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RESEARCH ARTICLE

Unsustainable anthropogenic mortality threatens the long-term viability of lion populations in Mozambique

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Abstract

Anthropogenic mortality is a pervasive threat to global biodiversity. African lions (*Panthera leo*) are particularly vulnerable to these threats due to their wide-ranging behaviour and substantial energetic requirements, which typically conflict with human activities, often resulting in population declines and even extirpations. Mozambique supports the 7th largest lion population in Africa, which is recovering from decades of warfare, while ongoing conflicts and broad-scale socio-economic fragility continue to threaten these populations. Moreover, there are concerns that Mozambique represents a regional hotspot for targeted poaching of lions which fuels a transnational illegal wildlife trade. This study aimed to quantify the longitudinal impact of anthropogenic mortality on lion populations in Mozambique. Using national population estimates and monitoring records, we performed forward simulation population viability modelling incorporating detection-dependent population trends and varying scales of anthropogenic mortality. Between 2010–2023, 326 incidents of anthropogenic mortality involving 426 lions were recorded. Bushmeat bycatch and targeted poaching for body parts were the greatest proximate causes of lion mortality (i.e., 53% of incidents),

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increasing significantly over time and acting as cryptic suppressors of regional population recovery, followed by legal trophy hunting (i.e., 33%), and retaliatory killing (i.e., 13%). Our findings suggest that resilience to anthropogenic threats is largely a function of lion population size as well as resource and management capacity. For instance, projections suggest that the lion population in Niassa Special Reserve will likely remain stable despite comparatively high levels of anthropogenic mortality, although further escalation may precipitate decline. Conversely, the lion population in Limpopo National Park is projected to become extirpated by 2030 without the buffering effect of its neighbouring source population in Kruger National Park. These unsustainable levels of anthropogenic mortality threaten the long-term viability of lion populations in Mozambique, requiring urgent national-level action and public-private partnerships to support site security, monitoring, and policy enforcement.

Introduction

Escalating anthropogenic mortality arguably poses the greatest threat to global biodiversity [1], portending a sixth mass extinction crisis [2], with significant impacts on vital ecological and socio-economic services [3]. In Africa, anthropogenic threats to wildlife are severe and pervasive at the continental (e.g., land/sea-use change, natural resource extraction, pollution, climate change [4,5]), regional (e.g., illegal wildlife trade [IWT], poorly regulated legal harvest [6]), and local (e.g., poaching [7] and human-wildlife conflict [HWC; 8]) scales. Understanding the spatio-temporal patterns of such direct and indirect mortality, and how current or planned policy may potentially mitigate these scale-dependent threats, is critical for effective monitoring and intervention strategies [9,10]. This applies particularly to large carnivores, which are inherently elusive and often occur at low densities, while their substantial metabolic and ranging requirements tend to exacerbate persecution and conflict [11,12], which often results in significant demographic impacts, population declines and even extirpations [7,13,14].

African lions (*Panthera leo*) are ecologically, economically, and culturally significant [12,15,16], and yet, these large carnivores continue to suffer widespread population and range declines [17–20], with an estimated 23,000 mature individuals occurring in ~6% of their historic range [17,21]. Despite being listed as 'Vulnerable' globally (International Union for Conservation of Nature Red List of Threatened Species [17]), successful lion conservation resulted in a ~ 12% increase between 1993 and 2014 across Botswana, Namibia, South Africa and Zimbabwe, largely due to the proliferation of reintroductions into relatively small (i.e., < 1,000 km^2), fenced, and well-funded metapopulation reserves [18,22]. Nevertheless, this is not the case for most lion range states, where protected areas (PAs) are relatively large (i.e., > 1,000 km^2), unfenced, and underfunded [23]. These range states are often unable to keep pace with mounting anthropogenic threat levels, experiencing a ~ 60% decline over the same period, with a notable increase in anthropogenic mortalities [18]. Unfortunately, similar declines are predicted for many lion populations across their African range,

especially in the most ecologically and socio-politically fragile countries [23,24], which may be without adequate resources and management capacity to ameliorate these threats [18,25].

Mozambique (~800,00km^2) is an important range state for lions in Africa, harbouring ~1,500 mature individuals [African Lion Database, unpublished data, 2024] and represents one of only nine African countries with >1,000 lions (i.e., 7th largest African lion population). With 29% of the country formally designated for conservation [26], there is an opportunity for population recovery and range restoration. However, in the shadow of historical armed conflict and political instability, Mozambican conservation continues to grapple with ongoing localized conflict, human settlement within or around PAs and unprecedented growth of resident communities. When coupled with severe and ongoing shortages in funding for PA management, these challenges have driven unsustainable levels of resource extraction [27,28]. Exacerbated by a rapidly growing human populus, post-war large carnivore and prey numbers have continued to decline across many parts of Mozambique [29–32]. Lions currently occur in six resident populations across Mozambique. Of these populations, Niassa Special Reserve (SR) in the northern region is considered the only lion stronghold (i.e., > 500 lions; [17,33]) in the country, with stable to increasing populations occurring in the central region, largely due to post-war population recovery or subsequent reintroductions and significant private or non-governmental investment [30,31]. Mozambican lion populations are largely restricted to PAs and hunting concessions [34], and while these landscapes are relatively large, most are not sufficiently protected, monitored, or managed, as a result of limited resources and management capacity [20,23]. Mozambique also appears to have become a regional hotspot for IWT in lion derivatives, both as a source and transit state [35,36], that is particularly vulnerable to corruption and poor enforcement [14,37]. While the precise drivers of demand remain speculative, studies suggest that lion body parts are typically sought for use in zootherapeutic traditional medicine (i.e., zootherapy), and social or cultural purposes (e.g., clothing, curios, ornaments, trinkets, and other regalia) in both Asian and African markets [35,36,38]. Poaching of lions for body parts has thus raised significant concerns for lion conservation throughout the region [38,39].

Determining population size, as well as the proximate cause and extent of anthropogenic mortality for lions across Mozambique presents complex methodological and logistical challenges [36,40]. Approaches to estimating lion population size vary from non-individual-based techniques including traditional (e.g., call ups and spoor counts [41]) and more recent density estimation approaches (e.g., random encounter models [42]) to individual-based capture-recapture frameworks (e.g., search encounter [43]). Traditional approaches remain the most commonly applied across lion range states and provide sufficient information for estimating population trends [44]. Although, such methods carry inherent detection limitations and biases in addition to the substantial skilled capacity and operational costs of intensively monitoring such vast landscapes [43,45]. Similarly, the comparable detection of anthropogenic mortalities requires direct and consistent monitoring efforts [14,29,36,38], such that rapid and evidence-based reporting can distinguish among the proximate causes of lion mortality (i.e., natural, bushmeat bycatch, retaliatory killing, targeted poaching to supply the IWT, or legal trophy hunting). While regional consolidation and interpretation of such trends is objectively valuable, limited resources and capacity often force PAs and statutory authorities to prioritize immediate challenges like HWC and law enforcement over addressing knowledge gaps for adaptive management. Indirectly, PA management is also responsible for ensuring local food security and socio-economic development, where such resilience affords a greater capacity to coexist with lions and incentivizes alternative economic opportunities outside of poaching [23].

Understanding how lion populations are affected by anthropogenic mortality is critical to addressing this current conservation crisis and developing regional-level intervention strategies. This study aims to quantify the threat of anthropogenic mortality to the long-term viability of lion populations in Mozambique. Using longitudinal population estimates and mortality records collected between 2010–2023, we describe the recent trends and impact of anthropogenic mortality on current and future national lion population projections. We hypothesise that the proportion of anthropogenically linked lion mortality in Mozambique directly threatens the long-term viability of resident populations. We also predict that relative protected area size and perceived threat, as well as management resources and capacity contribute to the resilience of lion these

populations. While the targeted poaching of lions for the illegal wildlife trade significantly contributes to resident lion extirpation risk. We discuss our findings in the context of anthropogenic mortality relative to PA size, lion population viability, the detectability of mortalities and the scale of lion derivative trade, while evaluating resource and management capacity towards mitigating these threats across Mozambique. Importantly, we identify prioritized lion populations for strategic conservation management intervention and regional policy development.

Methods

Study areas

This study reports on longitudinal lion population and mortality data collected from various areas prioritized for conservation in Mozambique (Table 1). Of the national terrestrial conservation estate, formal PAs (i.e., national parks [NPs],

Table 1. Summary of lion populations in Mozambique and anthropogenic mortality record. Indicated by population, is the relevant management type (i.e., PA = Protected Area, WMA = Wildlife Management Area, MUL = Mixed-Use Landscape), area size, whether there is active trophy hunting, the latest population estimate and trend, the reported annual anthropogenic mortality and trend, as well as predominant causes of mortality and important contextual notes.

