



**HUMANE SOCIETY
INTERNATIONAL**

African Lion

(*Panthera leo*)

This factsheet is part of a series highlighting species vulnerability to trophy hunting and lethal offtake.



© Vanessa Mignon

IMPACTS OF TROPHY HUNTING

- Unsustainable offtake
- Social disruption resulting in infanticide, decreased reproductive output, and earlier male dispersal
- Drawing males from protected areas ('vacuum effect')
- Captive-bred lion hunting

POPULATION

The current population trend is decreasing with an estimated population size of 20,000 mature lions in Africa.¹ The lion has been classified as Vulnerable by IUCN since its first assessment in 1996, which was most recently reconfirmed in 2016, highlighting long-term population declines. Species are classified as Vulnerable if they face a high risk of extinction in the wild in the *immediate* future. Globally, lion populations have declined approximately 43% over the past three generations (21 years: 1993-2014).¹ IUCN notes that if the fenced, managed areas were excluded from estimated population trends, overall decline rate in Africa would be 49%.¹ This would nearly qualify the lion as Endangered, classified by a decline of 50% or greater.

The status of African lion populations varies across regions, although nearly all are declining. Populations in West, Central, and East Africa have declined by 61%.¹ This estimate is likely conservative, given that the populations sampled were monitored, and declines tend to be greater at unmonitored, unfenced sites due to lack of funding and conservation efforts.^{1,2} Although limited data are available for lion populations outside of fenced, intensively managed, and funded reserves, it is clear that they are experiencing the greatest declines.² Populations in West, Central, and East Africa are projected to decline 50% over the next two decades.² In West Afri-

QUICK FACTS:

Population Size:	Estimated 20,000 mature individuals in Africa; global population decreasing, estimated decline of 43% in last three generations (21 years); Africa population estimated decline of 61% except in four southern Africa countries with increase of 8%
Range:	87-92% of historic range lost
IUCN Red List:	Vulnerable (2016)
CITES:	Appendix II (since 1977)
International Trade:	7,667 lion trophies traded internationally from 2009-2018
Threats:	Conflict with livestock owners, habitat loss, prey depletion, poorly managed trophy hunting trade in bones and body parts

ca, the lion is Critically Endangered due to extremely small population size and habitat loss.³ As of 2014, only 250 mature individuals remained in the West African population, which is geographically isolated.³ Lions in Central and East Africa are considered regionally Endangered.²

Lion populations in four southern African countries (Botswana, Namibia, South Africa, and Zimbabwe) comprise approximately 1/3 to 1/4 of the total African lion population.¹ These populations increased by 8% between 1993 and 2014¹ and are regionally considered Least Concern.² This region is unique in that there are many fenced reserves where populations require intensive management to resemble

natural systems and management tactics introduce additional complications.^{4,5,6,7} Fenced populations are entirely different from those that are unfenced in that the former are comparatively well-funded and heavily managed.^{1,2} However, there are many concerns with fenced reserves including overpopulation, inbreeding, disrupted social structure, inbreeding, overpopulation, breakouts, conflict with communities, and an unbalanced ecosystem.^{4,5,7,8,9,10} Translocation is a better management intervention than hunting for long-term population control, but hunting has a stronger financial motivation.⁷ Yet both management options may necessitate continued and more frequent intervention.⁷ In addition, fencing threatens biodiversity through disruption of migrations routes and dispersal, blocking animals from accessing critical resources, limiting gene flow, and physical injury or death.^{11,12}

RANGE

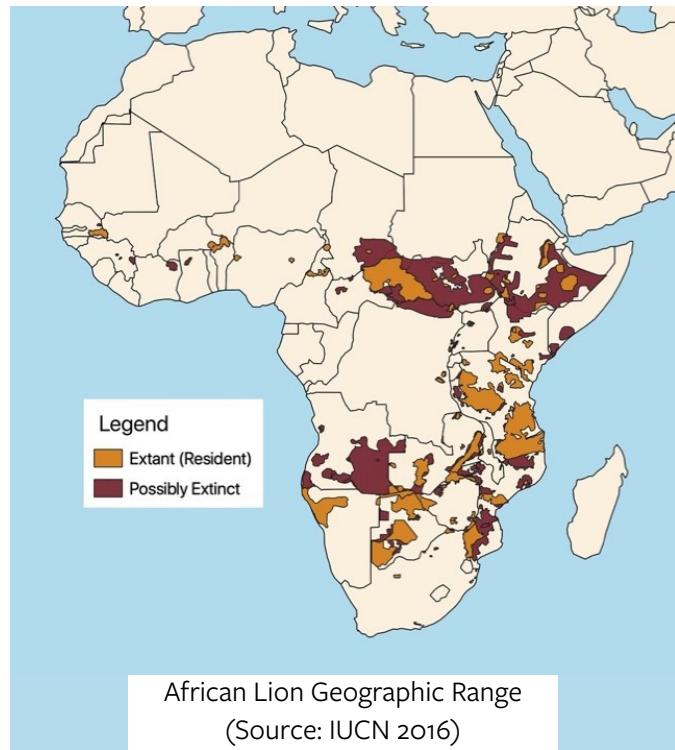
Lion populations are currently found in only 8%¹ - 12.5%² of their historical range. West and Central African populations have experienced the largest range declines, representing only 2.9% of their historical size.² Even within protected areas, populations of lions and their prey are below carrying capacity and declining.⁴

