POPULATION ASSESSMENT AND CONSERVATION STATUS OF AFRICAN LIONS (*Panthera leo)*

by

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Submitted in fulfilment of the academic requirements for the degree

Doctor of Philosophy

in the

School of Life Sciences

University of KwaZulu-Natal,

Pietermaritzburg, South Africa

January 2024

ABSTRACT

For several decades, the lion (*Panthera leo*) has undergone significant population decline across its range. The aim of this dissertation was to critically assess the current conservation status of Africa's most iconic carnivore. This included determining methods used to survey them, the conservation status of the global population, how fragile lion subpopulations are, and the perceived threats to the species across their African range.

As with most carnivores, several survey methods have been developed to estimate lion population abundance. To assess the current state of lion survey methodologies, I conducted a systematic literature review of peer reviewed scientific publications. The strengths and weaknesses of each method were considered, as well as their reliability and applicability in determining abundance and distribution. Building on from how lions are surveyed, I used current data that are available to assess the current population and distribution of lions to produce the updated IUCN Red List Assessment (RLA). RLAs provide a standardised and comprehensive tool to evaluate the status of species, prioritise conservation efforts, and drive informed decision-making at the global, national, and local levels. Extant lion range was estimated to be ~1,571,296 km² - an estimated 36 % range decline since 2002 (three lion generations). Based on this significant decline in range, which is synonymous with a decline in population size and abundance, a 36 % decline in population numbers for the lions was suspected. Therefore, the species met the requirements for a Vulnerable listing (Red List criteria A2abcd). As effective species conservation is about more than just understanding how many there are, I, in collaboration with other experts in large carnivore conservation, examined the socio-political and ecological fragility (hereafter fragility: defined as a species vulnerability to extinction) of known lion populations. By combining ecological and socio-political metrics, an overall fragility index demonstrated which lion populations were more vulnerable to extinction. The analysis revealed several populations were highly fragile and lion populations in Somalia were the most fragile while those in Botswana are the least. Populations that had the highest fragility included Bush-Bush (Somalia) and Maze National Park (Ethiopia). As the RLA indicated that populations are declining, I sought to determine the severity of the existing anthropogenic threats to lions driving these declines. To do this, I conducted an online questionnaire of experts across lion range. A threat severity index was developed for each subpopulation, and I assessed how this varied between subpopulations and across regions. A resource availability index was also developed to identify lion subpopulations which are not sufficiently resourced (e.g., funding, anti-poaching equipment, vehicles). This allowed me to highlight populations that are perceived as highly threatened and that are under-equipped. I found the total threat index differed significantly among regions, being highest (i.e. most severe) in Central

Africa and lowest (i.e. least severe) in southern Africa. Perceived resource availability was highest in Rwanda, Chad and Benin and lowest in six countries including Angola, Burkina Faso, Niger, South Sudan, Sudan and Uganda. This analysis identified how specific threats differ between regions.

I offer valuable insights into the species' status and provide innovative recommendations that could enhance the management of lions across their range. This includes conservation interventions that target specific threats while incorporating socio-political and ecological factors which contribute to a population's fragility. As lions remain listed as Vulnerable, and lion populations continue to decline, I recommend that the regional strategies be updated based on improved data and information available. To ensure that population data gathered and reliable and robust, harmonised survey methods need to be developed and implemented across the species range, especially in areas where survey data are poor or lacking. In a world where we are losing species at an unprecedented rate, effective and targeted conservation is needed, that is guided by the best available data, to ensure that the lion isn't one of those species that disappears.

PREFACE

The work described in this thesis was carried out by the author between June 2021 and December 2023, through the School of Life Sciences, University of KwaZulu-Natal, Westville campus, under the supervision of Professor Rob Slotow (University of KwaZulu-Natal), Dr Hans Bauer (Oxford University) and Dr Lizanne Roxburgh (Endangered Wildlife Trust).

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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8 January 2024

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I, Samantha Nicholson, declare that:

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Declaration 2 – publications

Publication 1: (Chapter 2 – Towards effective and harmonised lion survey methodologies: a systematic review of practice across Africa)

Published in April 2024 in the Journal of Global Ecology and Conservation (Impact factor 3.97)

Samantha K. Nicholson, David R. Mills, Erin C. Adams, David G. Marneweck, Hans Bauer, Lizanne Roxburgh & Rob Slotow

Author contributions:

SN and RS conceptualised the study. SN, EA and DM collected and analysed the data. Samantha Nicholson wrote the draft manuscript. The other authors provided editorial input.

Publication 2: (Chapter 3 – Global Lion, *Panthera* leo, Red List Assessment)

The Red List Assessment was published in December 2023.

Assessor(s):
Nicholson, S., Bauer, H., Strampelli, P., Sogbohossou, E., Ikanda, D., Tumenta, P.F., Venktraman, M., Chapron, G. & Loveridge, A.

Author contributions:

SN and HB led the assessment. GC completed the Bayesian Analysis. The other authors provided editorial input, provided data and applied the IUCN Red List Criteria.