Population	Management type	Area size (km^2)	Trophy hunting of lions	Latest resident population estimate	Lion population trend	Anthropogenic mortality annual trend	Average annual anthropogenic mortalities	Main causes of anthropogenic lion mortality	Notes
Banhine National Park	**PA**	7,290	Inactive	Unknown	Unknown	No data	2	Illegal wildlife trade	*NA*
Coutadas 9 & 13	**WMA**	9,724	Active	44 [(1)]	Increasing	Increasing	2.72	Poaching	Coutada 13 is considered a transient population
Gorongosa National Park	**PA**	3,708	Inactive	183 (163-200) [(2)]	Increasing	Constant	3.13	By catch in snares	*NA*
Greater Lebombo Conservancy	**WMA**	2,483	Active	70 [(3)]	Stable	Constant	No data	Legal trophy hunts	*NA*
Limpopo National Park	**PA**	10,544	Inactive	22 [(4)]	Decreasing	Decreasing	4.42	Human-wildlife conflict & illegal wildlife trade	*NA*
Mahimba Game Farm	**WMA**	349	Inactive	< 5 [(5)]	Stable	No mortalities	0	No anthropogenic mortalities observed	*NA*
Muanza Game Farm	**WMA**	329	Inactive	17 [(5)]	Stable	No mortalities	0	No anthropogenic mortalities observed	*NA*
Niassa Special Reserve	**MUL**	42,353	Active	932 (810−1,054) [(6)]	Decreasing	Increasing	19	Poaching	*NA*
Tchuma Tchato Community Programme	**MUL**	38,000	Active	Unknown	Unknown	No data	No data	No data	*NA*
Zambezi Delta	**MUL**	9,750	Inactive	64 [(7)]	Increasing	Constant	3.33	By catch in snares	Lions reintroduced in 2018 after being extirpated
Zinave National Park (Sanctuary)	**PA**	59	Inactive	6 [(8)]	Increasing	No mortalities	0	No anthropogenic mortalities observed	Lions naturally recolonized Zinave Sanctuary in 2021 after being extirpated

(1) Rio Save Safaris Ltd. Unpublished Data. 2022 (Pers Comm), (2) Gorongosa Restoration Project. Unpublished Data. 2022, (3) Sabie Game Park. 2020. Unpublished Report, (4) Everatt, K. T., Kokes, R., Pereira, C. L. 2019. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. Biological Conservation. 28: 4099–4114, (5) Taylor. Personal Communication. 2023, (6) Niassa Carnivore Project, TRT Conservation Foundation, 2018 Annual Report, (7) Zambeze Delta Conservation. Unpublished Data. 2022, (8) Abrao. Pers Comm. 2024.

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national and forest reserves) and wildlife management areas (i.e., hunting concessions, mixed-use areas, community areas, and game farms) comprise approximately 233,249 km^2 (i.e., 29% of the country; [26]). In particular, we investigate comparatively large and well-monitored resident lion populations (i.e., a demographically cohesive group of lions occupying the same geographic area) occurring in Niassa SR, Gorongosa NP, Tchuma Tchato Community Programme, Zambezi Delta, Coutada 9 and 13 (hereafter, Coutadas 9/13), and Limpopo NP (Fig 1). Lions predominantly occur within these areas, yet some small resident or transient populations are still found outside of this estate [34]. While most lion populations in Mozambique were naturally founded, lions were reintroduced into Coutada 9 in 2010 and the Zambezi Delta in 2018, following post-war functional extirpation [31]. Where lions are considered to be damage-causing animals or are involved in severe cases of HWC, the standing policy of the national wildlife authority (i.e., the Administração Nacional das Áreas de Conservação; ANAC) is to either translocate or euthanize these individuals to mitigate the threat to community lives and livelihoods [34]. Legal trophy hunting quotas for lions are also assigned and regulated by ANAC, with validation by independent partners [46].

Data collection

We quantified the longitudinal impact of anthropogenic mortality on lion populations in Mozambique using national population estimates and monitoring records between 2010 and 2023. These data were collaboratively complied directly by conservation area managers or research representatives from as many of the Mozambican PAs, wildlife management areas, and mixed-use landscapes as possible. Population size and trend data were derived from intensive monitoring and call-up

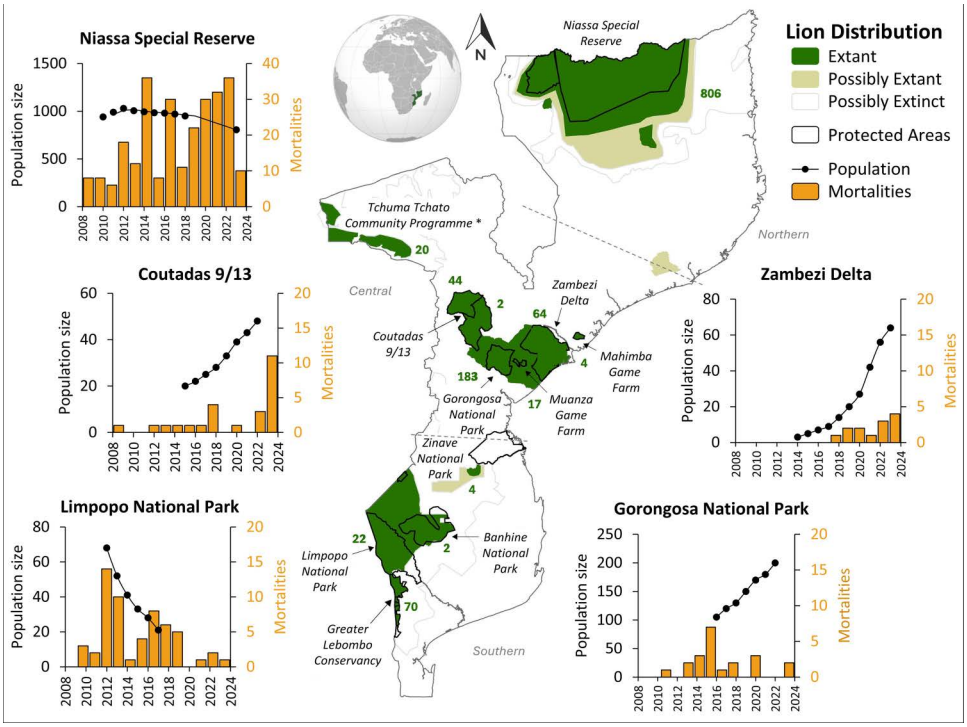

Fig 1. Resident lion populations in Mozambique, with associated population and anthropogenic mortality trends over time (2010–2023). The map shows the current IUCN lion range (extant, dark green; possibly extant, beige; possibly extinct, clear; S1 Appendix in S1 File), and protected areas (grey outlines), indicating known lion populations (labelled) and their most recent population sizes (green numbering). Where longitudinal trend data were available for the 13-year study period, annual lion population size estimates (black circles) and anthropogenically induced mortality incidents (orange bars) are presented. *Data were only available for Chawalo Safari Area as a proxy for the Tchuma Tchato Community Programme.

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surveys, while mortality records included the number and demographics of lions killed, cause of mortality (i.e., snared, trapped, poisoned, shot, or vehicular collisions) and, where possible, motivations behind the incident (i.e., accidental, bushmeat by-catch, damage-causing animal, retaliation, targeted poaching, and trophy hunting). Targeted poaching of lions was defined as an anthropogenic mortality with i) no evidence of HWC, ii) evidence of deliberate attempts to kill lions, and iii) body parts removed [38]. Due to the complex nexus of suspected motives, we could not reliably confirm this for all incidents of anthropogenic mortality from the information provided. Incidents where lions were injured but survived following veterinary intervention, were not included in mortality analyses, but were considered in population modelling to demonstrate the value of ongoing intervention efforts.

In addition to population estimates and mortality records, we used information gathered through a range-wide structured questionnaire survey (University of KwaZulu-Natal Human and Social Sciences Research Ethics Committee; HSSREC/00003076/2021; recruitment period: 01-08-2021–31-07-2022), with informed, written consent from participants, to present baseline information on the anthropogenic threats to lions within their Mozambican range, and the resources available to reduce anthropogenic mortalities. Surveys were completed at a subpopulation level, which we define as the non-transboundary lion area that is clearly separated by either political or formal protection boundaries [47]. One completed survey represented one lion subpopulation. We targeted managers of lion subpopulations within formal protected areas, recognised conservancies and game management areas, hunting concessions, and other wildlife areas. A total of 187 experts were invited to participate in the survey, of which 132 responded, yielding a response rate of 71%. Two broad indices were developed from this survey: i) a perceived Anthropogenic Threat Index (ATI) was developed to score the perceived severity of anthropogenically driven threats to lions within a population. From a list of threats, survey respondents were required to indicate whether a particular threat occurred in the area for the past five years and provide a score as to its severity (i.e., ranging from '0', where the threat to lions does not occur in the area, to '4' where the threat is severe enough to potentially result in extirpation). High ATI scores indicated increasingly severe threat intensity, while lower scores (i.e., closer to 0) indicated reduced severity; ii) a perceived Resource and Capacity Index (RCI) was developed in parallel to determine the perceived availability of resources and capacity within PA, wildlife management area, or mixed-use landscape management towards reducing lion mortality. The RCI was based on a series of four trichotomous questions where respondents answered whether area management had sufficient funding and staff, correct anti-poaching gear, and enough vehicles to reduce the illegal killing of lions. For the purpose of this study, we utilized the results of both indices, gathered for Mozambique only, to provide further contextual understanding of threats to lions in Mozambique and the capacity of area managers to reduce the impacts of those threats in their landscapes.