Due to numerous threats across their range, African lions have been extirpated in 12 countries and likely extirpated in four additional countries.¹ Major threats include indiscriminate killing as a result of human-wildlife conflict, habitat loss, prey base depletion, population fragmentation, and trophy hunting.¹ An emerging threat is the trade in lion bones and body parts such as teeth and claws.¹

LIFE HISTORY AND REPRODUCTION

Lion population growth is slow due to long lifespans, low reproductive rates, long intervals between births. Sexual maturity is reached around the age of four when females have their first litter, and males leave to join a male coalition. Females remain in their home territories, while males disperse to compete for access to prides of females.¹³

Females give birth every 20 months if cubs survive to maturity. Cub mortality is high; more than 50% of cubs die under the age of one.¹⁴ Cub mortality is also highly dependent on maternal survival.¹⁵ Gestation



lasts 110 days, and the average litter size is 1-4 cubs.¹⁴ Cubs are weaned at 5-8 months but are dependent on their mothers for food until 1.5-2 years old.¹⁴ Females do not resume mating activity until their cubs reach 1.5-2 years old.¹⁶

The maximum lifespan for females is 18 years and 14 years for males.¹⁷ Females can continue to give birth until their death, although reproductive activity declines around 14.^{15,6} Cub survival does not change with female age, but litter size decreases at 14 years.¹⁵ Therefore, even the oldest females are important for population growth. Reproductive success is positively correlated with pride size,^{17,18} fewer male takeovers,¹⁹ and higher quality habitat.¹⁹

Infanticide occurs when adult males take over a new territory and kill the dependent cubs in order to increase mating opportunities with resident females that have dependent offspring (see Social Structure section). Rates of infanticide increase when males are removed from the population due to trophy hunting.^{20,21,22} Females that lose their cubs during a male takeover (see Social Structure) take a median of 134 days to conceive their next litter. In comparison, females that lose dependent cubs due to other circumstances only take a median of 24 days to conceive.¹⁶ Therefore, repeated male takeovers, such as those caused by trophy hunting, clearly decrease reproductive output and slow population growth.

SOCIAL STRUCTURE

Lions live in social groups called prides, generally comprised of 2-18 related females, their dependent offspring, and transient coalitions of 1-7 adult males.^{14,23} Females typically remain in their home territory, while males leave their natal prides to form a coalition with other males or become solitary. Male coalitions compete to control female prides for several months or years, until leaving or being ousted by another coalition.²⁴ When a coalition is replaced by another it is called a “male takeover.” Larger coalitions have longer tenure than smaller ones.²⁴

Pride composition is mostly stable; however, changes occur when new males take over the pride. Within the pride, lions form smaller social groups that exhibit fission-fusion dynamics, where group membership is continually changing as individuals from the pride join and leave the smaller subgroups.¹⁴ Individual lions maintain stronger social bonds with preferred social partners and generally prefer to associate with individuals of the same sex.²⁵ The strength and frequency of these associations are also influenced by prey availability.²⁵

Following a male takeover, cub mortality is high and reproductive rates are low.²⁴ When new males takeover a pride, they kill the dependent cubs in order to bring females into estrus, thereby increasing their mating opportunities with females.^{24,26} Cubs under the age of two are especially vulnerable.²² During these male takeovers, females may be injured or killed while trying to protect their cubs.²⁴ Females also experience a period of infertility following takeovers: the median time it takes to give birth is 110 days later than for females who lost their cubs outside of an infanticide event.²⁴ Regardless of reproductive state during the takeover, female lions experience a median 102-day period of infertility following a male takeover.²⁴ The duration of male tenure has profound effects on survival, reproduction, and population growth rate. Females need to be protected from male takeover for at least 25 months to raise cubs successfully.²⁴ Therefore, maintaining social stability to prevent male takeover is critical for cub survival and reproductive rates.