Publication 3: (Chapter 4: Socio-political and ecological fragility of threatened, free-ranging African lion populations)

Published in August 2023 in Nature: Communications Earth and Environment (Impactor 7.9).

Samantha K. Nicholson, Amy Dickman, Amy Hinks, Jason Riggio, Hans Bauer, Andrew Loveridge, Matthew Becker, Colleen Begg, Shivani Bhalla, Dawn Burnham, Alayne Cotterill, Stephanie Dolrenry, Egil Dröge, Paul Funston, Leela Hazzah, Dennis Ikanda, Fikirte Gebresenbet, Philipp Henschel, Roseline L. Mandisodza-Chikerema, Moreangels Mbizah, Luke Hunter, Kim Jacobsen, Peter Lindsey, Nakedi Maputla, Ewan Macdonald, David W. Macdonald, Resson Kantai Duff, Craig Packer, Claudio Sillero-Zubiri, Tutilo Mudumba, Paolo Strampelli, Etotépé A. Sogbohossou, Peter Tyrrell, Andrew P. Jacobson

(2023). Socio-political and ecological fragility of threatened, free-ranging African lion populations. *Communications Earth Environment,* 4, 302 (2023). https://doi.org/10.1038/s43247-023-00959-3

Author contributions:

SN and AD contributed equally to the work and are joint lead co-authors. AD and AJ jointly supervised the work. AD, AH, DB, EM and DM conceived the study and wrote the early drafts. All authors were involved in study design and contributed data for use in the study. SN, AD, AH, HB, JR, and AJ compiled the datasets. SN, AD, AH and JR carried out data preprocessing. AL ran the carrying capacity results required for the study analysis. SN, AD, and AJ analysed the data. SN prepared figures, maps and tables. SN, AJ and AD led the writing of the final manuscript. All authors contributed to writing, reviewing, and editing the manuscript. SN and AD contributed equally. AD and AJ jointly supervised the work.

Publication 4: (Chapter 5 - Perceived threats and pressures to lions across African regions, and resource availability for their mitigation)

Samantha K. Nicholson, Lizanne Roxburgh, Tyson Asfaw, Erin C. Adams, Hans Bauer & Rob Slotow

Author contributions:

SN, LR and RS conceptualised the study. SN and EA completed the geographical analysis. The other authors provided editorial input. LR, HB and RS supervised the work.

[redacted]

Samantha Nicholson

8 January 2024

ACKNOWLEDGEMENTS

My PhD journey has been strongly guided by my supervisors, to whom I am indebted and owe sincere gratitude. Dr Rob Slotow, thank you for your invaluable advice and guidance. Through this process, you have helped me to "think bigger" and ask the questions that really helped to apply my work to the bigger conservation picture. You have helped me grow as a scientist and I am grateful for that. Dr Hans Bauer, from the day I first embarked on the journey as manager of the IUCN SSC Cat Specialist Group's African Lion Database and stepped into the world of lion conservation, you have provided me with the foundation and knowledge to succeed. You have been, and continue to be, a mentor, thank you for taking up this role. I look forward to continuing to learn from you. Lastly, Dr Lizanne Roxburgh, not only have you been my manager at the Endangered Wildlife Trust for the last nine years, but you have been a fundamental part of my PhD journey. You have continued to provide endless support, guidance, encouragement and help whenever it was needed.

My first significant career chapter has been at the Endangered Wildlife Trust (EWT). I am grateful to the individuals within the organisation for helping to shape the formative years of my career and allowing me to pursue my passion for carnivore conservation, no matter which team I sat it. Special thanks must go to the following people, who guided me and helped me grow as a carnivore scientist during my time at EWT: Dr Lizanne Roxburgh, Dr Harriet Davies-Mostert, Dr Kelly Marnewick, Dr David Mills, Constant Hoogstad, Lourens Leeuwner, Dr David Marneweck, Derek van der Merwe, Marnus Roodbol and both the Conservation Planning and Science Unit and the Carnivore Conservation Programme teams.

Thank you to the incredible researchers, organisations and people along the way that I have met and have worked with for the last few years, there are certainly too many to name but some of which are co-authors on chapters within this PhD.

I could not have gotten through this PhD journey without my village. Taking on a PhD, on top of a full-time job and being a new mom was not easy and at times, it felt like an insurmountable amount of pressure that would never ease and workload that would never get lighter. But with the unwavering support, love and strength from my family and friends, I made it to the light at the end of the tunnel and am able to proudly hand in this PhD. A special thank you to my close friends and my brother and sister-in-law (Craig and Ashleigh Page), who were always there to offer support, love and encouragement. Oftentimes they kept me sane and reminded me to have fun, and were often checking in. To my parents, Jacklin and Gary Page, a special thank you for all the endless support and love, not just with my PhD, but with absolutely everything. I am grateful for it all. To my husband, my co-captain and pillar of strength, there are no words that I could put on this page that would truly capture how grateful I am for you. Your love, your support, your endless strength and your encouragement pushed me further than I thought possible - and I could not have done this without you. To Kaylan Grace, you have brought more joy and love into our lives than I could have imagined, and your presence motivated me to keep going and not to give up.