Statistical analysis

All statistical analyses were run using *R* v4.2.1 statistical software [48]. Spatio-temporal differences in motives and methods behind anthropogenic mortality events were explored through linear or multinomial logistic regression models using the 'multinom' function in the *nnet* package [49]. Where the overall significance of each factor was assessed using Type III ANOVAs implemented in the *car* package [50]. The relative effect of each variable (i.e., motive or method) was plotted by region and year using the *effects* package [51]. Tukey *post-hoc* analyses were then performed in the *lsmeans* package [52] to test for pairwise differences in the relative proportion of each motive or method comparison by region and year.

To evaluate the sustainability of anthropogenic mortality within the local context of Mozambique, we used the individual-based lion population model, which is available as the *pop.lion* package, developed by Loveridge et al. [53]. It is unlikely that all cases of anthropogenic mortality were detected within PAs, wildlife management areas, or mixed-use landscapes, thus we aimed to quantify the approximate rate of detection by comparing model projections based on recorded cases of mortality with recorded population size trends. We ran simulations with five different hypothetical detection probabilities (i.e., 20%, 40%, 60%, 80% and 100%); for example, scenarios that assumed the rate of

detection was 20%, the anthropogenic mortality estimates were multiplied by five for each population, whereafter we visually assessed which scenario aligned most closely with the known lion population size estimates recorded between 2010 and 2023.

We then modelled future projections (i.e., between 2023 and 2040) for each population with varying annual anthropogenic mortality rates (i.e., 0%, 5%, 10%, 15%, 20% and 40%) to provide insight into possible future population trends under the varying levels of proposed mortality. We identified the most likely scenarios based on the recorded trend data corrected by the approximate rate of detection from the first stage of the modelling process (e.g., if the anthropogenic mortality rate based on available data was calculated to be 5% and the rate of detection was estimated to be 60%, estimated anthropogenic mortality would be 8.3%). We calculated the ecological carrying capacity for each lion population to evaluate populations changes relative to these thresholds [54]. All scenarios were run with 1,000 iterations where the mean and quantile range between 0.025 and 0.975 were plotted for each population. For Limpopo NP, we included an additional set of models (i.e., Limpopo NP + K) which accounted for the buffering connectivity effect of lion movement from Kruger NP [38]. This was done by modelling the Limpopo NP and northern Kruger NP as one system and setting Limpopo NP as the edge/sink zone (i.e., the area where offtake occurs [53]). A 17% protected core area was also defined for Niassa SR, leaving 83% 'edge' of the population at modelled risk to anthropogenic mortality. Further details regarding the specific parameters used for each model are provided (S2 Appendix in S1 File).

Results

Status, threats and resource availability

We identified 11 conservation areas currently supporting extant lion populations in Mozambique, including a total conservative estimate of approximately 1,208–1,489 lions, covering over 125,970 km^2 (i.e., 54% of the available conservation estate across Mozambique). Of these lion populations (Table 1), 37% were reported by conservation managers as currently increasing, 27% were considered stable, 18% were decreasing, and 18% were unknown (Fig 1). Mortality trends for all populations were reported as no mortality (27%), decreasing (9%), constant (28%), increasing (18%) or as having no data (18%) and legal trophy hunting was conducted in approximately 36% of populations across Mozambique.

The perceived ATI revealed the highest threat scores for Coutada 13 and Niassa SR, whereas the Greater Lebombo Conservancy (i.e., Karingani Game Reserve, Sabie Game Park, Massintonto Concession, Mbhatse Concession; Greater Lebombo Conservancy) and Banhine NP reported the lowest threat scores (Fig 2a). In terms of perceived RCI, Niassa SR, Coutadas 9/13, and the Tchuma Tchato Community Programme (i.e., data were only available for Chawalo Safari Area as a proxy for the conservation area) reported the lowest resource and management capacity scores, while Gorongosa NP, Greater Lebombo Conservancy, and the Zambezi Delta reported relatively high scores. After accounting for area and population size, the annual anthropogenic mortality rate of lions per 100 km^2 was highest for Muanza Game Farm, followed by Niassa SR, Limpopo NP, and the Greater Lebombo Conservancy (Fig 2b).

Impact of anthropogenic mortality

A total of 326 anthropogenic mortality incidents (i.e., comprising of 426 individual lions) were recorded across Mozambique between 2010 and 2023 (Fig 3). An additional 16 successful interventions (i.e., comprising of 17 individual lions) were recorded. This constitutes an average of approximately 30 mortalities (i.e., ~2.3% of the total population) and 1.31 interventions (i.e., ~0.1% of the total population) per year (at a mean of 5.77 ± 2.67 [SE] lions per population). There was a significant increase in the number of annual anthropogenic mortalities observed ($F = 6.99$, df = 1 and 12, $P < 0.05$), increasing from 9 to 49 mortalities (i.e., 1–4% of the total population) over the 13-year period. Since 2012, the number of anthropogenic mortalities has exceeded 26 individuals each year, with the highest numbers recorded in 2015 ($n = 49$), 2017 ($n = 48$), 2020 ($n = 41$), and 2022 ($n = 49$). Demographically, males (68%) were killed more frequently than females

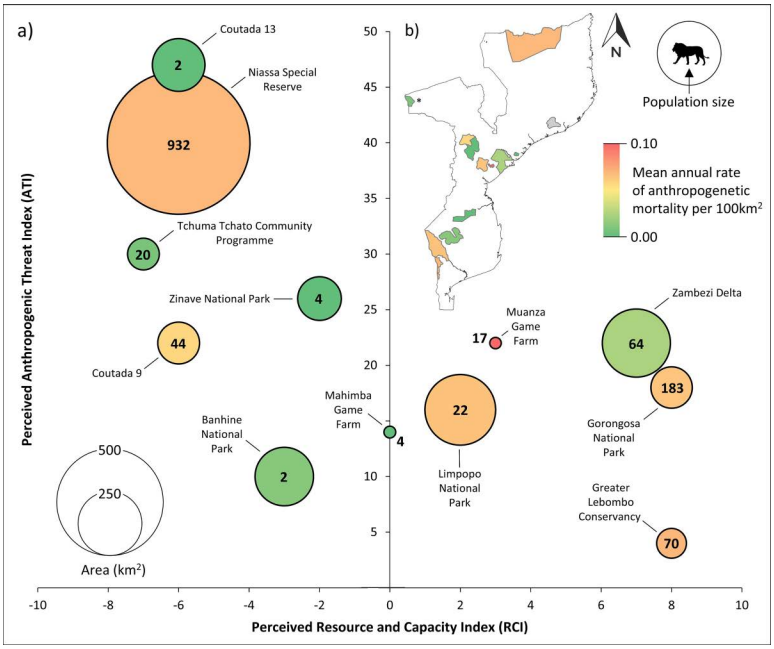

Fig 2. Lion population size by area-based anthropogenic mortality rate relative to perceived threat, resource and management capacity indices across Mozambique. a) Lion population size (bold number inside bubbles) for each area (bubble size) and b) mean annual rate of anthropogenic mortality per 100km^2 between 2010 and 2023 (green-yellow-red colour gradient) are indicated relative to perceived anthropogenic threat index (ATI), and resource and capacity index (RCI). ATI is the perceived severity of anthropogenically-driven threats to lions within a population, with higher index values indicating higher anthropogenic threats. RCI is the perceived availability of resources to management for reducing lion mortality, with higher values indicating greater resource and management capacity.

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(32%) based on known sexes, while 83% of mortalities were adults, followed by subadults (14%), and cubs (3%) based on known ages.

The greatest proximate causes of lion mortalities were illegal motives (i.e., 65% of incidents), comprising bushmeat bycatch (27%), targeted poaching for parts (25%), and retaliatory killing (13%), followed by legal trophy hunting (33%). There was a significant difference in motive for anthropogenic mortality over time ($F = 30.065$, df = 6, $P < 0.001$; S1 Table in S1 File), with the prevalence of bushmeat bycatch and targeted poaching increasing, and trophy hunting decreasing over time (Figs 3–4). There was also a significant difference in the method used for lion killings over time ($F = 152.97$, df = 65, $P < 0.001$; S1 Table in S1 File), with the most prominent changes being an increase in poisoning and decrease in shooting of lions over time. There were significant differences in motives for lion killings across regions ($F = 226.22$, df = 18, $P < 0.001$). Lion mortalities in the southern region comprised largely of targeted poaching and retaliatory killing, while bushmeat bycatch predominated the central region, and the northern region was mostly affected by trophy hunting and targeted poaching (S1 Table in S1 File). There were also significant differences in methods used between regions ($F = 217.21$, df = 15, $P < 0.001$), with poisoning and snaring used in the south, gin trapping and snaring in the central region, and trophy shooting in the north.

Targeted poaching of lions for body parts increased significantly over time ($F = 5.22$, df = 1 and 10, $P < 0.05$), with an average of one lion killed per year between 2010 and 2017, to an average of 7 lions per year between 2018 and 2023 (Fig 5). While illegal wildlife trade related poaching was evident in all populations, most incidents of body part removal were reported in the northern (e.g., skins, paws, and whole bodies) and southern (e.g., paws, face/head/skulls, and flesh/meat) regions.