Anthropogenic, or human-caused, factors such as trophy hunting, disrupt social structure by artificially increasing the rate of male takeovers which alters reproduction and dispersal.²⁷ This social disruption artificially increase the rate of male takeovers and

depress population growth by removing male lions from the population. Offtake of breeding aged males due to trophy hunting results in increased levels of infanticide.^{20,21,22} Removal of individuals from a pride can also negatively impact reproduction and survival, as pride size is positively correlated with reproductive success,^{17,18} female survival,¹⁹ and higher quality habitat.¹⁹ Indeed, following a moratorium on trophy hunting in Zambia, pride sizes increased.²⁸ Therefore, maintaining social stability to prevent male takeovers is critical for cub survival and reproductive rates.

In lion societies, males disperse from their natal range to establish new territories, and females stay in their home territories.¹³ Dispersal is important because it decreases the chances of inbreeding, or mating with a close relative, due to the physical separation of related individuals. Inbreeding in lions negatively affects population growth due to decreased reproductive success^{29,9} and increased susceptibility to disease.³⁰ Small, isolated reserves can experience high rates of inbreeding due to small populations sizes and limited dispersal.⁹ This is a major concern for the future of lions since many populations across Africa are becoming increasingly fragmented and isolated.

After new males takeover a pride, they force sub-adult males to disperse out of the pride at young ages.²⁷ Sub-adult males that disperse young are smaller and less successful at establishing new territories.²⁷ Younger males are also less likely to survive dispersal.²⁷ In a population that is impacted by trophy hunting and retaliatory killings, males disperse young, must travel long distances to find new territories, and are regularly killed by humans.²⁷ Young, lone males who have not yet established territories are more likely to be “problem-lions” involved in conflict with humans and livestock.^{31,32,33} Therefore, not only does trophy hunting disrupt successful male dispersal, but it may also increase the rate of human-lion conflict.

HABITAT AND ECOLOGY

Lions are carnivores that require an abundance of prey for survival. They are opportunistic hunters that prefer medium to large prey such as gemsbok (*Oryx gazella*), buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*), and zebra (*Equus burchellii*).³⁴ Lions also prefer to hunt prey much larger than themselves,

which is a benefit of hunting in groups.³⁴

Large carnivores, such as lions, provide important ecosystem and economic services.³⁵ Lions are important apex predators that shape the ecosystem and control prey populations.^{35,36,37,38} Loss of these apex predators can result in widespread cascading impacts throughout the ecosystem due to direct and indirect effects.^{35,39} Lions are also one of the most population species for tourists and attract people from all over the world.^{40,41}

Human impacts and prey availability are the two strongest predictors of lion presence.^{42,43} Lions are most likely to occupy habitats far from human settlements⁴³ where cattle are absent,⁴² which is a sign of human avoidance or exclusion from these areas due to persecution.⁴² Lions are also more likely to occupy habitats closer to the center of protected areas.⁴² The potential future availability of these preferred habitats is concerning given the rapid increase of human populations in Africa.

Lion population density and occupancy are closely related to prey biomass; thus, prey depletion is a significant threat.^{1,44,45,42} Large prey declines have occurred across Africa, including 52% in East Africa, and 85% in West Africa.⁴⁶ Bushmeat poaching and habitat loss have led to a widespread decline of ungulates across Africa.^{47,44,48} There is a critical threshold where areas with prey declines too great can no longer support lion populations.⁴³ Indeed, lions avoid habitats where bushmeat poachers are present, likely due to prey depletion.⁴² Further, decreased availability of natural prey can result in more opportunities for human conflict and persecution as lions seek out livestock.⁴⁴

DIRECT ANTHROPOGENIC THREATS

Human population growth is an underlying cause of multiple threats facing lions, including habitat loss, population fragmentation, genetic isolation, prey reduction, and human conflict.^{44,49} However, the primary human-caused, or anthropogenic, threat to lions is persecution from livestock owners to protect livestock, humans, or in retaliation.¹ Lions are killed by poisoning, trapping, and shooting.^{44,50,51}

Despite this being a primary threat, there are insufficient records on the number of lions killed by local livestock owners.¹ Retaliatory killings can be exces-

sive; studies have reported that following a single livestock conflict incident, entire lion prides have been killed.^{52,50} Without proper management and recording of offtake due to conflict with livestock owners, it is impossible to ensure that other sources of offtake, such as trophy hunting, are sustainable.

Lethal responses to human-lion conflict severely threaten lion populations.^{50,51} Poisoning, which is commonly used to kill lions, is indiscriminate and kills other species as well.⁵¹ However, non-lethal solutions to human-lion conflict can significantly decrease livestock loss and reduce conflict.⁵³ Livestock owners were more satisfied with a lion alert system that provided warnings in order to prevent conflict than they were with state-funded compensation after loss.⁵³ There is also evidence that lethal control may actually increase human-wildlife conflict in other carnivores.^{54,55,56,57}