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LIST OF ABBREVIATIONS

AI	Artificial Intelligence
ALD	African Lion Database
APNR	Associated Private Nature Reserves
Cat SG	Cat Specialist Group
CBD	Convention on Biological Diversity
CITES	Convention on International Trade in Endangered Species of Wild Fauna & Flora
CMS	Convention on the Conservation of Migratory Species of Wild Animals
CR	Critically Endangered
DRC	Democratic Republic of the Congo
United Nations DESA	United Nations Department of Economic and Social Affairs
EOO	Extent of occurrence
FLIR	forward looking infrared (FLIR) thermal monocular spotlights
GADM	Global Administrative Areas database
GCLA	Guidelines for the Conservation of Lions in Africa
GDP	Gross Domestic Production
GR	Game Reserve
GTI	Global Threat Index
HDI	Human Development Index
IUCN	International Union for Conservation of Nature
IUCN SSC	IUCN Species Survival Commission
LTI	Local Threat Index
NBSAP	National Biodiversity Strategies and Action Plans
NP	National Park
PA	Protected Area
PCR	Polymerase chain reaction
PNR	Private Nature Reserve
PPP	Purchasing Power Parity
Prisma	Preferred Reporting Items for Systematic Reviews and Meta-Analyses
SADC	Southern African Development Community
SD	Standard deviation
SECR	Spatially Explicit Capture-Recapture
REM	Random Encounter Models

SMR	Spatial Mark Resight
TFCA	Transfrontier Conservation Area
TTI	Total Threat Index
USD	United States Dollar
USFWS	United States Fish and Wildlife Service
USFWS ESA	USFWS Endangered Species Act
VU	Vulnerable
WDPA	World Database on Protected Areas
WMA	Wildlife Management Area
WoS	Web of Science

CHAPTER 1

General Introduction

1.1 The importance of large carnivores

Large carnivores occur naturally at low densities, have large spatial requirements, and experience high levels of conflict with humans, resulting in them being among the taxa that are the most threatened with extinction (Obbard *et al.,* 2010; Ripple *et al.,* 2014; Wolf & Ripple, 2017). These traits increase their risk to local level extirpations and population declines resulting from anthropogenic pressures (Fernández-Sepúlveda & Martín, 2022; Wolf & Ripple, 2017). Large carnivores play critical ecosystem roles, and their presence has a cascading impact on various ecological processes, such as trophic cascades (Carter *et al.,* 2007; Ripple *et al.,* 2010). A well-documented example of a trophic cascade is of wolves (*Canis lupus*) in Yellowstone National Park following their reintroduction in the 1990's (Miller *et al.,* 2012; Ripple *et al.,* 2001, 2010). Essentially, by preying on elk (*Cervus canadensis*), wolves altered their behaviour, allowing vegetation to regenerate, which benefited riparian ecosystems, revived beavers (*Castor canadensis*), diversified habitats, attracted songbirds, and enhanced aquatic biodiversity (Miller *et al.,* 2012; Ripple *et al.,* 2001). Wolves, as apex predators, played a pivotal role in rebalancing and enriching Yellowstone's ecosystem (Miller *et al.,* 2012; Ripple *et al.,* 2001). Another example is that of sea otters (*Enhydra lutris*) in coastal ecosystems where they prey on sea urchins, preventing overgrazing of kelp forests and promoting biodiversity, including increasing fish populations (Miller *et al.,* 2022). Another vital role of large carnivores is through maintaining an ecological balance in systems by regulating mesopredator populations, preventing their unchecked dominance and unnatural pressures on the lower levels of the food chain (Kamler *et al.,* 2020; Welch *et al.,* 2022). For example, mesopredator release occurs when apex predators (such as lions, *Panthera leo*) decline or are completely absent and this can disrupt ecosystems, by increasing mesopredator (such as black-backed jackal, *Lupulella mesomelas*) numbers leading to imbalances in prey populations (Kamler *et al.,* 2020; Prugh *et al.,* 2009).

The benefits of large carnivores are far reaching and have numerous instrumental benefits which are those that generally have monetary measure (van de Water *et al.,* 2022). Large carnivores have high economic value and are one of the major drawcards for tourists (di Minin *et al.,* 2013; Kellert *et al.,* 1996; van der Meer *et al.,* 2016). In the Zimbabwe component of the Kavango Zambezi Transfrontier Conservation Area, for example, lions and leopards (*Panthera pardus*) were the most well-liked by tourists and held the most potential to be utilised as a flagship species to raise funds and promote areas to attract tourists (van der Meer *et al.,* 2016). Another financial value from large carnivores, is that they are widely sought after for trophy hunts which generates income, not only to hunting operators and concessions, but to local communities and protected areas (Brink *et al.,* 2016; Dickman *et al.,* 2019; Whitman *et al.,* 2004). However, it should be noted that if not managed correctly, negative impacts on local carnivore populations will be evident (Becker *et al.,* 2013; Groom *et al.,* 2014; Packer & Whitman, 2006). Beyond ecological and instrumental value, large carnivores have deep rooted value from an intrinsic, existence, spiritual, cultural perspective (Coals *et al.,* 2022; Macdonald *et al.,* 2015; Mech, 1996; Ripple *et al.,* 2014; van der Meer *et al.,* 2016). Carnivores, including lions, have been found to have significant cultural importance in traditional medicinal and cultural practices (Coals *et al.,* 2022). Large carnivores have high existence value, spiritual significance, and cultural importance which are dimensions of a species broader value that extend beyond the tangible and measurable (van de Water *et al.,* 2022). From snow leopards, *Panthera uncia*, in Kazakhstan where they are an ever-present political, economic, cultural symbol (White, 2020), to lions, in Africa where they are a cultural symbol of power in Kenya and Benin (Tumenta, 2012) and to Bengal tigers (*Panthera tigris*) in India where they have cultural and spiritual value as they are perceived to be the animal transport of the Goddess Durga (Reddy & Yosef, 2016).