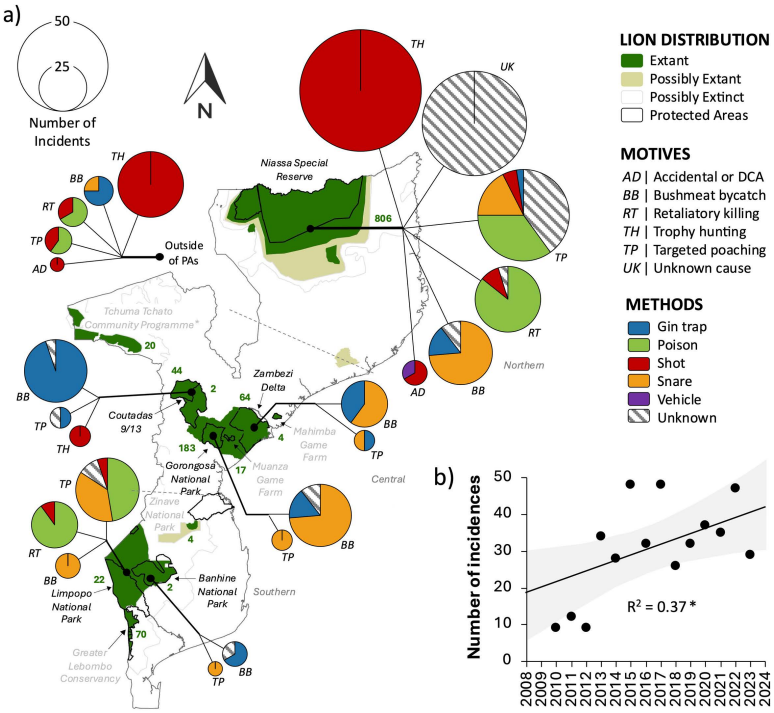

Fig 3. Typology of anthropogenic lion mortality across Mozambique between 2010 and 2023. Indicated are the typological motives (i.e., AD – accidental or damage-causing animal, BB – bushmeat bycatch, RT – retaliatory killing, TH – trophy hunting, TP – targeted poaching, and UK – unknown cause) and methods (i.e., blue – gin trap, green – poison, red – shot, orange – snare, purple – vehicle, and grey hashing – unknown) of anthropogenic mortalities. **a)** The map shows the current IUCN lion range (extant, dark green; possibly extant, beige; possibly extinct, clear; S1 Appendix in S1 File), and protected areas (grey outlines), indicating known lion populations (labelled) and their most recent population sizes (green numbering). The circle size indicates the number of incidents by reported motive and method. Indicated also are the b) significantly increasing trend of anthropogenic mortality incidents over time.

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Population viability modelling

Visual assessment of the population projections for each area under varying detectability levels of anthropogenic mortality (Fig 6) showed that Gorongosa NP, Coutadas 9/13 and the Zambezi Delta aligned best with population size trends when detection was set around 100%. This validation of near-complete detection indicates that a relatively greater degree of confidence may be assigned to projections for these populations. For Niassa SR, the scenario with detection rate set at 20% aligned most closely with the observed population trend, while all larger detection rates produced projections that far exceeded population estimates between 2010 and 2023. The 20% detection rate scenario was also the best fit for Limpopo NP when the buffering effect of Kruger NP was included, while the scenario with a slightly higher detection rate of 40% was the closest fit for Limpopo NP when Kruger NP was excluded.

The annual anthropogenic mortality rate in Gorongosa NP is projected to remain low and stable at approximately 1.5%, with ongoing interventions likely further reducing this rate (Fig 7). Coutadas 9/13 and the Zambezi Delta are projected to remain low to moderate with anthropogenic mortality rates at approximately 9% and 8% respectively, although current levels of intervention appear to reduce these rates by 2–3%. In Niassa SR, the annual anthropogenic mortality rate outside the well-protected core area is projected at approximately 3.2%, however, given the relatively low detection rate (i.e., 20%), the true annual anthropogenic mortality rate for Niassa SR is likely to be much higher at around 16%. In Limpopo NP, the annual anthropogenic mortality rate is projected as being low to moderate at approximately 8%, however, as the detection rate is likely very low (i.e., 20–40%), the actual rate of annual anthropogenic mortality could be high at 19.8% (i.e., excluding Kruger NP) to extremely high at approximately 40% when accounting for connectivity with Kruger NP.

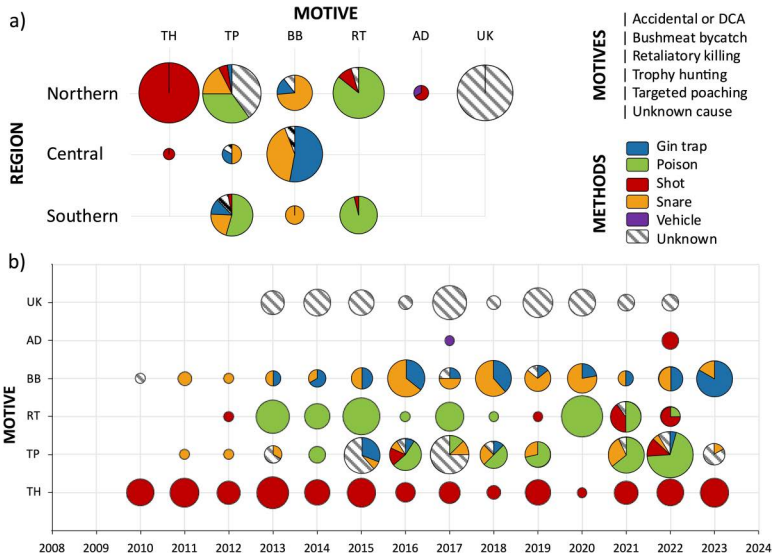

Fig 4. Typology of anthropogenic lion mortality summarized by a) region and b) over time in Mozambique between 2010 and 2023. Indicated are the typological motives (i.e., AD – accidental or damage-causing animal, BB – bushmeat bycatch, RT – retaliatory killing, TH – trophy hunting, TP – targeted poaching, and UK – unknown cause) and methods (i.e., blue – gin trap, green – poison, red – shot, orange – snare, purple – vehicle, and grey hashing – unknown) of anthropogenic mortalities.

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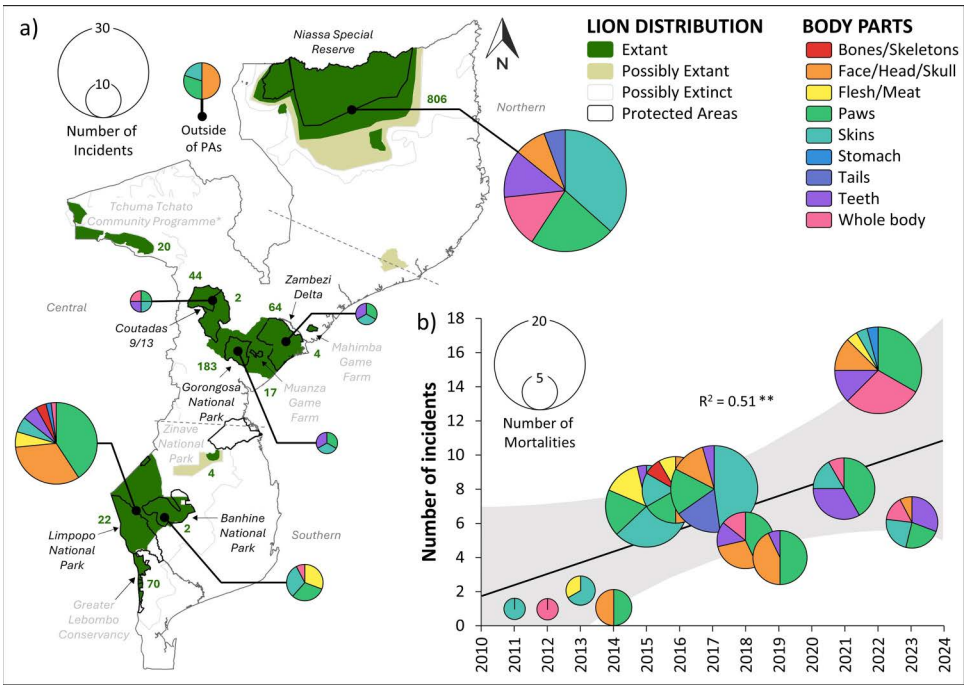

Fig 5. Lion body parts removed for illegal wildlife trade across Mozambique 2010–2023). The map shows the current IUCN lion range (extant, dark green; possibly extant, beige; possibly extinct, clear; S1 Appendix in S1 File), and protected areas (grey outlines), indicating known lion populations (labelled) and their most recent population sizes (green numbering). Indicated are the number of confirmed incidents (circle size) of anthropogenically driven lion mortality from which body parts were taken and presumably intended for the illegal wildlife trade, and the proportion of body parts (red – bones/skeletons, orange – face/head/skull, yellow – flesh/meat, green – paws, aquamarine – skins, blue – stomach, purple – tails, violet – teeth, and pink – whole body) taken by a) area and b) year.

