted	Male	Male & female	Male	Male	Male
Minimum age/size	6 years in Niassa; No restriction elsewhere	Skull size: 52 cm	6 years	None	None yet, though age restrictions are being considered
General	Must be shot >150 m from a vehicle; illegal to hunt problem lions as trophies	Lions must only be hunted in areas of at least 10 km ² in size; no hunting of captive- bred animals	Must be shot >200 m from a vehicle, >2 km from a national park boundary and >500 m from a water source	Must be shot >200 m from a vehicle	Must be shot >50 m from a vehicle, >400 m from a water source

Table 2. Rules and processes relating to the allocation of hunting blocks and management of lion hunting in Central and West Africa (derived from legal documents).

	Benin	Burkina Faso	Cameroon	CAR
Source	[47], [50], [51]	[51], [52]	[12], [51], [53]	[24], [51], [54]
Concession allocation process	Hunting Zones are leased to hunting operators via a call for tender	Hunting concessions attributed via a call for tender	Hunting Zones are leased to hunting operators via a call for tender (highest bid wins)	Hunting Zones are leased to hunting operators via a call for tender (first bid wins)
Lease period	5 years (renewable)	20 years	10 years (renewable)	10 years (renewable)
Community benefits from hunting in areas occupied by people	Community associations accrue 30% of income from hunting and tourism	Communities accrue 50% of the hunting block lease fee (\$5/km²), translating to 3–4% of total hunting revenues	Communities accrue 50% of the trophy fees (40% go to local authorities, and 10% to local populations)	Communities accrue 60% of hunting block lease fee and 25% of trophy fees in 'classic' privatized hunting blocks, and 80% of hunting block lease fees and 65% of trophy fees in community hunting blocks
Basis for establishing lion quotas	Initially based on demand, but after perceived lion declines in 1990s, based on a lion survey conducted by independent researchers in 2002	Quotas allocated annually, based on size of the hunting zone and quotas and extent of utilization in previous years	Quotas allocated annually, based on size of the hunting zone and quotas and extent of utilization in previous years	Quotas are set annually based or quotas of previous years, extent of utilization of previous quotas, and operator needs
Mandatory quota payments required by operators ('Fixed quota')	None – only pay for hunted animals	None – only pay for hunted animals	None – only pay for hunted animals	50% of total quota regardless of off-take
Monitoring	Official observer, Hunt return form	Hunt return form	Hunt return form	Official observer, Hunt return form
Season	15 Dec-15 May	1 Dec-31 May	1 Dec-31 May	15 Dec-31 May
Time	Sunrise – Sunset, (no artificial light)	Sunrise – Sunset, (no artificial light)	Sunrise – Sunset, (no artificial light)	Sunrise – Sunset, (no artificial light)
Minimum stipulated length of lion hunts (in days)	12–14	12	12–14	12–21
Sex of lions hunted	Male	Male	Male	Male
Minimum age/size	Age restrictions agreed in principle, but not yet enforced	None	None	None
General	Must be shot >1 km from a water source or salt-lick	Not specified	Cannot be shot from a vehicle	Cannot be shot from a vehicle

of lion hunting is not impartial. The US Fish and Wildlife Service is now undergoing a 12-month review process to determine whether ESA listing is warranted, having earlier found that there was sufficient evidence to consider the proposal.

Trade restrictions on lion trophies would have a significant impact on lion hunting by limiting imports of trophies into key markets. The US and the EU together represent the bulk of the market for African trophy hunting [17], and most lions hunted in Africa are exported as trophies to the US or EU (85.0% of non-South African [i.e. trophies of non captive-bred lions], accessed January 2012) [18]. Trade restrictions could reduce a direct source of mortality of lions and potentially allow lion populations depleted due to over-hunting to recover in the short term (assuming that nationals from other countries did not hunt lions instead of those from the US and EU). However, lion hunting generates significant returns (e.g. USD60,000 to >US\$120,000 per lion hunt, [13], [19]) and is conducted over vast areas where ecotourism is often unviable [20], [21]. Removing the EU and US markets for lion hunting would likely result in a significant drop in the price of lion hunts and could make it difficult for operators to sell lion hunting safaris. Such changes would render trophy hunting less viable in many areas, and in extreme cases could result in a conversion to less conservation-compatible land uses such as agriculture and pastoralism [12]. In Kenya, where trophy hunting has been banned since 1977, for example, protected areas now lack the buffers that are provided by hunting blocks in many other African countries, and wildlife populations have declined by 60–70% since the hunting ban [21]. While it is not possible to determine whether, or to what extent, the trophy hunting ban contributed to negative wildlife population trends, the prohibition certainly failed to improve the conservation status of wildlife (including lions) in Kenya.

In this paper, we review the extent of lion hunting in Africa, the way it is managed and identify issues which undermine sustainability. This paper complements a sister manuscript which provides consensus on steps needed to make lion hunting more sustainable Hunter et al. in prep.

Results

Management of Lion Hunting and of Hunting Blocks

Hunting blocks are typically allocated via a closed tender process, with the exception of state-owned blocks in Namibia and Zimbabwe (Tables 1, 2). State and community hunting blocks are typically leased for five years in Namibia, Tanzania, Zimbabwe (in

the latter with the option of a performance-related 5-year extension) and Benin, and 10 or more years in Burkina Faso, Cameroon, Central African Republic (CAR), Mozambique, and Zambia (Tables 1, 2). In hunting blocks occupied by communities, full devolution of user-rights to communities has only occurred in Namibia, where 79 community conservancies covering 160,000 km² have developed, resulting in rapid increases in wildlife populations [22] partly due to incentives created by trophy hunting [23]. In most other countries, community benefits are limited (Tables 1, 2). In several countries, at least a proportion of hunting quotas is fixed, such that operators pay trophy fees irrespective of whether the animals (including lions) are hunted (Tables 1, 2). Lion quotas are typically based on the opinion of state wildlife agency representatives and hunting operators, using past utilization of quotas, and with guidance from status reports where available (Tables 1, 2). In Namibia, Mozambique and Zimbabwe, reports of human-lion conflict are also purportedly used to inform quotas, with higher quotas allocated to areas with higher levels of conflict (Table 1). The hunting of lionesses is permitted in some hunting blocks in Namibia (Table 1), and was permitted in Zimbabwe until 2011 (after which no quotas for females were issued). Only male lions may be hunted in all other