Despite their ecological, cultural and spiritual importance, carnivores have suffered one of the most significant declines of all species groups (Wolf & Ripple, 2017). Intact carnivore guilds once occupied 96 % of the world's terrestrial area and this has declined to just 34 % (Wolf & Ripple, 2017). This decline is largely because of a loss of natural habitat, leading to unnatural range contractions (Wolf & Ripple, 2017), decline in natural prey base (Wolf & Ripple, 2016), conflict with humans (Holland *et al.,* 2018; Seoraj-Pillai & Pillay, 2017) and poaching (Montgomery, 2020). Carnivores are more threatened than other mammals and have a significantly higher proportion of species that have declining populations (Fernández-Sepúlveda & Martín, 2022). In the period between the 1990s and 2000s, a substantial reduction in Red List Index value was observed among numerous carnivore families, with Felidae suffering the greatest decline (Fernández-Sepúlveda & Martín, 2022). While Felidae is the second largest carnivore family, it is one of the most threatened with 76.3 % of species in decline and 47 % being listed as either Endangered or Vulnerable (Fernández-Sepúlveda & Martín, 2022). The decline across carnivore species globally has not occurred uniformly (Fernández-Sepúlveda & Martín, 2022), with some populations recovering such as in the global North (Chapron *et al.,* 2014; Fernández-Sepúlveda & Martín, 2022; Ripple *et al.,* 2001; Wolf & Ripple, 2017). There are many species of large carnivores in Europe, for example, that are mostly stable or increasing as is the case with brown bears (*Ursus arctos*), gray wolves and wolverines (*Gulo gulo*) (Chapron *et al.,* 2019).

1.2 Lion status through the years and challenges with determining abundance

The lion in Africa is one of the world's most iconic and charismatic species (Macdonald *et al.,* 2015) yet has undergone one of the largest range declines of all (Figure 1-1; Loveridge *et al.,* 2022; Wolf & Ripple, 2017). Outside sub-Saharan Africa, lions formerly ranged across North Africa through Southwest Asia (where they disappeared from most countries within the last two centuries), west into Europe (where the species became extinct approximately 2,000 years ago), and east into India (Nowell & Jackson, 1996). Today, the only lions found outside of Africa occur in a single isolated subpopulation in the Gir Forest National Park and surrounding landscape, in north-western India (Nicholson *et al.,* 2023a). Historically, lion range was estimated to be 21,257,422 km^2 (IUCN, 2006b, 2006a) and presently, lions only occur in only 6 % of that range. In the last three lion generations alone (~21 years, 2002 to 2023), lion range has declined by 36 %, leading the species to be listed as Vulnerable on the IUCN Red List (Nicholson *et al.,* 2023a).

A critical question for conservation management is understanding the status and trends in species distribution and abundance. However, this is not always straightforward, and results may be unreliable and often imprecise (Creel *et al.,* 2016; Elliot & Gopalaswamy, 2017). Although lions are one of the most charismatic felid species on the continent, robust population estimates are lacking across much of their range (Elliot & Gopalaswamy, 2017), even though multiple survey methods exist (Braczkowski, Gopalaswamy, Elliot *et al.,* 2020). Most lion population surveys, for example, have extensive caveats, significant uncertainty, and have largely been based on differing methodologies at a population and continental level (Bauer *et al.,* 2018; Dröge *et al.,* 2020; Riggio *et al.,* 2013). To survey lions, various methods are used to determine population abundance, including direct observations that use individual identification with capture-recapture (Beukes *et al.,* 2017; Rosenblatt *et al.,* 2014) or without capture-recapture (Bouley *et al.,* 2018; Kissui & Packer, 2004), genetic-based surveys (Tende *et al.,* 2010), spoor counts (also called spoor transects or track counts (Bauer *et al.,* 2014; Henschel *et al.,* 2010; Stander, 1998), call-up surveys (Mohammed *et al.,* 2019; Ogutu & Dublin, 2002), and camera trap studies with capture-recapture analysis (Elliot & Gopalaswamy, 2017; Kane *et al.,* 2015; Strampelli *et al.,* 2022; Western *et al.,* 2022). Despite the widespread use of many of these methods, there has historically been some disagreement regarding the appropriate choice, implementation, and interpretation of these survey methods (Dröge *et al.,* 2020; Braczkowski *et al.,* 2020; Elliot *et al.,* 2020). Reliable assessments of population status are critical to guide management and policy makers and will ultimately influence the success of conservation of lions (Elliot & Gopalaswamy, 2017; Braczkowski *et al.,* 2020). Without them, conservation decision- making, and the implementation of adaptive management frameworks are hindered (Braczkowski *et al.,* 2020).