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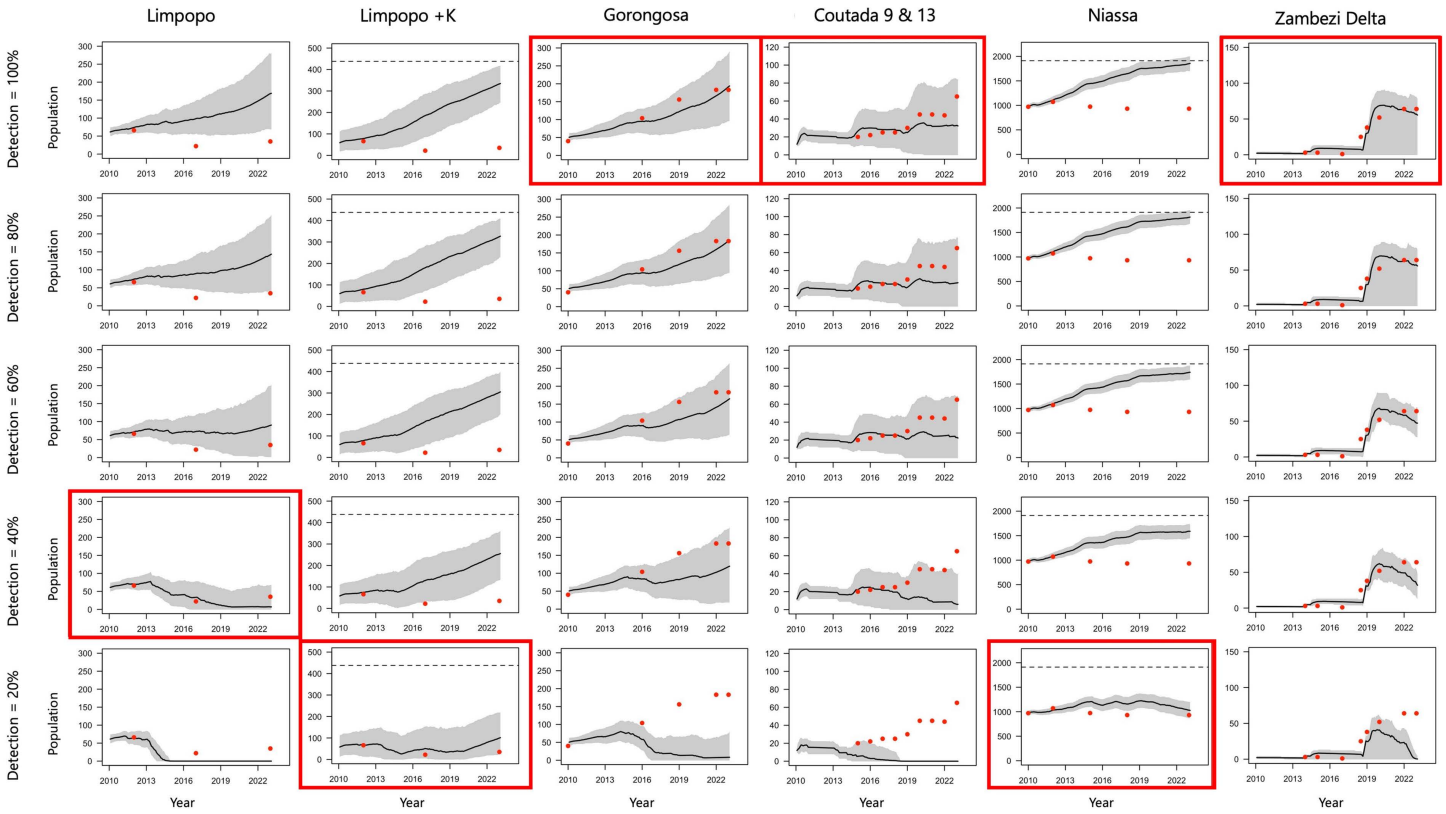

Fig 6. Lion population projections in Mozambique based on recorded levels of anthropogenic mortality with varying levels of assumed mortality detection. Plots outlined with red squares indicate the most likely scenarios based on visual assessment of model fit (black line with 95% CIs in grey). Red dots represent annual population estimates for each lion population and horizontal dashed lines indicate estimated ecological carrying capacity. The K (Kruger National Park) associated with Limpopo National Park represents the model run with the inclusion (+) of Kruger NP as a buffering effect to Limpopo NP, given the connectivity between these two PAs.

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Future simulations indicate that for all populations, eliminating anthropogenic mortality would lead to natural population growth such that by 2040 these populations would approach ecological carrying capacities. Gorongosa NP was projected as having the highest annual population growth rate of 6.5% and is projected to reach its ecological carrying capacity by 2040. The Zambezi Delta and Coutadas 9/13 support projected growth rates of approximately 0.8% and 0.4% per annum respectively and are not likely to achieve their ecological carrying capacities by 2040, although these populations are projected to display increasing trends if intervention capacity is maintained. The annual population growth rate projected for Niassa SR is −0.2%, indicating a population at stability tending towards decline, where projected levels of anthropogenic mortality are likely to keep suppressing the population at around half of its ecological carrying capacity by 2040. In Limpopo NP, the projected annual population growth rate is −0.1% to −0.4%, with and without the buffering effect of Kruger NP respectively, indicating that without this effect, the population will likely be extirpated by 2040.

To secure projected stable or growing annual population growth rates, given varying degrees of confidence in detection, annual anthropogenic mortality targets should be maintained at ≤5% for Gorongosa NP, whereas the Zambezi Delta and Coutadas 9/13 should set their annual anthropogenic loss targets at ≤5% (S2 Table in S1 File). Niassa SR should aim to keep annual anthropogenic mortality at ≤ 10% outside of the well-protected core area. In contrast, the Limpopo NP should take drastic steps to reduce annual anthropogenic mortality rates by half and keep these at ≤5% (without Kruger NP) or at ≤20% (with Kruger NP) to remain stable and viable or support recovery by 2040.

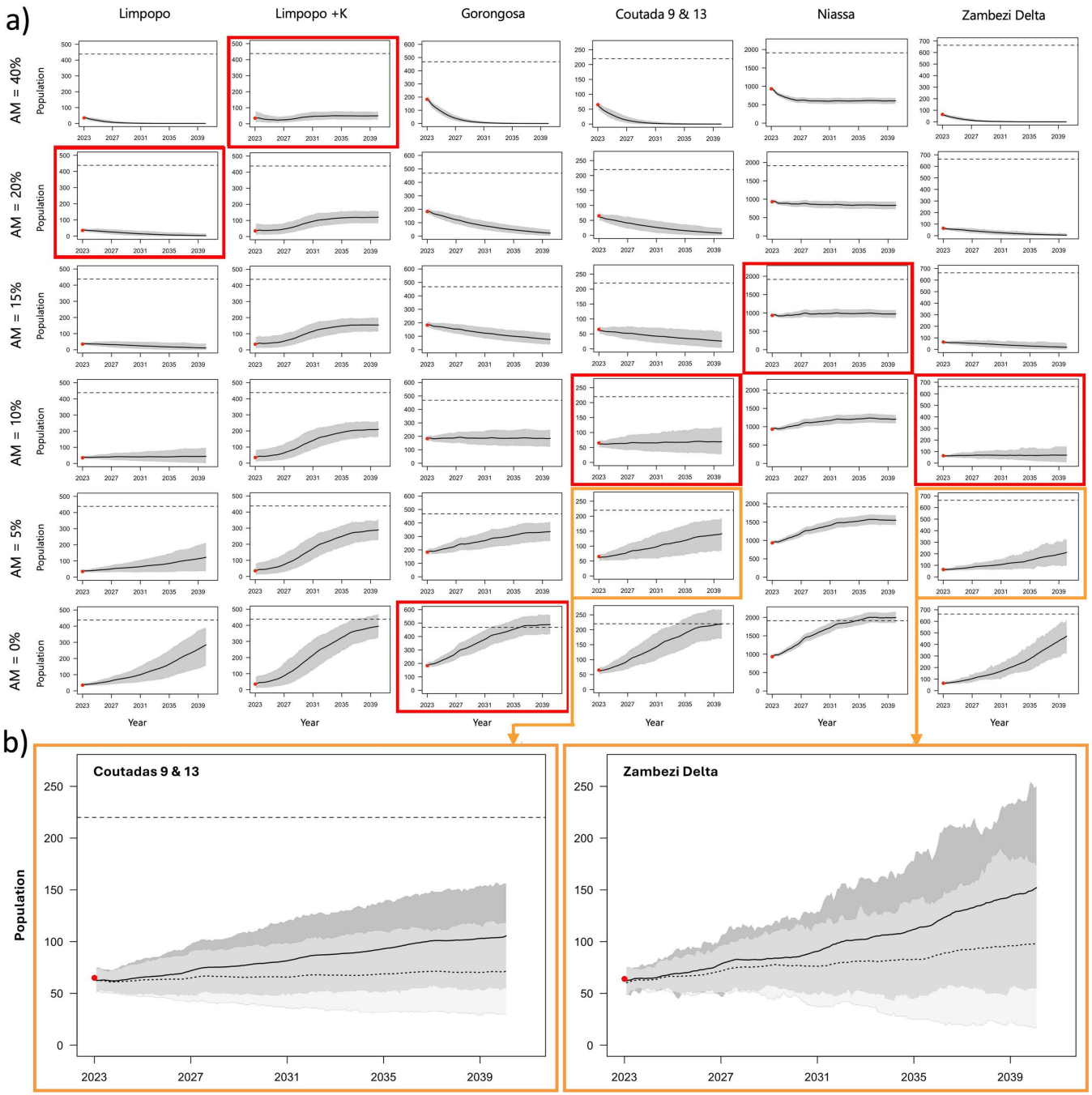

Fig 7. Lion population projections for in Mozambique under varying rates of anthropogenic mortality and management intervention. **a)** Plots with red squares indicate the most probable outlook based on current anthropogenic mortality rates corrected by estimated rates of detection (black line with 95% CIs in grey). Horizontal dashed lines indicate ecological carrying capacity as calculated for each of the populations. **b)** Plots with orange squares indicate the most probable outlook based on current anthropogenic mortality rates corrected by estimated rates of detection and the reported degree of intervention.