Spatial Extent of Lion Hunting, Hunting Blocks, Quotas and Off-takes, Success Rates

Lions are hunted across an area of $\sim 558,000~\rm km^2$ in Africa which represents $\sim 16\%$ of their total African distribution and 27–32% of the distribution of the species in the countries in which they are hunted (Table 3). Lions are hunted in the majority of the area used for trophy hunting in Benin, Burkina Faso, Mozambique, Zambia, Tanzania and Zimbabwe and in smaller proportions of hunting areas elsewhere (Table 3). Lions are hunted across the highest proportions of the species' range in Cameroon, Zimbabwe, Burkina Faso and Tanzania (Table 3).

Quotas per km² are highest in Burkina Faso, Zimbabwe, Cameroon and Tanzania (Table 4). Off-takes of lions per km² are highest in Burkina Faso and Zimbabwe. Mean off-takes per unit area were higher than the 0.5/1,000 km² recommended by [8] in Burkina Faso, Zimbabwe, Zambia and Namibia. However, off-takes are higher than that threshold in a significant proportion of hunting blocks in all countries for which data on block-by-block off-takes were available (Table 4). Data were not available on the numbers of females on quota in Namibia, though two respondents (of 12 interviewed) indicated that they had females on quota (one had a quota of 4 females on 800 km² of private land, and the other 1 female on 3,493 km² of communal conservancy).

Moratoria and Quota Cuts

There have been a number of steps taken by wildlife authorities and conservation organisations to reduce the detrimental impacts and extent of lion hunting. For example, Benin and Central African Republic imposed 2-year and 3-year moratoria on lion hunting during the early 2000s respectively, in response to research highlighting declining populations [24], [25]. Both countries subsequently cut quotas: in Central African Republic, a maximum of one lion per block is now generally allocated (blocks being a mean of $3,026\pm303~\rm km^2$ in size) [25]; and, in Benin, quotas were cut from 10 before the 2-year moratorium to 5 presently [26]. Botswana removed lions from quota during 2001–2004, and again from 2008 to the present [27]. Zambia cut quotas from ~ 100 in 2007 to 74 in 2012 and then imposed a moratorium in 2013 (Lindsey unpublished data). Tanzania reduced quotas from 520 in 2008/2009 to 315 in 2012 and introduced restrictions

on the ages of lions that may be hunted [28]. Zimbabwe stopped female hunting and is in the process of implementing trophy monitoring of lion hunting. We are not aware of any steps taken to improve sustainability in Burkina Faso or Cameroon, despite evidence of reduced lion densities in hunting areas and in the latter, declining populations [12], [29].

Latest data available on lion harvests suggests that \sim 244 lions per year are hunted in Africa (Table 4), whereas a mean of 350–550 were exported from Africa during 1995–2005 ([30], accessed April 2012, the number depending on which search terms are included when accessing the CITES database). For example, Packer et al [8] estimated that 243 wild lions were hunted per year in Tanzania during 1996–2006, 96 in Zimbabwe and 55 in Zambia, compared to our more recent estimates of 85, 43 and 47 for those countries (Table 4).

Monitoring of Lion Hunting

According to state-wildlife officials, all countries have implemented (or in the case of Mozambique are in the process of implementing) reporting systems to capture basic information on lions hunted (Tables 1, 2), though the rigour with which these data are collected, and whether they are analysed and the results actually used is not clear. Zimbabwe is in the process of implementing a rigorous trophy monitoring programme for lions whereby operators are required to complete hunt return forms and submit multiple photographs of the lion's face, body and skull as a prerequisite for obtaining export permits for lion trophies (Table 1).

Age Restrictions

Tanzania has implemented a six-year minimum age limit for trophy lions at a national scale. There, age restrictions are enforced such that: trophies from six year old lions are accepted with rewards, those from 4 and 5 year old lions are accepted with penalties and those from lions of <4 years old are rejected and attract deterrent penalties [28]. Age restrictions in Tanzania are enforced via assessment of: hunt return forms; skull measurements; qualitative assessments of skulls; x-rays of the upper pre molar PM2; and inspection of photos of the animal (assessing mane development, facial markings, nose and teeth colour) [28]. The age assessments are conducted by a panel which includes government representatives, an NGO, and scientists from Tanzanian universities [28].

Age restrictions are also in place in Niassa National Reserve in Mozambique. There, independent scientists monitor lion trophies and allocate varying numbers of points to operators for hunting lions of different categories (which correspond to those used in Tanzania), or for not hunting a lion [31]. The lion quota for the following year is then increased, kept the same, or reduced, depending on the number of points awarded. Age restrictions are planned in Benin (Table 1). Zimbabwe is currently considering introducing age restrictions (and held a workshop on the topic in mid-2013). Namibia requires that lions hunted have a skull measurement (length plus breadth) of at least 52 cm, though that restriction is unlikely to prevent the harvesting of young mature male lions in their reproductive prime under the 6-year threshold [32]

Most (73.4%) operators claim to adopt a conservative approach to trophy selection over and above legal restrictions to reduce the impacts of harvest, most commonly: shooting only old lions (60.0%), shooting only non-pride males (46.0%) and where females are on quota, avoiding hunting lionesses with cubs (6.0%).

Most (73.2%) operators felt that they are able to reliably age lions in the field to within the following age categories: (<4 years, 4–6 years, >6 years). There was no difference among perceptions

Table 3. The area in which lions occur, total area in which trophy hunting occurs and the area across which lions are hunted.