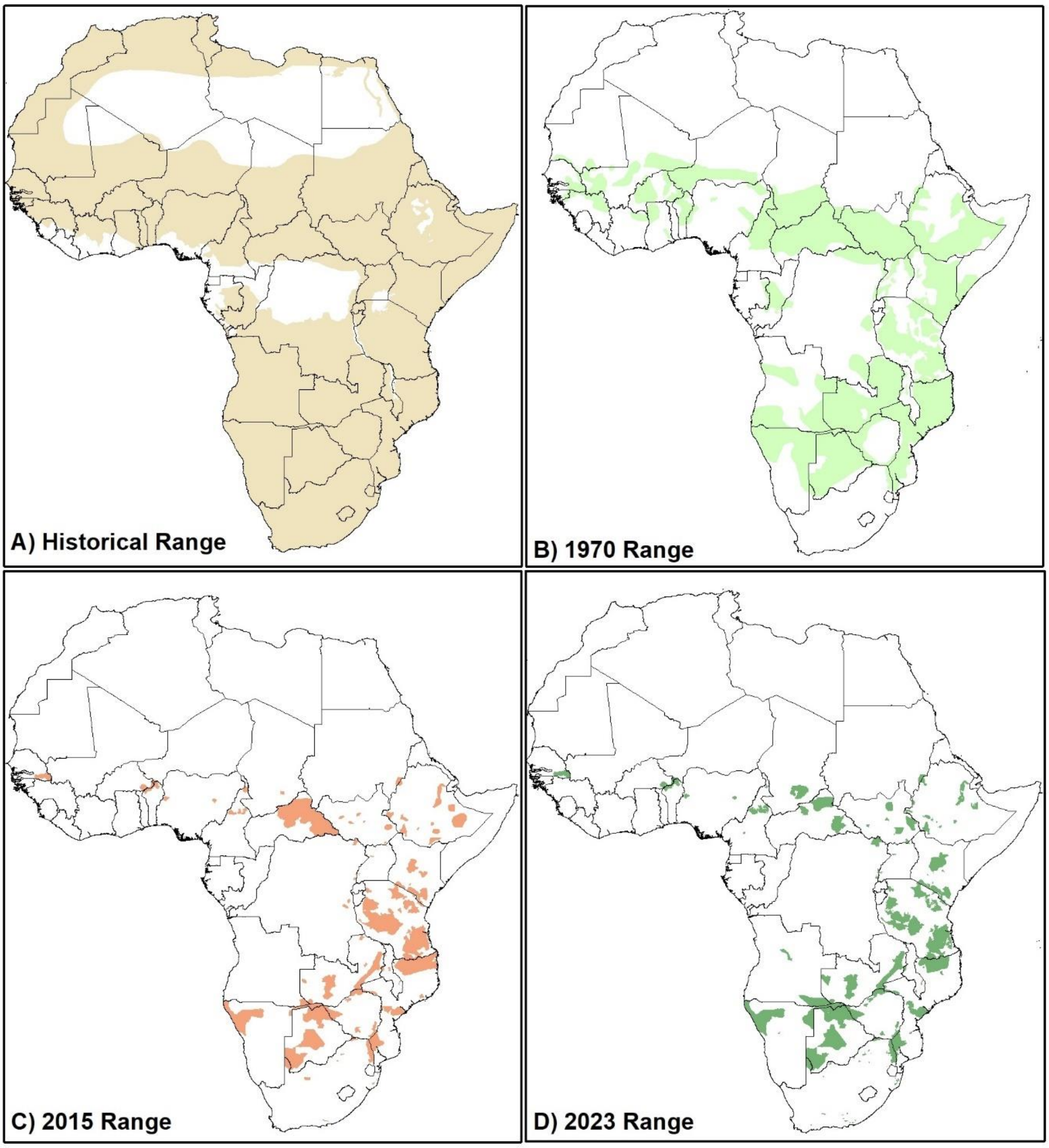

Figure 1-1. The distribution range of the lion (*Panthera leo*) in Africa has changed significantly over time, with a 36 % loss of range over the last 21 years. Historical range (Nowell & Bauer, 2004), range for c1970 (Loveridge *et al.,* 2022), 2015 (Bauer *et al.,* 2016) and 2023 (Nicholson *et al.,* 2023a) are shown.