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Discussion

Anthropogenic mortality has driven large carnivore population declines and extirpations across their range [12]. The inherent resilience of these populations is generally a function of population size and landscape integrity, but also resource and management capacity (i.e., security, monitoring, and funding) relative to the scale of these threats (i.e., coexistent human density, socio-economic dependencies, and tolerance; [12,23,55]). Quantification of anthropogenic mortality throughout post-war Mozambique revealed that bushmeat poaching, among other threats, is a significant suppressor of regional lion population recovery. Predictive modelling based on recent population trends, considering relative anthropogenic mortality rates, suggests that most resident lion populations in Mozambique will remain suppressed below ecological carrying capacity or suffer further declines over the next 15–20 years. These trends are further compounded in comparatively large populations (e.g., Niassa SR and Limpopo NP), as anthropogenic mortality remains under-detected and there is arguably an unstable dependency on well-protected core areas or buffering populations. In contrast, management capacity in comparatively smaller populations (e.g., Gorongosa NP and Zambezi Delta), improves detection and effective mitigation of anthropogenic mortality; but the long-term sustainability of these models will be increasingly challenged by growing lion populations. Moreover, the ubiquity and significant increase of targeted poaching of lions to supply IWT in body parts [38,39], itself often intertwined with bushmeat poaching and retaliatory killing [56], presents a rapidly growing threat. Our documented levels of illegal anthropogenic mortality (i.e., retaliatory persecution, as well as bushmeat and targeted poaching for body parts), exacerbated in smaller populations with limited management capacity, and populations with high transfrontier threats for illegal killing of lions for parts (i.e., Niassa SR and Limpopo NP), threaten the long-term viability of Mozambique's lion populations.

Of the 426 anthropogenically-driven lion mortalities recorded between 2010–2023, 65% of incidents were of illegal causes (i.e., bushmeat bycatch, as well as targeted and retaliatory killing), reiterating concerns raised over largely cryptic and unregulated threats to lions throughout Mozambique. In Niassa SR, which supports 62–77% of the national lion population, anthropogenic mortality rates range from low to high (3.2–16%), with the precision of these estimates constrained by low detection rates (~20%). While current efforts appear sufficient to maintain this population size at approximately half of its ecological capacity, any increase in the annual anthropogenic mortality rate (i.e., 15–20%) or fragmentation of the core area is likely to precipitate future population decline [46]. Niassa SR management should aim to increase overall detection and reduce these mortality rates to ≤10% to ensure population growth and resilience. With near complete detection, Gorongosa NP represents confident post-war lion population recovery, with projections approaching ecological capacity by 2040 given the lowest annual anthropogenic mortality rate (2%). Such site security and restoration is likely a result of the comparatively small area, intensive lion-specific monitoring efforts, and anti-poaching coverage facilitated by long-term investment through public-private partnerships [30,57,58]. As both Coutadas 9/13 and Zambezi Delta populations are reintroduced into relatively large areas, their growth is substantial, but will likely not attain ecological capacity within the projection timeframe. However, given increasing annual anthropogenic mortality rates in both areas, populations may begin to stabilize or decline. Management in these areas should maintain overall detection and reduce these mortality rates to ≤5%, especially as these populations continue to grow and their exposure to illegal anthropogenic threats intensifies [31]. Of greatest concern, however, is that predictive models, at low detection rates (~40%), suggest that without the buffering effect of Kruger NP, the lion population in Limpopo NP will likely be functionally extirpated by 2030, a compounding result of a relatively small population size and unsustainable levels of anthropogenic mortality [29,38]. This collective status and projection of lion populations in Mozambique highlights the severity of the monitoring and enforcement crisis currently threatening these and other regional strongholds [24,38,40,47].

Monitoring population dynamics and threats are challenging for elusive carnivores in expansive landscapes, and predicting long-term trends pose several caveats and limitations [43,59,60]. Firstly, perceived anthropogenic threat indices are dependent on population persistence and may be lower than reality if these populations are reduced or extirpated (e.g., Banhine NP and Limpopo NP). Secondly, while the significant increase in anthropogenic mortality identified in this

study may be an artefact of increased monitoring efforts, these findings corroborate growing evidence of increased legal and illegal trade in lion body parts regionally [35,36,40,61]. Thirdly, while more robust methods for estimating lion population size are increasingly recommended [43,44], consistent application of traditional methods provided sufficient insights into longitudinal population trends [18]. Fourthly, efforts to monitor lion mortality and indicators of specific threats (e.g., lion conflict events, and anti-poaching coverage) vary substantially across landscapes and depend on various factors such as PA size and accessibility, as well as monitoring capacity and efficacy [13,62], resulting in variable detection rates and therefore confidence in projections [7,25,40,55]. Finally, while the number of reported lion mortalities has fluctuated over time, some of this variability may be attributed to seasonal accessibility or temporal variability in retaliatory killing, and demand for bushmeat or lion body parts for trade [13,62]. In addition, the detection of lion mortality may also be masked by cryptic poaching (i.e., poachers concealing their activities and avoiding detection) in response to increased antipoaching efforts [63]. In contrast, legal trophy hunting is comparatively well documented and regulated, thus these lion mortalities are likely near complete records [46]. Nevertheless, such regional population trend modelling accounts for such variability and provides important insights into the impact of this pervasive threat to lions across Mozambique.

That Mozambique is vulnerable to bushmeat poaching and increasingly threatened by IWT, is not unique, as many lion range States have experienced turbulent political histories with ongoing socioeconomic fragility which challenge conservation efforts [14,18,27]. However, there are many factors predisposing Mozambique to these threats, most of which are driven by protracted multi-dimensional poverty, that continues to suppress large carnivore populations [29,31]. The rapidly growing human population continues to exert increasing pressure on natural resources through further encroachment into conservation areas [32,64,65], deforestation for logging and agriculture, and bushmeat poaching to fuel consumptive and commercial trade demands [29,35,66]. Relatively weak and poorly implemented penal systems, inadequate and corrupt law enforcement, as well as a lack of wildlife-based benefits and opportunities for local enterprise are also highlighted as potential drivers of bushmeat poaching [14,67]. Mozambique is geographically vulnerable with an exposed coastline which is generally poorly monitored, and long borders with neighboring countries who experience similar transnational wildlife crime [68]. Furthermore, the susceptibility of lion populations to anthropogenic mortality is likely exacerbated by existing poaching syndicates, and wide-reaching criminal economies, with accessibility to international ports and trade routes [37,68]. For instance, between 2012 and 2017, Everatt et al. [38] estimated a 66% lion population decline in Limpopo NP, with targeted lion poaching contributing to 61% of anthropogenic mortalities. This declining population trend was matched by an increasing demand for lion body parts in the IWT, particularly from 2014 [38], alongside a near five-fold parallel increase in legal exports of lion skeletons from southern Africa to south-east Asia [36,61]. This is likely evidence of expanding trader and consumer markets, with lions increasingly used to supplement previously targeted species, especially tigers (*Panthera tigris*), which have become less accessible due to population declines and improved protection efforts in Asia [35]. Though such informed speculation should not be conflated with interpretation [56]. Such Asian influence in regional lion body part trade is not limited to end-user demand, rather, there is a chain of local exploitation and influence which feeds into syndicated international IWT, that is particularly pronounced in Mozambique [35,38]. Similar trends have been recorded for Niassa SR since 2015 [39]. This largest PA in the country, remains under-resourced resulting in a poor detection of anthropogenic mortalities and is at the projected threshold of unsustainable offtake. Comparably, Limpopo NP has greater detection, though this is likely an artefact of a severely compromised lion population [38] which shows a significant transnational source dependency on Kruger NP to avoid functional extirpation [38]. In an effort to combat wildlife-related crime, Mozambique enacted the Conservation Areas Law (Act Nº7 of 2017), which amends and strengthens provisions from Act 16 of 2014. This new legislation aligns with international conservation standards and imposes more stringent penalties for wildlife crimes, particularly those involving species, like lions, that are listed under the Convention on International Trade in Endangered Species of Wild Fauna and Flora, with prison sentences up to 12 years. However, law enforcement in the field and consistent application of the law in the courts remains problematic [68]. Despite a quarter of the country being formally designated for conservation [69],

only ~16% of the total funding required for effective PA management is available, making Mozambique one of the most under-funded countries for lion conservation [23].