	Total lion range (where 2 figures are presented they represent permanent/ permanent +occasional	Total hunting	Area across which lions are	% of lion range where lions are	% of hunting area with lion on	6
Country	lion presence) (km²)	area (km²)	hunted (km²)	hunted	quota	Source of data
Tanzania	516,000–750,000	300,000	254,207	33.9–49.3	84.7	Lion range, lion hunting area - [55], hunting area - [8]
Mozambique	515,000-610,000	120,932 ^b	69,465 ^e	11.4–13.5	57.4	Lion range, lion hunting area - [56], hunting area - Lindsey unpublished data
Central African Republic	338,475	223,924 ^c (114,524)	59,738	17.7 ^c	26.7 (52.2) ^c	Lion range [6], lion hunting area – [46], [57]; hunting area - [57]
Zambia ^a	200,237	167,000	89,035	44.5	53.3	Lion range - [3]; hunting area – Lindsey unpublished data, lion hunting area, Zambia Wildlife Authority 2012 quotas
Namibia	74,270	274,057 ^d	22,889	30.8	8.4	Lion range - [3]; hunting area – Lindsey unpublished data, lion hunting area - WWF- Namibia pers. comm., 2010
Zimbabwe	51,078	64,945	32,810 ^f	64.2	50.5	Lion range - [3], hunting area - [17], lion hunting area - Zimbabwe Parks and Wildlife Management 2012 quotas
Cameroon	26,809	52,815	18,260	68.1	34.6	Lion range - [7] hunting area: [58]; lion hunting area calculated from [58] and [7]
Benin	20,080	4,338	4,338	21.6	100	Lion range [6], hunting area, lion hunting area - [47]
Burkina Faso	13,387	9,510	7,148	53.4	75.2	Lion range – [6], total hunting area – [51], lion hunting area, calculated from [6] and [51]
TOTAL	1,755,336–2,084,336	1,108,121– 1,217,521	557,890	26.8–31.8	45.8–50.3	

^aln January 2012, a moratorium was imposed on the hunting of lions and leopards in Zambia;

of operators from different countries about their ability to age lions ($\chi^2 = 2.1$, df. = 4, p = 0.711). Operators were asked what percentage of lions that they had previously hunted fell in each of three age categories: a mean of $8.51\pm2.49\%$ of trophies were estimated to have been <4 years old; $35.6\pm4.0\%$ 4–6 years old, and $55.9\pm4.61\%$ >6 years old.

When asked to indicate whether they considered a lion's nose to be an accurate indicator of its age, 57.1% of operators answered in the affirmative and 19.0% were unsure. Of respondents who did not consider noses to be an accurate indicator of lions' ages (23.9%), 54.5% indicated that they had shot old lions with pink noses and 9.1% said that they had seen young lions with black noses. Only 31.1% of operators considered it practically feasible to gauge the colour of a lion's nose in the field, because hunting normally occurs under low light conditions (48.2%); because lions are sometimes facing away when they are hunted (13.8%) or are hunted in thick bush (10.3%). Operators use a variety of other cues to age lions, including *inter alia*: the head size/shape (44.4%); body size/shape (44.4%); the extent of facial scarring (44.4%); presence/absence of spots on the fur (22.2%); shape of the mane (15.3%); and body colour (14.8%).

Sixty-four per cent of operators felt that it would be/is a good idea to have a legal minimum age limit on male lion trophies at a national level (Namibia –88.8% of operators; Tanzania –84.6%; Zambia –83.3%; Zimbabwe –53.3%; Mozambique –50.0%).

However, 22.2% of operators who supported national minimum age limits expressed concern over how such a regulation would be enforced and 21.1% stressed that some error must be accommodated. Respondents supporting minimum age limits suggested the following as means of enforcement: imposition of fines for shooting under-age lions (34.3% of operators); cutting quotas (15.1%); or temporary loss of license (12.5%). Of respondents who felt that a national minimum age limit was not a good idea: 35.3% felt that aging lions was too difficult and that new techniques for aging are required; 17.6% felt that it would be impossible to enforce and 17.6% felt that it would be preferable to rather establish sustainable quotas.

Respondents were subsequently asked to indicate if they felt that the system currently in place in Niassa National Reserve in Mozambique (whereby the lion quota is dictated by the quality of the trophies taken in the previous year) would work in their area. Most (64%) operators responded in the affirmative.

Operators' Perceptions of Hunting Success Rates and Trends in Lion Populations

During surveys, 34.1% of operators felt that the success rate of lion hunting had changed in their areas during the last five years, of whom 64.3% indicated that their success rate had declined. Forty-four and 33.3% of the operators that documented declining success rates were from Tanzania and Mozambique, of which

^bExcluding 27 hunting blocks of unknown size (mostly game ranches);

The smaller figure represents the actual area where hunting has occurred recently (due inter alia to political instability): in the recent past hunting (and lion hunting) was conducted over an area almost twice as large;

dExcluding 2 state concessions of unknown size and potentially some private ranches where lions may be hunted;

Excluding 5 blocks of unknown size where lions are on quota and game ranches where lions may be on quota;

^fExcluding 24 blocks of unknown size where lions are on quota (mainly community areas for which size data are lacking).

Table 4. Square kilometres/lion on quota and lion hunted, and the percentage of hunting blocks with >0.5 lions on quota and lions hunted.