Throughout the past three decades, multiple assessments have estimated the number of remaining lions in Africa with great variability. In 1996, educated guesses estimated between 30,000 and 100,000 free-roaming lions in Africa (Nowell *et al.,* 2006; Nowell & Jackson, 1996). In 2002, the population was estimated to have been ~37,945 individuals (Chardonnet, 2002), while in 2004, a conservative estimate was between 16,500 and 30,000 (Bauer & van der Merwe, 2004) and in 2006, ~33,160 lions were estimated (IUCN, 2006b, 2006a). In 2013, estimates for free-roaming lions in Africa were estimated at 32,000 (Riggio *et al.,* 2013). The recent Red List assessment estimates between 20,000 and 25,000 lions remaining (Bauer *et al.,* 2018; Nicholson *et al.,* 2023a). Regardless of survey related challenges (Belant *et al.,* 2019; Dröge *et al.,* 2020; Elliot & Gopalaswamy, 2017), there is a broad consensus that wildlife numbers in Africa are declining, which includes both lions and their prey (Bauer *et al.,* 2015).

1.3 Threats to lions and the causes of declines

Most instances of local lion population extinctions before the 20th century can be attributed to the combined effects of an expanding global human population (Wolf & Ripple, 2017), heightened pressure on natural resources, increased availability of hunting tools, and subsequent declines in prey populations, human-wildlife conflict and the degradation of natural habitats (Bauer *et al.,* 2020). Lion populations are suspected to have endured the longest outside of sub-Saharan Africa in more secluded regions characterised by lower human population densities and slower technological progress (Black *et al.,* 2013; Nowell & Jackson, 1996). In Morocco, lions might have survived until the 1960s in the High Atlas Mountains, despite the last confirmed visual sighting dating back to 1925 (Black *et al.,* 2013). Similarly, remote populations may have persisted into the 1960s in small and remote areas of Iraq, Pakistan, and Iran (Nowell & Jackson, 1996).

One of the most significant threats to lions is loss and conversion of natural habitat, which is driven by expanding human activities such as agriculture, urbanisation, and infrastructure development (Bauer *et al.,* 2020; Geldmann *et al.,* 2013; Riggio *et al.,* 2013). The loss of natural prey threatens many carnivores globally, especially lions (Wolf & Ripple, 2016). The "bushmeat poaching crisis" is a significant and increasing local threat to wildlife in Africa, particularly snaring (Loveridge *et al.,* 2020; Mudumba *et al.,* 2021). Snares are typically targeted at species suitable for bushmeat, but as they are indiscriminate, many species are caught as by-catch, including carnivores (Becker *et al.,* 2013; Loveridge *et al.,* 2020; Montgomery, 2020; Montgomery *et al.,* 2023; Mudumba *et al.,* 2021). The motivational drivers fuelling this crisis range from small-scale subsistence poaching for bushmeat (Luiselli *et al.,* 2019; Martins & Shackleton, 2019), to local sale in markets for financial incentives, traditional medicine (Manqele *et al.,* 2018; Williams *et al.,* 2017) and international trade (Everatt *et al.,* 2019). Lions are frequently caught as by-catch in snares and this has been recognised to negatively impact populations either by limiting population growth or causing local population declines (Mudumba *et al.,* 2021). For example, snaring has been considered as the leading cause of mortality of lions in Murchison Falls National Park in Uganda (Montgomery *et al.,* 2023). Modelling exercises have demonstrated that the removal of snaring pressure from Murchison would potentially allow the lion population to double within 18 years and, if poaching pressures were eased by half, the population would increase by 40 % (Montgomery *et al.,* 2023).

Like other carnivores, lions experience high levels of human-wildlife conflict where they are killed, either pre-emptively or through retaliation, to protect livestock or human life (Beck *et al.,* 2019; di Minin *et al.,* 2021; Gueye *et al.,* 2022). In some systems, retaliatory killings are the leading anthropogenic cause of mortality, such as in Limpopo National Park (Mozambique) where these killings made up 51 % of recorded mortalities (Everatt *et al.,* 2019). In other areas, local extinctions have been attributed to unsustainably high levels of retaliatory killings. This includes Swaga Swaga in Tanzania (Ikanda, D., pers comm. 2022) and Akagera National Park in Rwanda (African Parks. 2023). While the targeted poaching of lions for parts has not been observed in some parts of Africa, such as Hwange National Park and the Ruaha landscape in Tanzania (Coals *et al.,* 2020), it has contributed to the decline of local populations in other areas such as Limpopo National Park (Everatt *et al.,* 2019). A study by Everatt *et al.,* (2019), revealed that 35 % of lion mortalities were because of targeted poaching of lions for their parts across the Greater Limpopo Lion Conservation Unit and for 61 % of mortalities in Limpopo National Park itself.