The importance of Mozambique among lion range States in Africa cannot be neglected, and yet these resident populations are under significant pressure, requiring urgent national-scale action. To address these threats, we encourage improved monitoring of lion populations, allowing for greater responsiveness when problems arise and providing a stronger basis for evidence-based quota setting. Additionally, improved detection of anthropogenic mortality, through standardized monitoring systems, would help to generate more accurate data to assess impacts on lion population trends and evaluate the efficacy of current conservation interventions [40,70]. Site security remains an ongoing issue and coordinating anti-poaching operations more effectively may reduce pressure on lion populations locally, while developing integrated inter-agency task forces to coordinate joint patrol operations and review investigations may improve regional security [63]. Tackling bushmeat poaching and IWT requires significant efforts from local and national authorities towards identifying weak points for targeted investigations to disrupt IWT networks [71]. Direct intervention with judiciary systems through sensitization of magistrates is required to ensure a robust understanding of the impact of wildlife crimes, as well as courtroom monitoring to flag inconsistencies in the application of the law [14]. Furthermore, appropriate zonation of PAs is required on a national scale through more accurate delineation, and enforcement of these policies to prevent further inward immigration [27,28]. Trophy hunting represents an important land-use practice in Mozambique [69], funding approximately 30% of the annual operational costs for Niassa SR, along with anti-poaching and management activities, while supporting local communities and government initiatives [72]. While we are cautious in recommending reduced legal offtake quotas, especially given that legal offtake is comparatively well-monitored and detected in Niassa SR [46], compensating for current illegal anthropogenic mortalities in quota setting, even temporarily, may benefit local population recovery [31]. Refining opportunities for alternative modes of wildlife-related investment opportunities in wildlife management areas and mixed-use landscapes, as well as developing tripartite partnerships between government, hunting operators and NGOs can help bridge the gap between revenues from hunting and funds needed for effective management. Mozambique must attract more inward investment into the conservation space, although, this is dependent on ANAC creating a long-term enabling environment for potential investors by developing and adhering to clear policy on public-private partnerships, including simplifying bureaucracy and processes for engaging in the country. The systemically low resource capacity and high threat levels across these large PAs requires a significant upscaling of co-management intensity which will rely on external operational and financial support [23]. However, given the underlying socio-economic fragility of many rural landscapes alongside PAs, it is essential that these actions and funding models be built around the needs and opportunities of impacted communities, such that they become enfranchised stakeholders in lion conservation with clear incentives to coexist.

Supporting information

S1 File. S1 Appendix. Descriptions of lion populations in Mozambique. **S2 Appendix.** Population modelling details. **S1 Table.** Tukey post-hoc test results derived from the multinomial linear regression models. **S2 Table.** Details of estimated detection rates, anthropogenic mortality rates (AMR) and recovery targets for lion populations within Mozambique. Included are current AMRs, trends in AMRs, and targets for AMR reduction needed to promote lion recovery. Effects of interventions on AMRs are also provided to highlight the importance of monitoring and veterinary capacity.
(DOCX)

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References

1. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. Defaunation in the Anthropocene. Science. 2014;345(6195):401–6. https://doi.org/10.1126/science.1251817 PMID: 25061202
2. Ceballos G, Ehrlich PR. Mutilation of the tree of life via mass extinction of animal genera. Proc Natl Acad Sci U S A. 2023;120(39):e2306987120. https://doi.org/10.1073/pnas.2306987120 PMID: 37722053
3. Ripple WJ, Wolf C, Newsome TM, Hoffmann M, Wirsing AJ, McCauley DJ. Extinction risk is most acute for the world's largest and smallest vertebrates. Proc Natl Acad Sci U S A. 2017;114(40):10678–83. https://doi.org/10.1073/pnas.1702078114 PMID: 28923917
4. Searchinger T, Peng L, Zionts J, Waite R. The Global Land Squeeze: Managing the Growing Competition for Land. 2023. https://www.wri.org/research/global-land-squeeze-managing-growing-competition-land
5. Jaureguiberry P, Titeux N, Wiemers M, Bowler DE, Coscieme L, Golden AS, et al. The direct drivers of recent global anthropogenic biodiversity loss. Sci Adv. 2022;8(45):eabm9982. https://doi.org/10.1126/sciadv.abm9982 PMID: 36351024
6. Packer C, Brink H, Kissui BM, Maliti H, Kushnir H, Caro T. Effects of trophy hunting on lion and leopard populations in Tanzania. Conserv Biol. 2011;25(1):142–53. https://doi.org/10.1111/j.1523-1739.2010.01576.x PMID: 20825444
7. Loveridge AJ, Sousa LL, Seymour-Smith J, Hunt J, Coals P, O'Donnell H, et al. Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. Biol Conserv. 2020;244:108504. https://doi.org/10.1016/j.biocon.2020.108504
8. Treves A, Karanth KU. Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv Biol. 2003;17(6):1491–9. https://doi.org/10.1111/j.1523-1739.2003.00059.x
9. Bauer H, Dickman A, Chapron G, Oriol-Cotterill A, Nicholson SK, Sillero-Zubiri C, et al. Threat analysis for more effective lion conservation. Oryx. 2020;56(1):108–15. https://doi.org/10.1017/s0030605320000253
10. Becker MS, Creel S, Sichande M, de Merkle JR, Goodheart B, Mweetwa T, et al. Wire-snare bushmeat poaching and the large African carnivore guild: impacts, knowledge gaps, and field-based mitigation. Biological Conservation. 2024;289:110376. https://doi.org/10.1016/j.biocon.2023.110376
11. Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, et al. Trophic downgrading of planet Earth. Science. 2011;333(6040):301–6. https://doi.org/10.1126/science.1205106 PMID: 21764740
12. Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, et al. Status and ecological effects of the world's largest carnivores. Science. 2014;343(6167):1241484. https://doi.org/10.1126/science.1241484 PMID: 24408439
13. Becker M, McRobb R, Watson F, Droge E, Kanyembo B, Murdoch J, et al. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biol Conserv. 2013;158:26–36. https://doi.org/10.1016/j.biocon.2012.08.017
14. Lindsey PA, Balme G, Becker M, Begg C, Bento C, Bocchino C, et al. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. Biol Conserv. 2013;160:80–96. https://doi.org/10.1016/j.biocon.2012.12.020
15. Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW. Conservation inequality and the charismatic cat: Felis felicis. Global Ecol Conserv. 2015;3:851–66. https://doi.org/10.1016/j.gecco.2015.04.006

16. Lindsey PA, Balme GA, Booth VR, Midlane N. The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. PLoS One. 2012;7(1):e29332. https://doi.org/10.1371/journal.pone.0029332 PMID: 22247772
17. Nicholson SK. The IUCN red list of threatened species. In: IUCN red list of threatened species. 2023. Accessed 2024 August 14. https://www.iucnredlist.org/en
18. Bauer H, Chapron G, Nowell K, Henschel P, Funston P, Hunter LTB, et al. Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. Proc Natl Acad Sci USA. 2015;112(48):14894–9. https://doi.org/10.1073/pnas.1500664112
19. Henschel P, Coad L, Burton C, Chataigner B, Dunn A, MacDonald D, et al. The lion in West Africa is critically endangered. PLoS One. 2014;9(1):e83500. https://doi.org/10.1371/journal.pone.0083500 PMID: 24421889
20. Packer C, Loveridge A, Canney S, Caro T, Garnett ST, Pfeifer M, et al. Conserving large carnivores: dollars and fence. Ecol Lett. 2013;16(5):635–41. https://doi.org/10.1111/ele.12091 PMID: 23461543
21. Loveridge AJ, Sousa LL, Cushman S, Kaszta Ż, Macdonald DW. Where have all the lions gone? Establishing realistic baselines to assess decline and recovery of African lions. Diversity and Distributions. 2022;28(11):2388–402. https://doi.org/10.1111/ddi.13637
22. Selier J, Miller SM, Coverdale B, Ferreira S, Kruger J, Parker DM. Wild lions in small, fenced reserves in South Africa conform to a meta-population. Ecol Sol and Evidence. 2024;5(3). https://doi.org/10.1002/2688-8319.12341
23. Lindsey PA, Miller JRB, Petracca LS, Coad L, Dickman AJ, Fitzgerald KH, et al. More than $1 billion needed annually to secure Africa's protected areas with lions. Proc Natl Acad Sci U S A. 2018;115(45):E10788–96. https://doi.org/10.1073/pnas.1805048115 PMID: 30348785
24. Nicholson SK, Dickman A, Hinks A, Riggio J, Bauer H, Loveridge A, et al. Socio-political and ecological fragility of threatened, free-ranging African lion populations. Commun Earth Environ. 2023;4(1). https://doi.org/10.1038/s43247-023-00959-3
25. Lindsey PA, Petracca LS, Funston PJ, Bauer H, Dickman A, Everatt K, et al. The performance of African protected areas for lions and their prey. Biological Conservation. 2017;209:137–49. https://doi.org/10.1016/j.biocon.2017.01.011
26. IUCN ESARO. The state of protected and conserved areas in Eastern and Southern Africa. 2nd edition. Gland, Switzerland: IUCN; 2024.
27. Hatton J, Couto M, Oglethorpe J. Biodiversity and war: a case study of Mozambique. Washington D.C., USA: Biodiversity Support Program; 2001.
28. Soto B. Protected areas in Mozambique. Evolution and innovation in wildlife conservation: Parks and game ranches to transfrontier conservation areas. Earthscan. 2009. p. 85–100.
29. Everatt KT, Moore JF, Kerley GIH. Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. Global Ecol Conserv. 2019;20:e00758. https://doi.org/10.1016/j.gecco.2019.e00758
30. Bouley P, Poulos M, Branco R, Carter NH. Post-war recovery of the African lion in response to large-scale ecosystem restoration. Biol Conserv. 2018;227:233–42. https://doi.org/10.1016/j.biocon.2018.08.024
31. Briers-Louw WD, Kendon TA, Rogan MS, Naude VN, Leslie AJ, Gaynor D. Anthropogenic pressure limits the recovery of a post-war leopard population in central Mozambique. Conserv Sci Pract. 2024.
32. Roque DV, Macandza VA, Zeller U, Starik N, Göttert T. Historical and current distribution and movement patterns of large herbivores in the Limpopo National Park, Mozambique. Front Ecol Evol. 2022;10. https://doi.org/10.3389/fevo.2022.978397
33. Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, Dickman A, et al. The size of savannah Africa: a lion's (Panthera leo) view. Biodivers Conserv. 2012;22(1):17–35. https://doi.org/10.1007/s10531-012-0381-4
34. Chardonnett P, Mésochina P. Conservation status of the lion (Panthera leo Linnaeus, 1758) in Mozambique. Maputo, Mozambique: DNAC/MITUR & DNTF/MINAG; 2009.
35. Williams VL, Newton DJ, Loveridge AJ, Macdonald DW. Bones of contention: an assessment of the South African trade in African lion (Panthera leo) bones and other body parts. TRAFFIC & WildCRU; 2015.
36. Williams VL, Loveridge AJ, Newton DJ, Macdonald DW. Questionnaire survey of the pan-African trade in lion body parts. PLoS One. 2017;12(10):e0187060. https://doi.org/10.1371/journal.pone.0187060 PMID: 29073202
37. Hübschle AM. The social economy of rhino poaching: Of economic freedom fighters, professional hunters and marginalized local people. Curr Sociol. 2016;65(3):427–47. https://doi.org/10.1177/0011392116673210
38. Everatt KT, Kokes R, Lopez Pereira C. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. Biodivers Conserv. 2019;28(14):4099–114. https://doi.org/10.1007/s10531-019-01866-w
39. Niassa Carnivore Programme. Annual report. 2023. Available at: https://niassalion.org/wp-content/uploads/2024/07/2023-NCP-Annual-Report.pdf
40. Coals P, Dickman A, Hunt J, Grau A, Mandisodza-Chikerema R, Ikanda D, et al. Commercially-driven lion part removal: What is the evidence from mortality records?. Global Ecol Conserv. 2020;24:e01327. https://doi.org/10.1016/j.gecco.2020.e01327
41. Midlane N, Justin O'Riain M, Balme GA, Hunter LTB. To track or to call: comparing methods for estimating population abundance of African lions Panthera leo in Kafue National Park. Biodivers Conserv. 2015;24(6):1311–27. https://doi.org/10.1007/s10531-015-0858-z
42. Cusack JJ, Swanson A, Coulson T, Packer C, Carbone C, Dickman AJ, et al. Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. J Wildl Manage. 2015;79(6):1014–21. https://doi.org/10.1002/jwmg.902 PMID: 26640297
43. Elliot NB, Gopalaswamy AM. Toward accurate and precise estimates of lion density. Conserv Biol. 2017;31(4):934–43. https://doi.org/10.1111/cobi.12878 PMID: 27958641