Country	Quota	Year(s) of data	km²/lion (quota) ± S.E. (area used for lion hunting/ lions on quota)ª	% with >0.5 lions/ 1000 km² on quota	Actual off-takes	Year(s) of data	Km²/lion hunted ± S.E. (area used for lion hunting/ lions hunted) ^b	% of blocks with >0.5 lions shot/1,000 km² where block by block data were available (excluding blocks where lions were on quota but not harvested)	Source of data
Burkina Faso	20±0	2006–2009	357	100	13.3±1.45	2006–2009	537	100	Quota and off-takes - [59]
Zimbabwe	101	2011	463	100	42.5±7.5	2008–2011	714	No data	Quota data – ZPWMA unpublished data 2010–2011, off-takes – CITES export data
Namibia ^c	14.5	2010	1,769	64.3	14.0±3.2	2008–2011	1,635	No data	Quotas – WWF-Namibia unpublished data; off-takes – CITES export data
Zambia ^d	74	2012	1,203	78.3	47	2012	1,894	60.0	Quotas and off-takes, Zambia 2012
Benin	5.0+0	2007-2009	898	100	2.0±0.4	2007-2009	2,169	9.99	Quota and off-take data – [47]
Mozambique	42-60	2013	2,399	47.6	19.2±7.3	2008–2011	2,584	18.2	Quotas – Mozambique Ministry of Tourism, [56], off-takes – CITES export data, off-takes per block [56], C. Begg pers. comm.
Cameroon	29.2 ± 2	2006–2010	625	;	6.9±1.0	2006–2010	2,646	No data	Quota and off-takes - [12]
Tanzania	315	2011–2012	807	;	85	2011–2012	2,991	No data	[28]
CAR	31	2009	1,927	35.4	13.7±6.9	2008–2011	4,358	50.0	Quotas [46], total off-takes – CITES export data, off-takes per block – [46]
Total	632–650				244				

Except Zimbabwe, Mozambique and Namibia where there were missing data on the size of some hunting blocks: in those countries we took the mean area per lion on quota for blocks that we had data for;

Phote that for Mozambique, Namibia and especially Zimbabwe, the area per lion hunted represents an underestimate as data on the sizes of some hunting blocks where lions are hunted were unavailable and thus not included in

doi:10.1371/journal.pone.0073808.t004

the analysis;

for some Namibian conservancies, lion trophy quotas are only issued every second year. The quota figure may exclude some lions hunted on private lands;

for some Namibian conservancies, lion trophy quotas are only issued every second year. The quota figure may exclude some to collect information on populations of the species as a basis for establishing quotas;

for some lion and in the past. In 2009, for example, the national quota including game

for state and community areas in 2013 was 42, but we could not access data for game ranches where lions have been hunted in the past. In 2009, for example, the national quota including game ranches means that we may have under-estimated the area across which lions are hunted and the area per lion on quota and lion hunted may be over-estimated somewhat as game ranches are typically somewhat smaller than state hunting blocks.

75% and 100% respectively attributed the decline to the implementation of age restrictions for lion trophies.

Respondents were asked if it was possible to re-sell lion hunts in the same year if a hunt was unsuccessful. Most (58.0%) answered in the affirmative, with the proportion of positive responses varying among operators from different countries (Zambia and Zimbabwe -100%, Mozambique -44.4%, and Tanzania -16.7%) $(\chi^2 = 24.4, d.f. = 4, p < 0.001)$.

Fifty-five (54.5%) per cent of operators considered lion populations to be increasing in their areas, 25.8% considered numbers to be stable, 9.1% thought numbers were declining, 9.1% were not sure of the trends, and the remainder felt there were no resident lions in their hunting blocks (though quotas were still issued for the species in those areas) (Figure 1). Lions were considered to be increasing in most hunting areas in Zimbabwe and Mozambique, and to be declining in a significant proportion of Zambian and Tanzanian hunting areas (Figure 1).

The most common explanations given for increasing lion populations were: recovering/large prey populations (37.5% of respondents reporting increasing lion populations); current or recent moratoria on lion hunting (9.4%); following the reintroduction of lions (9.4%); and, due to small/reduced quotas or good management of hunting (6.3%). Most common reasons given for declining lion populations were: human-wildlife conflict (40.0% reporting declining lion populations), human encroachment on hunting areas (40.0%) and communities killing lions (for various reasons including conflict, snaring and ritual killings) (20.0%).

Sixty-two per cent (62.2%) of operators felt that there were problems associated with the trophy hunting of lions in their country (Table 5). Inappropriate, unscientific or excessive quotas were the most commonly identified problems associated with lion hunting (Table 5). The most commonly suggested solutions to problems (provided to an open ended question) were: smaller quotas (32.2% of operators); the introduction of age restrictions (32.2%); more scientific quotas (22.8%) and stricter enforcement of existing quotas (32.0%).

Discussion

Limitations of Our Data

There is uncertainty regarding some of our quota and off-take data. Data on quotas and off-takes from several countries are somewhat dated. The exclusion of zero values when calculating the percentage of hunting blocks where 0.5 lions per 1,000 km² are hunted may over-estimate the intensity of harvest. However, we feel that in most cases (where age restrictions are not in place), failure of operators to secure a lion is more likely to be due to there being few or no lions present than operators abstaining from shooting lions or being unable to sell lions on quota. In Zimbabwe, Namibia and Mozambique estimates of the area per lion shot are under-estimates because we did not have data on the size of a number of hunting blocks in those countries (and thus under-estimated the area used for lion hunting).

A drawback with data on operators' perceptions is that such individuals clearly have a vested interested in the perpetuation of lion hunting and so their reflections on issues such as the trends in lion populations, causes for such trends, and the age of lions hunted must be treated with caution. Operators perceptions on conservation issues associated with trophy hunting were derived before implementation of age restrictions in Tanzania or quota cuts in Zambia.

Extent of Lion Hunting

African lions are hunted across 27-32% of the lion distribution in countries where trophy hunting of the species is permitted, and at least 16% of the total lion distribution in Africa [6]. Furthermore, these percentages do not include hunting blocks in Chad where the species is also hunted [17] and in some countries (notably Mozambique) we lacked data on some blocks where lions are hunted. Significantly, in Tanzania (which holds $\sim 15,500$ lions of a total population of $\sim 30,000$ individuals [6]) lions are hunted over 34-49% of their range. Consequently, trophy hunting has potential to impart either significant positive or negative conservation impacts on lions, depending on the way in which it is managed. Lion harvests have declined steeply in recent years, which may be due in part to quota cuts in some countries and the implementation of age restrictions in Tanzania and Mozambique.