Key pressures or enabling environments that can also threaten lion populations include a lack of funding (Lindsey *et al.,* 2018) or local war or violent extremism (Gaynor *et al.,* 2016; Lhoest *et al.,* 2022). Wildlife areas require significant financial support, and without it, fundamental operations and management implementation is limited (Bauer *et al.,* 2020; Lindsey *et al.,* 2017; Robson *et al.,* 2022). Insufficient funds increase an area's risk or likelihood of increased anthropogenic threats that could have been reduced with mitigation and the proper resources (Lindsey *et al.,* 2021). Forms of civil unrest, local war or violent extremism can have both direct and indirect impacts on a species and its conservation (Bouley *et al.,* 2018; Gaynor *et al.,* 2016; Lhoest *et al.,* 2022). In addition, they generate unique insecurity, and lawlessness can increase the severity and intensity of existing threats (Lhoest *et al.,* 2022). This type of environment has led to the local extinctions of lions and other wildlife species in Comoé National Park, Côte d'Ivoire, (Aglissi *et al.,* 2023), and historic population declines in Gorongosa National Park, Mozambique (Bouley *et al.,* 2018). The W-Arly-Pendjari complex (33,000 km^2, Benin, Niger and Burkina Faso) has the largest remaining number of Critically Endangered West African lion (*Panthera leo leo*) according to the most recent Regional IUCN Red List assessment (Henschel *et al.,* 2010, 2014; IUCN, 2006a). In 2022, 62 % of the complex was estimated to be under the control of violent extremist groups (Lhoest *et al.,* 2022). This threatens the persistence of lions and other wildlife through poaching, wildlife trafficking, and the prevention of effective conservation management of the area (Lhoest *et al.,* 2022).

1.4 Why understanding the status of lions and their threats is important to their conservation

To conserve species effectively, understanding their conservation status and threats to them is essential (Bauer *et al.,* 2020). Firstly, accurate and reliable knowledge regarding their abundance, including trends, and their conservation status is fundamental for developing and implementing targeted conservation strategies (Bauer *et al.,* 2020; IUCN, 2006b, 2006a). Conservation efforts and conservation projects need to be carefully tailored to specific challenges and threats faced by lion populations. Challenges and threats, both in severity and across socio-political and ecological landscapes, vary widely across regions (Kuiper *et al.,* 2018; Nicholson *et al.,* 2023b). Understanding the severity of threats and pressures on subpopulations allows for the prioritisation of effective and appropriate interventions that will yield impact. By identifying and understanding these threats and the drivers behind them, strategies and action plans can be developed that address the root causes and provide meaningful conservation of populations (Hazzah *et al.,* 2014; Janss & Ferrer, 2012; Sibanda *et al.,* 2021). For instance, the leopard population in Phinda Private Game Reserve (South Africa) was under pressure from high rates of persecution by farmers and trophy hunting. This resulted in high mortality rates for the species (Balme *et al.,* 2009), and a declining population. Targeted conservation work to address these specific threats, namely educating farmers on methods for reducing livestock losses, along with implementing stricter hunting policies, resulted in a decrease in the number of mortalities because of persecution and an increase in leopard density (Balme *et al.,* 2009). In the Amboseli Ecosystem, human-lion conflict was identified as one of the most significant threats to lions (Hazzah *et al.,* 2009, 2014). Lion killings were reduced by 87–91 % following the implementation of targeted conservation projects including compensation for livestock losses (Hazzah *et al.,* 2014). These killings were reduced by 99 % when compensation was combined with employing lion guardians (Hazzah *et al.,* 2014).

Understanding both the threats and conservation status of populations assists with efficient resource allocation for effective management required to effectively protect a given population. Resources for species conservation and protected area management are known to be unequally distributed and this poses challenges to conservation efforts (Lindsey *et al.,* 2017, 2018). Directing limited funds and resources to dealing with threats that are prioritised based on their severity ensures that interventions are implemented where they are most needed. This strategic allocation enhances the likelihood of success in mitigating threats and preserving lion populations.

A clear understanding of the status of lions and the threats to them, enables the formulation of evidence-based policies that contribute to their long-term survival. Policy-makers and international conventions (e.g. IUCN, CITES and CMS) regularly rely on information to establish regulations and guidelines for the conservation and management of wildlife species (Bauer *et al.,* 2018a; Hellinx, 2020). Trade in species that are threatened with extinction is more strictly regulated and are generally listed as “Appendix I” under CITES (Bauer *et al.,* 2018a) and these listings are based on available information in status assessments. Lions, for example, were historically not assessed, but as they faced substantial declines, they were uplisted to Vulnerable on the IUCN Red List in 1996. In response to this change, lions were added to the CITES Appendix II listing meaning that some regulation was required around their trade. The inclusion in CITES Appendix II emphasised the importance of enhanced monitoring and management of lion populations to address the range of threats (Bauer *et al.,* 2018a). Thus, scientifically sound knowledge forms the foundation for informed, evidence-based conservation practices (Walsh *et al.,* 2014) that can make a significant impact on the survival of these iconic and ecologically important species (Bauer *et al.,* 2020; Walsh *et al.,* 2014).

1.5 Thesis outline and broad methodology

The broad aim of this thesis was to critically assess the conservation status of Africa’s most iconic carnivore, the lion. This included determining the conservation status of the global population, how fragile these populations are, methods on how these populations are monitored, and the perceived threats to lions across their African range. Chapters two to five have been written as independent peer-reviewed scientific papers (see “List of publications” on page v), each with a full reference list. A synthesis of findings and conservation implications are presented in chapter six. I briefly present the context of each chapter, and its methodology, below.