Another emerging threat to lion populations is both the illegal and legal trade in bones, skins, and body parts for medicinal purposes.¹ There is increasing interest in the use of African lion bones in Asia,¹ and the poaching for lion body parts has likely contributed to unsustainable rates of mortality in parts of the lion's range.^{35,52} A study from 2011 to 2018 in Greater Limpopo Lion Conservation Unit (GLLCU), which includes Limpopo National Park in South Africa and Banhine National Park in Mozambique, found that 51% of known human-caused mortalities were due to retaliatory killing for livestock conflict and 35% were due to targeted poaching for body parts.⁵² The same study also found that 61% of lion mortality within Limpopo National Park was due to poaching.⁵² There is also evidence that the demand for body parts may incentivize retaliatory killings, as body parts were missing in 48% of conflict cases.⁵² Illegal trade and retaliatory killings are especially problematic, given that the number of lions taken is unknown and, therefore, cannot be considered in management plans.

Scientific studies have documented lion hunting quotas higher than what is biologically sustainable. One study found that lion hunting quotas in Tanzania's Selous Game Reserve were up to four times the sustainable rate in some hunting blocks.⁵⁸ Even offtake well below these quotas can lead to a decline in the proportion of males.⁵⁹ In one study, despite the average annual offtake representing only about a quarter of annual quotes, 72% of identified territorial adult males were taken by trophy hunt-

ers.⁵⁹ In 2013, Zambia enacted a 3-year ban on trophy hunting out of concern for mismanagement and excessive quotas. Following this 3-year ban, there were increases in lion abundance, male survival, cub production, coalition tenure, and pride size.²⁸ Population demographics also shifted from male-depleted and adult female-dominated to a younger population with more adult males.²⁸ Despite these improvements, Zambia lifted the ban on trophy hunting in 2016.

Numerous scientific studies have demonstrated that trophy hunting has negative impacts on lion populations. The latest IUCN assessment states that poorly managed trophy hunting contributed to population decline across their range.¹ Offtakes higher than scientific recommendations have been identified in nearly all countries where trophy hunting of lions occurs,⁶⁰ and 62% of hunting operators felt that there were problems associated with trophy hunting of lions in their country, most commonly “inappropriate, unscientific or excessive” quotas.⁶⁰ Excessive offtake from trophy hunting has contributed to lion declines in Zimbabwe,^{59,61,62} Zambia,^{20,63} Tanzania,⁶⁴ and Cameroon. A study in a Game Management Area in Zambia found that from 2008 to 2012, trophy hunting was the leading cause of death and contributed to decreased population size, low cub survival, low male survival, depletion of adult males, and an older female population that contributed less to reproduction.⁶³ Trophy hunting is especially problematic in populations that already face other threats.²⁰ Further, offtake of young lions and females can lead to population crashes.⁶⁵ As a way to lessen these negative impacts, scientific studies recommend offtake of males 6 years and older,^{21,65} or 7 years and older in some populations.²⁰ Yet, data are often unavailable on the age and sex of lion trophies.⁶³ The 6-year age minimum is now official government policy in Mozambique, Tanzania, Zambia, and Zimbabwe.⁶⁶

Despite recommendations to restrict hunting to adult males past reproductive prime,^{20,21} trophy hunters will also kill females and sub-adults.^{59,61} Hunting operators even self-reported that 44% of lion trophies they hunted were 6 years or younger.⁶⁰ Adult females are especially important to the survival of the species as the number of adult females in a pride is closely correlated with reproductive success.¹⁷ Allowing high quotas for hunting of subadult males is also unsustainable and will lead to population collapse due to decreased mating opportuni-

ties.^{21,20} One study in Hwange National Park, Zimbabwe, found that more than 30% of the males killed by trophy hunters were sub-adults (mean age = 3.2 years).⁵⁹ Further, removing only adult males over a certain age still does not guarantee sustainability.²⁰ Offtake of breeding aged males destabilizes the social structure, resulting in increased infanticide,^{15,16,17} depressed reproduction rates,²⁶ and disrupted male dispersal²⁷ (see *Social Structure*). Earlier male dispersal due to increased rates of male takeovers from trophy hunting offtake may also contribute to greater human-lion conflict.²⁷ Research from human-lion conflict also shows that when there are too few adult pride males, females and their cubs are not sufficiently protected from male takeovers.⁵⁰ Trophy hunting may also reduce genetic connectivity between lion populations by restricting movement patterns, especially where hunting pressure is high outside of protected areas.⁴⁹