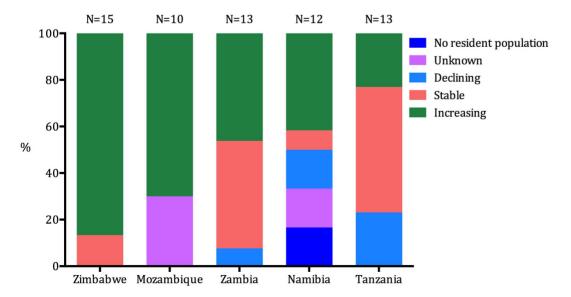


Figure 1. Operators' perceptions of lion population trends in their hunting concessions. doi:10.1371/journal.pone.0073808.q001

Table 5. Perceptions of hunting operators regarding problems associated with the trophy hunting of African lions.

	Mozambique	Namibia	Tanzania	Zambia	Zimbabwe
% of operators who believe there are problems associated with lion hunting in their country	22.2	60.0	76.9	100	61.5
Quotas too high/unscientific	40.0	28.6	46.2	66.7	50.0
Quotas too low	0	0	0	0	10.0
Lack of guidelines/rules on age of lion trophies	20.0	0	0	16.7	0
Incompetent parks authority	0	0	15.3	16.7	0
Political influence on quotas	0	0	7.8	0	30.0
Excessive off-take of problem animals and absence of trophy quotas	0	42.9	0	0	0
Lack of control over lion hunting	20.0	0	0	0	0

However, it is not possible to determine the extent to which improved management of lion hunting has contributed to such reductions, versus continued population declines.

Key Problems and Necessary Interventions

Our data highlights several weaknesses associated with the management of lion hunting.

i Arbitrary bases for establishing quotas and excessive harvests

Quotas have been reduced significantly in recent years in several countries, including Benin, CAR, Tanzania, and Zambia [24], [25], [26], [28], P. Lindsey unpublished data]. However, quotas are generally not established in a scientific manner and there is an over-reliance on subjective personal opinions during the process, including those of hunting operators. In Namibia, Zimbabwe and Mozambique, the size of quotas is apparently determined partly on the extent and location of problem animal reports, which need not have a close relationship to lion abundance. Such linkages create scope for false reporting of conflict, which further decouples quotas from what populations can necessarily support and are unlikely to help address humanlion conflict effectively. Lion quotas remain higher than the 0.5/ 1,000 km² recommended by [8] in all countries except Mozambique. Mean actual harvests are lower than the 0.5/1,000 km² threshold in most countries (with the exception of Burkina Faso, Zambia, Namibia and Zimbabwe). However, in all countries where data are available, harvests appear too high in a proportion of hunting blocks.

There is a need for decisive efforts to ensure that quotas and harvests are not excessive in any areas that lions are hunted; indeed, given the recent international scrutiny, range states would do well to adopt a conservative approach to managing lion hunting. Steps to improve sustainability could include the interim implementation of quota caps following the suggestions of [8], until age restrictions (as discussed below), trophy monitoring and adaptive quota management have been implemented. In West Africa, where lions are considered regionally endangered [33], efforts to prevent excessive harvests are most urgently required.

ii. Lack of enforced age restrictions

Based on dynamics of the Serengeti lion population, the restriction of trophy harvests to males of six-years or older effectively ensures sustainability of harvest in the absence of reliable population estimates [34], [35]. By six years, male lions have typically had the opportunity to sire at least one litter of cubs,

the recruitment of which is sufficient to maintain population stability [34], [35]. There is variability among countries in the presence, extent and type of restrictions imposed on trophy selection and operators admitted that many lions hunted are under six-years of age.

Hunting success rates declined in Niassa National Reserve following implementation of age limits ([31]). The number of lions shot as trophies in Tanzania also dropped after implementation of age restrictions (which commenced in 2011) from: 243 during 1996-2006 [8], 132 in 2009/2010; 101 in 2010/2011 and 85 in 2011/2012 [28]. Hunting operators suggested that declining offtakes in Tanzania were the result of greater selectivity among operators to avoid penalties for shooting young lions. However, quota cuts and continuing declines in lion populations also likely played a role [8]. Nonetheless, properly-enforced age restrictions are likely to reduce off-takes due to the need for greater selectivity and the scarcity of such individuals in lion populations [11]. In addition to increasing the sustainability of harvests, age restrictions could result in greater financial returns, as lions on quota could potentially be re-sold in the same year in the event of an unsuccessful hunt. For such age restrictions and trophy monitoring to be most effective and least likely to be undermined by corruption, they should be as transparent as possible and ideally involve input from multiple independent organisations.

There is general support among hunting operators for agebased restrictions, and specifically for the system implemented in Niassa National Reserve where quotas are managed adaptively based on the age of lions hunted in the previous year. Age restrictions are likely to be more effective than attempts to reduce the impacts of hunting by operators attempting to avoid shooting pride males or females with cubs as in both cases the ability of operators to identify such animals is questionable. Some operators expressed uncertainty regarding their ability to age lions and hunters performed poorly when attempting to age leopards [36]. However, experiences from Niassa indicate that hunters can learn to age lions effectively [31]. A key source of contention (among operators and some scientists) is whether the cues used to age lions vary regionally. Consequently, there is a need to further develop national or regional aging guidelines for lions (to complement those already produced for Tanzania and Zambia ([37]; White unpublished). These guidelines require the development of a suite of cues that can be used to age live animals [38], including characteristics such as nose colour, facial scarring, mane development and teeth wear. The use of a suite of cues reduces the likelihood of lions being aged incorrectly as a result of variation in individual characteristics [37] and addresses the contention associated with the validity of individual cues such as nose colour. Furthermore, employing a suite of cues reduces the difficulty of assessing individual characteristics under the low light conditions when lions are typically hunted.