44. Nicholson SK, Mills DR, Adams EC, Marneweck DG, Bauer H, Roxburgh L, et al. Towards effective and harmonized lion survey methodologies: a systematic review of practice across Africa. Global Ecol Conserv. 2024;51:e02908. https://doi.org/10.1016/j.gecco.2024.e02908
45. Dröge E, Creel S, Becker MS, Loveridge AJ, Sousa LL, Macdonald DW. Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. Ecol Evol. 2020;10(7):3276–92. https://doi.org/10.1002/ece3.6065 PMID: 32273986
46. Begg CM, Miller JRB, Begg KS. Effective implementation of age restrictions increases selectivity of sport hunting of the African lion. J Appl Ecol. 2017;55(1):139–46. https://doi.org/10.1111/1365-2664.12951
47. Nicholson SK, Roxburgh L, Ty. Percieved threats and pressures to lions accross African regions, and resource availibility for their mitigation. 2024.
48. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2022.
49. Venables WN, Ripley BD. Modern applied statistics. Springer; 2002.
50. Fox J, Weisberg S. An R companion to applied regression. Sage Publications; 2011.
51. Fox J, Hong J. Effect displays inrfor multinomial and proportional-odds logit models: extensions to the effects package. J Stat Soft. 2009;32(1). https://doi.org/10.18637/jss.v032.i01
52. Lenth RV. Least-squares means: ther package lsmeans. J Stat Soft. 2016;69(1). https://doi.org/10.18637/jss.v069.i01
53. Loveridge AJ, Wijers M, Mandisodza-Chikerema R, Macdonald DW, Chapron G. Anthropogenic edge effects and aging errors by hunters can affect the sustainability of lion trophy hunting. Sci Rep. 2023;13(1):95. https://doi.org/10.1038/s41598-022-25020-9 PMID: 36635294
54. Loveridge A, Canney S. African lion distribution modelling project: final report. Horsham, UK: Born Free Foundation; 2009.
55. Loveridge AJ, Valeix M, Elliot NB, Macdonald DW. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. J Appl Ecol. 2016;54(3):815–25. https://doi.org/10.1111/1365-2664.12794
56. Arias M, Coals P, Ardiantiono, Elves-Powell J, Rizzolo JB, Ghoddousi A, et al. Reflecting on the role of human-felid conflict and local use in big cat trade. Conservat Sci and Prac. 2024;6(1). https://doi.org/10.1111/csp2.13030
57. Pringle RM. Upgrading protected areas to conserve wild biodiversity. Nature. 2017;546(7656):91–9. https://doi.org/10.1038/nature22902 PMID: 28569807
58. Huntley BJ. Gorongosa National Park: wilderness, war and wildlife recovery. SpringerBriefs in Environmental Science. Springer Nature Switzerland; 2023. p. 39–51. https://doi.org/10.1007/978-3-031-24880-1_5
59. O'Kelly HJ, Rowcliffe JM, Durant SM, Milner-Gulland EJ. Robust estimation of snare prevalence within a tropical forest context using N-mixture models. Biol Conserv. 2018;217:75–82. https://doi.org/10.1016/j.biocon.2017.10.007
60. Liberg O, Chapron G, Wabakken P, Pedersen HC, Hobbs NT, Sand H. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc Biol Sci. 2012;279(1730):910–5. https://doi.org/10.1098/rspb.2011.1275 PMID: 21849323
61. Williams VL, Coals PG, de Bruyn M, Naude VN, Dalton DL, Kotzé A. Monitoring compliance of CITES lion bone exports from South Africa. PLoS One. 2021;16(4):e0249306. https://doi.org/10.1371/journal.pone.0249306 PMID: 33798210
62. Kendon TA, Comley J, Wilkinson A, Grobler MJ, Nieman WA, Leslie AJ, et al. Evaluating determinants of wire-snare poaching risk in the Boland Mountain Complex of South Africa. J Nature Conserv. 2022;70:126295. https://doi.org/10.1016/j.jnc.2022.126295
63. Rogan MS, Lindsey PA, Tambling CJ, Golabek KA, Chase MJ, Collins K, et al. Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. Biol Conserv. 2017;210:233–42. https://doi.org/10.1016/j.biocon.2017.04.020
64. Stalmans ME, Massad TJ, Peel MJS, Tarnita CE, Pringle RM. War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. PLoS One. 2019;14(3):e0212864. https://doi.org/10.1371/journal.pone.0212864 PMID: 30865663
65. Beilfuss RD, Dutton P, Moore D. Status and distribution of large herbivores in the Marromeu complex of the Zambezi Delta, Mozambique. Maputo, Mozambique: WWF; 2010. https://www.anac.gov.mz/wp-content/uploads/2017/07/Aerial-Survey-Report-Marromeu-2010-Beilfuss-et-al-2.pdf
66. Allen J, Grossmann F. Patterns of forest loss in one of Africa's last remaining wilderness areas: niassa national reserve (northern Mozambique). Parks. 2017;23:39–50.
67. Trouwborst A, Lewis M, Burnham D, Dickman A, Hinks A, Hodgetts T, et al. International law and lions (Panthera leo): understanding and improving the contribution of wildlife treaties to the conservation and sustainable use of an iconic carnivore. Nat Conserv. 2017;21:83–128. https://doi.org/10.3897/natureconservation.21.13690
68. Massé F. Police power in green: furthering political ecologies of the state. Polit Geo. 2022;97:102627. https://doi.org/10.1016/j.polgeo.2022.102627
69. Booth VR. Contribution of tourism hunting to the economy in Mozambique. Maputo, Mozambique. 2012.
70. Gavin MC, Solomon JN, Blank SG. Measuring and monitoring illegal use of natural resources. Conserv Biol. 2010;24(1):89–100. https://doi.org/10.1111/j.1523-1739.2009.01387.x PMID: 20015259
71. Gore ML, Griffin E, Dilkina B, Ferber A, Griffis SE, Keskin BB, et al. Advancing interdisciplinary science for disrupting wildlife trafficking networks. Proc Natl Acad Sci U S A. 2023;120(10):e2208268120. https://doi.org/10.1073/pnas.2208268120 PMID: 36848572
72. Jorge AA, Vanak AT, Thaker M, Begg C, Slotow R. Costs and benefits of the presence of leopards to the sport-hunting industry and local communities in Niassa National Reserve, Mozambique. Conserv Biol. 2013;27(4):832–43. https://doi.org/10.1111/cobi.12082 PMID: 23772986