Trophy hunting also threatens lions in protected habitats, such as National Parks, where trophy hunting is prohibited.^{58,62} Male lions that live in protected reserves are drawn out to fill territories in unprotected habitats that have been vacated due to trophy hunting. This creates a ‘vacuum effect’ where males will continuously be pulled out of protected habitats and risk being trophy hunted.⁵⁹ In Hwange National Park, Zimbabwe, where trophy hunting is prohibited in the park but occurs in surrounding areas, mortality rates were higher for lions living on the edge of the park compared to those living in the core of the park.⁶² The risk of mortality was 4.8 times higher for males, 2.5 times higher for females, and 3 times higher for cubs living towards the edge of the park.⁶² In Ghana, carnivore extinction rates were highest in small reserves and near reserve borders, consistent with hunting pressure at reserve edges.⁶⁷ At the Bénoué Complex in Cameroon, lion populations were well below carrying capacity in the National Parks (50% of potential population density) and the hunting zones (30% of potential population density), despite stable prey populations.⁶⁸ These low lion densities were attributed to excessive trophy hunting offtake, and highlight the importance of incorporating anthropogenic sources of morality in addition to habitat and prey availability when evaluating population status.⁶⁸ Scientists note the importance of recognizing that although populations may appear stable, they may not be at carrying capacity, which is an assumption frequently made when setting ‘sustainable’ offtake rates.⁶⁸

CAPTIVE-BRED LION HUNTING

There are also serious welfare and ethical concerns about captive-bred lion hunting, also known as ‘canned’ or ‘put and take’ hunting.^{44,69} Nearly all lions hunted for trophies in South Africa are captive bred and hunted in small, fenced areas.^{69,70} South Africa has an estimated population of 8,000 captive lions, although some reports suggest that number could be as high as 12,000, that are kept in small quarters, habituated to humans, and used for various purposes, including canned hunting.^{44,70} Captive lions may also be used for cub petting where cubs are taken from their mothers immediately after birth so tourists can pay to take photos with the cubs.⁷¹ The National Council for Societies for the Prevention of Cruelty to Animals (NSPCA) has opened numerous criminal cases against captive-breeding facilities for neglect and welfare concerns.⁷² In 2019, for example, inspectors found more than 100 lions neglected, diseased, overcrowded, and near death at a captive-breeding facility in South Africa.⁷³

In most captive-bred lion hunts, lions are released into the area less than 7 days before, and hunters have a 99% success rate, mainly because the lions are contained and habituated to humans.⁶⁹ According to the IUCN Cat Specialist Group and the African Lion Working Group, most scientists agree that captive lion hunting provides no conservation benefits, and the practice has been condemned by the IUCN, the Operators’ and Professional Hunters’ Associations of Africa (OPHAA), and the African Lion Working Group.⁴⁴ Even two of the largest trophy hunting clubs, Safari Club International and Dallas Safari Club, do not support captive lion hunting.⁷¹ Dallas Safari Club says that the practice is not in keeping with their “values of ethical and fair chase hunting.”⁷⁴ In addition, these lions are not candidates for reintroduction due to inbreeding and behavioral concerns.^{44,75} However, captive-bred lions have been released into fenced reserves and marketed as wild, which has led to incorrect CITES reporting.⁷⁰

This industry is not a significant source of local employment and provided less than 1% of tourism’s total GDP contribution in 2019.⁷⁶ Alternative economic opportunities, such as non-consumptive ecotourism, would provide significantly more job opportunities.⁷⁶ Operators indicated that 80% of income from captive-bred lion hunting goes to the breeder,⁶⁹ not into lion conservation. In 2017, nearly 30

lion researchers and conservationists from across the continent sent a letter to Secretary Zinke of the United States’ Department of the Interior, providing evidence that hunting captive-bred lions does not contribute to conservation.⁷⁷ According to the South African government’s Biodiversity Management Plan for the African Lion, “captive lions are bred exclusively to make money and managers actively manipulate all vital rates and demographics.”⁷⁰ They also receive fees from tourists who are misled to believe that cub petting and lion walks contribute to conservation, which is not true.⁷¹ Instead, at least 2-3 of these tame lions are killed daily for trophies or to be exported as skeletons.⁷¹

There are also serious concerns that the captive lion breeding industry fuel the lion and tiger bone trade. The increasing trade in lion bones is a significant threat to lions in Africa. Recently China has permitted the use of bones from captive lions to make medicinal wines, which traditionally contained tiger bone.¹ The captive lion breeding industry in South Africa has created a legal channel for lion bone that formerly did not exist in Asia. Captive-bred lions are the main supplement for the illegal tiger bone trade to Southeast Asia.⁷⁸ At the joint CITES/CMS African Lion Range State Meeting in 2016, concerns were raised that the legal trade in lion skeletons also acts as an incentive for illegal trade.⁷⁹ Bones from captive-bred lions are illegally combined with tiger bones to continue fueling this trade. Captive-bred lions are also traded illegally for this purpose, and there are concerns that demand for lion bones could increase poaching.

The South African Parliamentary Portfolio Committee of the Environment directed the South African government to end South Africa’s captive lion breeding due to ethical issues and concerns about loss of tourism revenue due to disagreement with the practice.⁷¹ Following a two day colloquium, “there was an overwhelming consensus” to end the captive lion breeding industry.⁷¹ However, the government has yet to act on the Parliament’s directive.