Operators will have to be educated on lion aging techniques if age-based hunting restrictions are to be successfully implemented. More than a quarter of operators feel unable to distinguish six-yearold males and some use unreliable cues such as the absence of spots, body colour and body size [37]. Lion aging techniques should be included in the curricula of appropriate hunting courses with the successful completion of an examination a prerequisite for licensing (as is the case for mountain lions Puma concolor in the United States; http://wildlife.state.co.us/Hunting/HunterEducation/MtnLion Educ/Pages/MountainLionExam.aspx, accessed November 2011). Similarly, hunting clients must be educated such that they understand the importance of, and reasons behind age restrictions. Clients should be encouraged to appreciate the experience of lion hunting more than the actual product and to understand that going on a lion hunting safari is no guarantee that a lion will be shot. Safari hunting clubs such as Safari Club International and Dallas Safari Club could play a key role in educational efforts involving clients. Furthermore, organisations that hold trophy record books (such as Safari Club International and Rowland Ward) could play an important role by ensuring that lion trophies must be from lions of a minimum age to qualify. Such measures motivate clients as well as professional hunters to avoid shooting young lions.

iii. The hunting of females is permitted in Namibia

The hunting of females creates a risk that dependent cubs will die, removes the most reproductively productive individuals, can increase the vulnerability of prides to loss of territory to neighbouring prides and can render cubs more vulnerable to infanticidal males [39]. Consequently, the hunting of lionesses should be prohibited, except where the express management objective is to control the size of a lion population [40].

iv. The prevalence of fixed quotas

Several countries have large 'fixed' quota, meaning that operators are charged for a proportion (40–100%) of lions on quota, irrespective of whether animals are actually hunted. Such a system is likely to encourage utilization of the entire fixed portion of the quota regardless of sustainability and potentially result in the harvest of underage individuals.

v. The lack of minimum hunt lengths in some countries

Several countries either have no limit on the length of lion hunting safaris, or have short minimum lengths (most notably in West and Central Africa). Minimum hunt lengths of least 21 days would allow hunters time to be selective and maximize the revenue earning potential from lion hunts.

vi. General problems associated with management of trophy hunting

Several other problems associated with the management of trophy hunting are likely to exacerbate negative impacts associated with the hunting of lions (where such impacts occur) and/or undermine conservation incentives created by trophy hunting. Corruption is a challenge that affects multiple aspects of the trophy hunting industry [41] and could undermine steps to reform the hunting of lions. Such possibilities stress the importance of transparency within the hunting industry and independent verification of processes such as quota setting, concession

allocation and trophy monitoring. There are other problems associated with the process of allocating hunting concessions, such as the use of closed tender systems which do not account for the conservation track record of operators [42]. Concessions are leased for periods that are too short, particularly in Tanzania, which encourages over-use of and underinvestment in hunting blocks [43]. Under-investment in anti-poaching for example, can result in rapid loss of wildlife resources in hunting concessions due to pressure from illegal hunting and the bushmeat trade [44]. The threat posed by poaching is elevated in many cases due to the fact that communities are often marginalized from the benefits generated by trophy hunting (and ecotourism) due to inappropriate legislation which does not recognize community ownership of land and wildlife resources [14], [17]. Furthermore, due to the high costs associated with effective law enforcement and severe threat from the bushmeat trade [44] there may be need for additional funding support for protection of wildlife regardless of whether trophy hunting and the hunting of lions occurs. That said, some revenue is better than none and in the absence of realistic alternatives, governments should be careful not to foreclose an important means of generating income from and for wildlife.

Conclusions

Some countries have made steps to make lion hunting more sustainable in recent years and off-takes have declined significantly. However, there remain several problems associated with the management of lion hunting which may perpetuate negative impacts. Consequently, further reforms are urgently needed. Key changes needed include: reduced quotas in some countries; implementing trophy monitoring and adaptive quota management; introducing enforced age restrictions where they are absent; and minimum hunt lengths for lion hunts of at least 21 days. Reforms are arguably preferable to trade bans because they would provide scope for the retention of financial and economic incentives for the retention of land for wildlife and for tolerance of lions, while reducing the negative impacts on lion populations. Given the resilience of lions, populations affected by excessive trophy harvests would likely recover rapidly if lion hunting was managed more sustainably [45].

Methods

This study excluded South Africa where the majority of lion 'hunts' are of captive (and captive-born) animals, [18]). Several methods were employed to assess the spatial and numerical extent of lion hunting, the way in which lion hunting is managed in each country, and hunting operators' perceptions of lion hunting.

Surveys of State Wildlife Officials

The individual in charge of administering trophy hunting in each of the five main wild lion hunting countries (Mozambique, Namibia, Tanzania, Zambia, Zimbabwe) was interviewed with a structured survey on the management of lion hunting and hunting blocks in their country in November 2010. Updated information was obtained from the same individuals at a meeting in Botswana at which they were gathered in September 2012. Refusal rate was zero.

Data on the Size of Quotas and of Hunting Areas

Data on hunting quotas and off-takes for lions were collected from as many different hunting areas in as many different countries as possible. In Zambia, 2012 quotas and off-take data were provided by Zambia Wildlife Authority (ZAWA). In Zimbabwe, quota data for 2010–2011 were provided by the

Zimbabwe Parks and Wildlife Management Authority (for some blocks 2011 data were available, whereas for others only 2010 data were available: we used the latest figure available for each block). Off-take data for Zimbabwe, Namibia, Mozambique and Central African Republic were based on estimates of trophy exports during 2008–2011 from the CITES trade database [30], accessed July 2013). In Namibia, data on quotas were provided by WWF-Namibia for communal conservancies and by private operators for three privately owned areas where lions are hunted (the species only occurs on 8.2% of Namibian farmlands and is rarely hunted on that land tenure category [13]. In Mozambique, quota data for 2013 were provided by the Mozambique Ministry of Tourism. In Benin, Burkina Faso, Cameroon, Central African Republic, and Tanzania, quota and/or off-take data were derived from [12], [25], [28], [46], [47].