MANAGEMENT IMPLICATIONS

African lion populations are decreasing and facing numerous ongoing threats, including habitat loss, prey declines, and persecution.¹ In addition to these threats lions are especially susceptible to population declines from trophy hunting. Lions have low reproductive rates, slow population growth, and

replacement of individuals takes a long time. Mismanagement of trophy hunting, where quotas are set too high, or restrictions on lion age and sex are not established or regulated, has led to population declines.

Yet, trophy hunting of adult males, the ‘preferred’ targets, still negatively impacts lion populations. Trophy hunting artificially increases rates of male turnover which increases rates of infanticide, depresses population growth rates, and disrupts male dispersal. Offtake of females and young lions results in population crashes. Trophy hunting also continually draws males out of protected reserves into unprotected habitats where they are at risk of being hunted. Males, females, and cubs all experience higher mortality rates on the edges of protected parks that are adjacent to areas where trophy hunting is permitted. However, hunting quotas do not take these important biological factors into consideration. Hunting quotas also assume that stable populations are at carrying capacity, which is not always the case. The negative effects of trophy hunting are especially exacerbated if populations are small and fragmented. Without proper monitoring and management, the compounding effects of trophy hunting can continue to threaten lion survival.

Lions in South Africa present a unique case where most lion hunts occur in small fenced facilities, and lions are exploited from birth to death. Captive-bred lion hunting is discouraged by international scientists and organizations due to welfare concerns and lack of conservation benefits. However, as of May 2021, South Africa has announced that they plan to phase out their captive lion breeding industry.

REFERENCES

1. Bauer, H., Packer, C., Funston, P. F., Henschel, P. & Nowell, K. *Panthera leo* (errata version published in 2017). *IUCN Red List Threat. Species* e. T15951A115130419 (2016).
2. Bauer, H. et al. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci.* **112**, 14894–14899 (2015).
3. Henschel, P. et al. The lion in West Africa is critically endangered. *PLoS One* **9**, (2014).
4. Slotow, R. & Hunter, L. T. B. *Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: the African lion in South Africa. Reintroduction of Top-Order Predators* (2009). doi:10.1002/9781444312034.ch3
5. Hayward, M. W. et al. Practical considerations reintroduction large terrestrial mammalian predators. *Open Conserv. Biol. J.* **1**, 1–11 (2007).
6. Miller, S. M. et al. Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. *South African J. Wildl. Res.* **43**, 138–154 (2013).
7. Kettles, R. & Slotow, R. Management of free-ranging lions on an enclosed game reserve. *African J. Wildl. Res.* **39**, 23–33 (2009).
8. Trinkel, M. et al. Inbreeding and density-dependent population growth in a small, isolated lion population. *Anim. Conserv.* **13**, 374–382 (2010).
9. Trinkel, M. et al. Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa. *Anim. Conserv.* **11**, 138–143 (2008).
10. Miller, S. M. & Funston, P. J. Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African J. Wildl. Res.* **44**, 43–55 (2014).
11. Hayward, M. W. & Kerley, G. I. H. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? *Biol. Conserv.* **142**, 1–13 (2009).
12. Woodroffe, R., Hedges, S. & Durant, S. M. To fence or not to fence. *Science* **344**, 46–48 (2014).
13. Packer, C. & Pusey, A. E. The evolution of sex-biased dispersal in lions. *Behaviour* **101**, 275–310 (1987).
14. Schaller, G. *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press (1972).
15. Packer, C., Tatar, M. & Collins, A. Reproductive cessation in female mammals. *Nature* **392**, 807–811 (1998).
16. Packer, C. & Pusey, A. E. Male takeovers and female reproductive parameters. *Animal Behaviour* **31**, 334–340 (1983).
17. Packer, C. et al. Reproductive success of lions. in *Reproductive Success. Studies of Individual Variation in Contrasting Breeding Systems.*(Ed. TH Clutton-Brock.) 363–383 (1988).
18. Packer, C. & Pusey, A. E. Intrasexual Cooperation and the Sex Ratio in African Lions. *Am. Nat.* **130**, 636–642 (1987).
19. Mosser, A. & Packer, C. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Anim. Behav.* **78**, 359–370 (2009).
20. Creel, S. et al. Assessing the sustainability of African lion trophy hunting, with recommendations for policy. *Ecol. Appl.* **26**, 2347–2357 (2016).
21. Whitman, K., Starfield, A. M., Quadling, H. S. & Packer, C. Sustainable trophy hunting of African lions. *Nature* **428**, 175–178 (2004).

22. Bertram, B. C. R. Social factors influencing reproduction in wild lions. *J. Zool.* (1975). doi:10.1111/j.1469-7998.1975.tb02246.x
23. Packer, C. & Pusey, A. E. Cooperation and competition within coalitions of male lions: Kin selection or game theory? *Nature* **296**, 740–742 (1982).
24. Packer, C. & Pusey, A. E. Adaptations of female lions to infanticide by incoming males. *Am. Nat.* **121**, 716–728 (1983).
25. Mbizah, M. et al. Effect of ecological factors on fine-scale patterns of social structure in African lions. *J. Anim. Ecol.* 1–37 (2020).
26. Packer, C., Pusey, A. E. & Eberly, L. E. Egalitarianism in female African lions. *Science* **293**, 690–693 (2001).
27. Elliot, N. B., Valeix, M., Macdonald, D. W. & Loveridge, A. J. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos* **123**, 1049–1056 (2014).
28. Mweetwa, T. et al. Quantifying lion (*Panthera leo*) demographic response following a three-year moratorium on trophy hunting. *PLoS One* **13**, e0197030 (2018).
29. Wildt, D. E. et al. Reproductive and genetic consequences of founding isolated lion populations. *Nature* **329**, 328–331 (1987).
30. Trinkel, M., Cooper, D., Packer, C. & Slotow, R. Inbreeding depression increases susceptibility to bovine tuberculosis in lions: An experimental test using an inbred-outbred contrast through translocation. *J. Wildl. Dis.* **47**, 494–500 (2011).
31. Patterson, B. D., Neiburger, E. J. & Kasiki, S. M. Tooth breakage and dental disease as causes of carnivore-human conflicts. *J. Mammal.* **84**, 190–196 (2003).
32. Patterson, B. D., Kasiki, S. M., Selempo, E. & Kays, R. W. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biol. Conserv.* **119**, 507–516 (2004).
33. Stander, P. E. A suggested management strategy for stock-raiding lions in Namibia. *South African J. Wildl. Res.* **20**, 37–43 (1990).
34. Hayward, M. W. & Kerley, G. I. H. Prey preferences of the lion (*Panthera leo*). *J. Zool.* **267**, 309–322 (2005).
35. Ripple, W. J. et al. Status and ecological effects of the world's largest carnivores. *Science* **343**, (2014).
36. Brashares, J. S., Prugh, L. R., Stoner, C. J. & Epps, C. W. Ecological and conservation implications of mesopredator release. in *Trophic cascades: predators, prey, and the changing dynamics of nature* 221–240 (2010).
37. le Roux, E., Kerley, G. I. H. & Crome, J. P. G. M. Megaherbivores modify trophic cascades triggered by fear of predation in an African Savanna Ecosystem. *Curr. Biol.* **28**, 2493–2499.e3 (2018).
38. Tambling, C. J. et al. Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology* **93**, 1297–1304 (2012).
39. Atkins, J. L. et al. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* **364**, 173–177 (2019).
40. Di Minin, E., Fraser, I., Slotow, R. & Macmillan, D. C. Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. *Anim. Conserv.* **16**, 249–258 (2013).
41. Hausmann, A. et al. Social media data can be used to understand tourists' preferences for nature-based experiences in protected areas. *Conserv. Lett.* **11**, 1–10 (2018).
42. Everatt, K. T., Moore, J. F. & Kerley, G. I. H. Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. *Glob. Ecol. Conserv.* **20**, e00758 (2019).
43. Everatt, K. T., Andresen, L. & Somers, M. J. Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PLoS One* (2014). doi:10.1371/journal.pone.0099389
44. IUCN SSC Cat Specialist Group. 2018. Guidelines for the Conservation of Lions in Africa. Version 1.0. Muri/Bern, Switzerland, 147 pages.
45. Hayward, M. W., O'Brien, J. & Kerley, G. I. H. Carrying capacity of large African predators: Predictions and tests. *Biol. Conserv.* (2007). doi:10.1016/j.biocon.2007.06.018
46. Craigie, I. D. et al. Large mammal population declines in Africa's protected areas. *Biol. Conserv.* (2010). doi:10.1016/j.biocon.2010.06.007
47. Lindsey, P. A. et al. The performance of African protected areas for lions and their prey. *Biol. Conserv.* (2017). doi:10.1016/j.biocon.2017.01.011
48. Ripple, W. J. et al. Collapse of the world's largest herbivores. *Sci. Adv.* **1**, (2015).
49. Creel, S. et al. Carnivores, competition and genetic connectivity in the Anthropocene. *Sci. Rep.* **9**, 1–8 (2019).
50. Trinkel, M., Fleischmann, P. H. & Slotow, R. Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *J. Zool.* **301**, 41–50 (2017).
51. Ogada, D. L. The power of poison: Pesticide poisoning of Africa's wildlife. *Ann. N. Y. Acad. Sci.* **1322**,