We calculated the percentage of hunting blocks with >0.5 lions/1,000 km² on quota and harvested (the threshold recommended by [8] for Tanzanian hunting blocks outside Selous Game Reserve). When calculating the percentage of blocks with 0.5 lions harvested per 1,000 km², we excluded areas where lions are on quota but were not hunted. The reason for this is that in some instances lions are put on quota in areas where there are no or too few lions for hunting. We thus felt that including those areas (which would make the estimate of the area per lion hunted larger) would paint an overly optimistic. We acknowledge that in some cases the converse may be true — lions may be present and on quota but not hunted due to conservatism on the part of operators or due to failure to sell lion hunts.

Surveys of Hunting Operators

Insights on various issues relating to lion hunting were obtained via a survey of hunting operators at US hunting conventions

References

- Ray J, Hunter L, Zigouris J. (2005) Setting conservation and research priorities for larger African carnivores. New York: Wildlife Conservation Society.
- 2. Nowell K. (2004) The cat specialist group at CITES 2004. Cat News 41: 29.
- Chardonnet P. (2002) Conservation of the African lion: Contribution to a status survey. Paris: Fondation IGF.
- Bauer H, Van Der Merwe S. (2004) Inventory of free-ranging lions Panthera leo in Africa. Oryx 38: 26.
- Riggio J. (2011) The African lion (Panthera leo): A continent-wide species distribution study and population analysis.
- Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, et al. (2012) The size of savannah Africa: A lion's (*Panthera leo*) view. Biodiversity and Conservation 22: 17–35. MSc thesis: Duke University.
- IUCN. (2006) Conservation strategy for the lion Panthera leo in southern and eastern Africa. Gland. Switzerland: IUCN.
- Packer C, Brink H, Kissui BM, Maliti H, Kushnir H, et al. (2011) Effects of trophy hunting on lion and leopard populations in Tanzania. Conserv Biol 25: 142–153.
- Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW. (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol Conserv 134: 548–558.
- Davidson Z, Valeix M, Loveridge AJ, Madzikanda H, Macdonald DW. (2011) Socio-spatial behaviour of an African lion population following perturbation by sport hunting. Biol Conserv 144: 114–121.
- Becker M, Watson F, Droge E, Leigh K, Carlson R, et al. (2012) Estimating past and future male loss in three Zambian lion populations. Journal of Wildlife Management DOI: 10.1002/jwmg.446.
- Croes BM, Funston PJ, Rasmussen G, Buij R, Saleh A, et al. (2011) The impact of trophy hunting on lions (*Panthera leo*) and other large carnivores in the Bénoué complex, northern Cameroon. Biol Conserv 144: 3064–3072.
- Lindsey P, Balme G, Booth V, Midlane N. (2012) The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. PLoS One: - e29332.
- Nelson F, Lindsey P, Balme G. (2013) Trophy hunting and lion conservation: A question of governance? Oryx: doi:10.1017/S003060531200035X.
- Frank L, Hemson G, Kushnir H, Packer C. (2006) Lions, conflict and conservation in eastern and southern Africa. Laikipia, Kenya: Living with lions.
- Packer C, Ikanda D, Kissui B, Kushnir H. (2005) Conservation biology: Lion attacks on humans in Tanzania. Nature 436: 927–928.

(Dallas and Houston Safari Clubs, Atlanta Africa hunting show) in 2011, using a structured survey, following the methods of [20]. The US is the largest market for African hunting safaris, and most hunts are sold at hunting conventions. Dallas Safari Club was selected because it is one of the largest hunting conventions in the world, Houston because it is also large in size, and Atlanta because it is a unique show focused specifically on African hunting safaris. An attempt was made to survey every African operator present at the shows that sells lion hunts, resulting in coverage of 73.8% of the operators present who offered lion hunts and a sample of 91 operators (2 of whom were from Central African Republic 10 from Mozambique, 12 from Namibia, 28 from South Africa, 14 from Tanzania, 7 from Zambia and 18 from Zimbabwe). Refusal rate was 2.2%.

Ethics Statement

The University of Pretoria Ethics Committee approved this research and approved the procedure for obtaining consent for the surveys conducted during the research. We were provided with written consent by the organisers of the hunting conventions and meeting that we attended to conduct surveys. From respondents we obtained verbal consent prior to conducting the surveys. Written consent from individual respondents was not considered practical or necessary. We documented any cases where respondents did not wish to participate in order to calculate refusal rates.

Author Contributions

Conceived and designed the experiments: PAL GB NM. Performed the experiments: PAL GB NM. Analyzed the data: PAL GB NM LH HM VN PF. Contributed reagents/materials/analysis tools: PAL GB NM LH HM VN PF. Wrote the paper: PAL GB NM LH HM VN PF.

- Lindsey PA, Roulet PA, Romañach SS. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. Biol Conserv 134: 455–469.
- Lindsey P, Alexander R, Balme G, Midlane N, Craig J. (2012) Possible relationships between the south African captive-bred lion hunting industry and the hunting and conservation of lions elsewhere in Africa. S Afr J Wildl Res 42: 11–22.
- Booth V. (2009) A comparison of the prices of hunting tourism in southern and east Africa. Budapest, Hungary: FAO/CIC.
- Lindsey PA, Alexander R, Frank LG, Mathieson A, Romañach SS. (2006) Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. Anim Conserv 9: 283–291.
- Norton-Griffiths M. (2007) How many wildebeest do you need? World Economics 8: 41–64.
- 22. NACSO website. (2013). Available: www.nacso.org. Accessed 2013 August 190.
- 23. Weaver C. (2011) The catalytic role and contributions of sustainable wildlife use to the Namibia CBNRM programme. In: Abensperg-Traun M, Roe D, O'Criodain C, editors. CITES and CBNRM. Proceedings of an international symposium on "The relevance of CBNRM to the conservation and sustainable use of CITES-listed species in exporting countries", Vienna, Austria, 18–20 May 2011. Gland, Switzerland: IUCN. pp. 1–172.
- 24. Roulet P. (2004) Chasseur blanc, cœur noir? la chasse sportive en Afrique Centrale. Une analyse de son rôle dans la conservation de la faune sauvage et le développement rural au travers des programmes de gestion communautaire». les cas du nord RCA et du sud-est Cameroun. Orleans: Université d'Orléans.
- Di Silvestre I. (2002) Dénombrement des grands carnivores au niveau de la réserve de biosphère de la Pendjari Rapport final de mission pour le projet Pendjari: Unpublished report.
- CENAGREF. (2013) Plan d'action pour la conservation du lion au Bénin. Cotonou, République du Bénin: CENAGREF.
- 27. Lindsey P. (2010) The future of wildlife-based land uses in Botswana. Current Conservation 3: 23.
- Tanzania Wildlife Division. (2012) Comment on ESA status review of the African lion. Dar Es Salaam, Tanzania: Wildlife Division.
- Henschel P, Kiki M, Sewade C, Tehou A. (2012) Improving the status of lions and cheetahs in their last stronghold in West Africa: The W-arly-pendjari complex. New York: Panthera.

- Cites Trade Database website. (2013) Available: www.cites.org/eng/resources/ trade.shtml. Accessed 2013 August 190.
- Begg C, Begg K. (2010) Monitoring of lion and leopard trophies in Niassa National Reserve, Mozambique: 2009 hunting season. Niassa National Reserve: Niassa Carnivore Project.
- Smuts G, Robinson G, Whyte I. (1980) Comparative growth of wild male and female lions (Panthera leo). J Zool 190: 365–373.
- 33. IUCN. (2012) IUCN red list of threatened species. Gland, Switzerland: IUCN.
- Whitman K, Starfield AM, Quadling HS, Packer C. (2004) Sustainable trophy hunting of African lions. Nature 428: 175–178.
- Whitman KL, Starfield AM, Quadling H, Packer C. (2007) Modelling the effects
 of trophy selection and environmental disturbance on a simulated population of
 African lions. Conserv Biol 21: 591

 –601.
- Balme GA, Hunter L, Braczkowski A. (2012) Applicability of age-based hunting regulations for leopards. PlosOne 7: e35209.
- 37. Packer C, Whitman K. (2006) A hunter's guide to aging lions in east and southern Africa. Huntingdon Beach: Conservation Force/Savannas Forever.
- 38. Ferreira S, Funston PJ. (2010) Age assignment to individual African lions. S Afr J Wildl Res 40: 1–9.
- Packer C, Scheel D, Pusey AE. (1990) Why lions form groups: Food is not enough. Am Nat: 1–19.
- Funston PJ, Groom RJ, Lindsey PA. (2013) Insights into the management of large carnivores for profitable wildlife-based land uses in African savannas. PloS One 8: e59044.
- Leader-Williams N, Baldus RD, Smith RJ. (2009) The influence of corruption on the conduct of recreational hunting. In: Dickson, B. Hutton, J. Adams, B. Recreational Hunting, Conservation and Rural Livelihoods. Oxford: Wiley-Blackwell. pp. 296–316.
- Lindsey P, Frank L, Alexander R, Mathieson A, Romanach S. (2007) Trophy hunting and conservation in Africa: Problems and one potential solution. Conserv Biol 21: 880–883.
- 43. Brink H. (2010) Hunting for sustainability: Lion conservation in Selous game reserve, Tanzania. PhD thesis, London: Imperial College.
- Lindsey P, Balme G, Becker M, Begg C, Bento C, et al. (2013) The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. Biological Conservation 160: 80–96.

- Loveridge AJ, Packer C, Dutton A. (2009) Science and the recreational hunting of lions. In: Dickson, B. Hutton, J. Adams, B. Recreational Hunting, Conservation and Rural Livelihoods. Oxford: Wiley-Blackwell. pp. 108–124.
- Mesochina P, Mamang-Kanga J, Chardonnet P, Mandjo Y, Yagueme M. (2010)
 The conservation status of the lion in Central African Republic. Paris: Fondation IGF
- Pellerin M, Kidjo F, Tehou A, Sogbohossou E, Ayegnon D, et al. (2009) Statut de conservation du lion au Benin. Paris: Fondation IGF.
- Simasiku P, Simwanza H, Tembo G, Bandyopadhyay S, Pavy J. (2008) The impact of wildlife management policies on communities and conservation in game management areas in Zambia. Zambia: Natural Resources Consultative Forum
- Taylor RD. (2009) Community based natural resource management in Zimbabwe: The experience of CAMPFIRE. Biodiversity and Conservation 18(10): 2563–2583.
- 50. République Populaire du Bénin. (1987) Loi n° 87–014 portant réglementation de la protection de la nature et de l'exercice de la chasse en en République Populaire du Bénin.
- IUCN/PACO. (2009) La grande chasse en Afrique de l'Ouest: Quelle contribution à la conservation? Ouagadougou, Burkina Faso: IUCN/PACO.
- 52. Burkina Faso. (1997) Décret N 96–061, portant réglementation de l'exploitation de la faune. loi N 006/97/ADP du 31 janvier 1997 portant code forestier.
- 53. Republic of Cameroon. (1994) Loi n° 94/01 portant régime des forêts, de la faune et de la pêche; décret n° 95–466 fixant les modalités d'application du régime de la faune.
- Central African Republic. (1984) Ordonnance no. 84.045, portant protection de la faune sauvage et réglementant l'exercice de la chasse.
- 55. Mesochina P, Mbangwa O, Chardonnet P, Mosha R, Mtui B, et al. (2010) The conservation status of the lion in Tanzania. Paris: Fondation IGF.
- Chardonnet P, Mesochina P, Renaud P, Bento C, Conjo D, et al. (2009) The conservation status of the lion in Mozambique. Paris: Fondation IGF.
- World Resources Institute. (2010) Interactive forest atlas for Central African Republic. Washington, DC: World Resources Institute.
- MINFOF/SDIAF/SC. (2012) Hunting areas of Cameroon. Douala, Cameroon: Ministry of Forestry and Wildlife in Cameroon.
- Chardonnet P. (2011) The conservation status of the lion in Burkina Faso. Paris: Fondation IGF.