- 1–20 (2014).
52. Everatt, K. T., Kokes, R. & Lopez Pereira, C. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodivers. Conserv.* **28**, (2019).
 53. Weise, F. J. et al. Lions at the gates: trans-disciplinary design of an early warning system to improve human-lion coexistence. *Front. Ecol. Evol.* **7**, 1–19 (2019).
 54. Treves, A. & Naughton-Treves, L. Evaluating lethal control in the management of human–wildlife conflict. *People Wildl.* 86–106 (2009). doi:10.1017/cbo9780511614774.007
 55. Slotow, R., Van Dyk, G., Poole, J., Page, B. & Klocke, A. Older bull elephants control young males. *Nature* **408**, 425–426 (2000).
 56. Milleret, C. et al. Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *J. Anim. Ecol.* **86**, 43–54 (2017).
 57. Borg, B. L., Brainerd, S. M., Meier, T. J. & Prugh, L. R. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. *J. Anim. Ecol.* **84**, 177–187 (2015).
 58. Caro, T. M., Young, C. R., Cauldwell, A. E. & Brown, D. D. E. Animal breeding systems and big game hunting: Models and application. *Biol. Conserv.* **142**, 909–929 (2009).
 59. Loveridge, A. J., Searle, A. W., Murindagomo, F. & Macdonald, D. W. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biol. Conserv.* **134**, 548–558 (2007).
 60. Lindsey, P. A. et al. The trophy hunting of African lions: scale, current management practices and factors undermining sustainability. *PLoS One* **8**, e73808 (2013).
 61. Groom, R. J., Funston, P. J. & Mandisodza, R. Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? *Oryx* **48**, 385–393 (2014).
 62. Loveridge, A. J. et al. Conservation of large predator populations: Demographic and spatial responses of African lions to the intensity of trophy hunting. *Biol. Conserv.* **204**, 247–254 (2016).
 63. Rosenblatt, E. et al. Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions. *Biol. Conserv.* **180**, 176–186 (2014).
 64. Packer, C. et al. Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conserv. Biol.* **25**, 142–153 (2011).
 65. Packer, C., Kosmala, M., Cooley, H., Brink, H. & Pintea, L. Sport hunting predator control and conservation of large carnivores. *PLoS One* **4**, (2009).
 66. Packer, C. The African lion: A long history of interdisciplinary research. *Front. Ecol. Evol.* **7**, 1–6 (2019).
 67. Brashares, J. S., Arcese, P. & Sam, M. K. Human demography and reserve size predict wildlife extinction in West Africa. *Proc. R. Soc. B Biol. Sci.* **268**, 2473–2478 (2001).
 68. Croes, B. M. et al. The impact of trophy hunting on lions (*Panthera leo*) and other large carnivores in the Bénoué Complex, northern Cameroon. *Biol. Conserv.* **144**, 3064–3072 (2011).
 69. Lindsey, P., Alexander, R., Balme, G., Midlane, N. & Craig, J. Possible relationships between the south African captive-bred lion hunting industry and the hunting and conservation of lions elsewhere in Africa. *African J. Wildl. Res.* **42**, 11–22 (2012).
 70. Funston, P. . & Levendal, M. *Biodiversity Management Plan For The African Lion*. (2015).
 71. Parliament Of The Republic Of South Africa. *Report of the Portfolio Committee on Environmental Affairs on the Colloquium on Captive Lion Breeding for Hunting in South Africa: harming or promoting the conservation image of the country*. No 167. (2018).
 72. “High Court Rules in Favour of Lions and NSPCA.” August 6, 2019. National Council of SPCAs (NSPCA). Available at: <https://nspca.co.za/news/high-court-rules-in-favour-of-lions-and-nspca/>.
 73. “Sick Neglected Lions Found at Captive Breeding Facility in South Africa.” May 8, 2019. National Geographic.
 74. Steinmetz, J. T. American trophy hunters condemn South African Lion Hunting. (2018). Available at: <https://www.eturbonews.com/175295/american-trophy-hunters-condemn-south-african-lion-hunting/>.
 75. Hunter, L. T. B. et al. Walking with lions: Why there is no role for captive-origin lions *Panthera leo* in species restoration. *Oryx* **47**, 19–24 (2013).
 76. Harvey, R. G. Towards a cost-benefit analysis of South Africa’s captive predator breeding industry. *Glob. Ecol. Conserv.* eo1157 (2020). doi:10.1016/J.GECCO.2020.Eo1157
 77. Open Letter to Secretary Zinke The African Lion Conservation Community’s Response to the South African Predator Association’s Letter. November 29, 2017.
 78. United Nations Office on Drugs and Crime (UNODC), 2020. World wildlife crime report: Trafficking in protected species.
 79. IUCN World Conservation Congress, 2020. Motion 072 - Combatting the illegal trade in lion body parts and derivatives. Available at: <https://www.iucncongress2020.org/motion/072>.