The results of this thesis offer insights into the current global status of lions in Africa, what threatens their populations, and recommendations that could enhance the management of lions across their African range. This thesis focuses on the lion population in Africa only and does not assess or consider the Asian population apart from in Chapter 2 where it is assessed in the Global Red List Assessment.

Chapter two: Towards effective and harmonised lion survey methodologies: A systematic review of practice across Africa

Currently, several methods exist to survey lion abundance and density (Midlane *et al.,* 2015; Mills *et al.,* 1978; Stander, 1998; Strampelli *et al.,* 2022). However, there is still significant discord in the literature regarding the suitability and reliability of each method (Belant *et al.,* 2017; Dröge *et al.,* 2020). In chapter two, I conducted a systematic literature review utilising the PRISMA method (Page *et al.,* 2021) to describe and assess the current state of knowledge regarding lion survey methodologies. We addressed four questions: (1) What survey methods are being used to survey lions and for what purpose? (2) What are the strengths and weaknesses of methods used to survey lions? (3) What are some of the potential knowledge gaps that exist relating to lion survey methodology? Lastly, (4) based on the literature we reviewed; what methods are recommended to estimate lion abundance? In addition to these research questions, we aimed to provide a comprehensive comparison of existing methods for estimating lion abundance in Africa. Along with my co-authors, we provide several recommendations on the most suitable application of each method and encourage the uptake of more effective and harmonised lion survey methods that will contribute to more reliable and accurate population estimates.

Chapter three: Lions remain as Vulnerable according to the IUCN Red List Assessment

The previous Red List Assessment was completed in 2016 (Bauer *et al.,* 2015, 2016) and required updating. Regularly updating the assessments ensures they remain a robust and reliable tool for guiding conservation efforts worldwide in their efforts to protect biodiversity (IUCN 2022). Reassessments are important to enable the Red List as an indicator of biodiversity over time, using the Red List Index, and after a decade, an assessment is considered to be outdated (IUCN 2022). To ensure that the most accurate reflection of their status is used to guide conservation and policy decisions, I led the latest global Red List Assessment for lions using the best available data for lion populations across Africa. This assessment was conducted with the permissioned use of the IUCN SSC Cat Specialist Group's African Lion Database, and through the consultation with more than 100 experts in the field.

In this thesis chapter, I present the published assessment (for which I was the lead assessor), provide a narrative for the assessment process, and contextualise the outcome in terms on conservation and threat mitigation. I discuss the influences of the Red List status on listings from CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), CMS (Convention on the Conservation of Migratory Species of Wild Animals) and the United States Fish and Wildlife Services' Endangered Species Act (USFWS ESA).

Chapter four: Socio-political and ecological fragility of threatened, free-ranging African lion populations

Conservation threats in general are driven and affected by a multitude of wider-scale socio-political factors (including poverty, governance, human population growth etc.) but are very rarely considered in conservation planning and status assessments (Dickman *et al.,* 2015; Kuiper *et al.,* 2018).

In chapter three, I present a novel approach developed for lions, with the possibility to apply to other taxa, that incorporates both socio-political and ecological factors (Nicholson *et al.,* 2023b). The ecological and socio-political fragility (defined as a species' vulnerability to extinction) at both a national and geographic population scale is presented in this chapter and its implications for conservation explored. This approach provides a tool to allow for the increased understanding of the fragility of lion populations and will inform decision-makers regarding choices around lion conservation, such as funding strategies and priorities for action. These insights can inform more nuanced and appropriately targeted conservation plans for the species.

Chapter five: Perceived threats and pressures to lions across African regions, and resource availability for mitigation

Lion populations across Africa are declining rapidly, with instances of local populations becoming extinct entirely (Bauer *et al.,* 2018b). In chapter five, I determined which threats are perceived to be important for lions across their range by surveying large panel of experts across 132 lion subpopulations in Africa. I assessed how these threats differ at a continental, regional, national and subpopulation level. Data for this chapter was gathered between 2021 and 2022 through a structured questionnaire survey based on existing literature (Lindsey *et al.,* 2017; Page *et al.,* 2015; Page-Nicholson *et al.,* 2017; Robson *et al.,* 2022). Included in the analysis were 132 lion subpopulations across Africa. To broadly measure the severity of threats and pressures, I developed a "threat severity index" using the perceived severity rating of these threats by survey participants. I also sought to understand the scale at which specific threats occurred. This included how prevalent targeted poaching for parts was, and what is known about the target markets and target body parts. Perceptions on past, present and future lion subpopulation trends were gathered, and the perceived level of resources available to prevent the illegal killing of lions. Through this survey, I also developed a resource availability index to identify lion areas which were perceived to be insufficiently or sufficiently equipped with resources (e.g., funding, anti-poaching equipment, vehicles) to implement effective conservation. This allows us to highlight areas that are perceived as highly threatened and that are under-equipped. Key existing knowledge gaps that, when filled, would allow the increased understanding of these threats and, therefore, interventions likely to effectively improve the conservation status of lions, were identified.

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CHAPTER 2

Towards effective and harmonised lion survey methodologies: a systematic review of practice across Africa

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2.1 Abstract

Understanding the population status of a species is vital for their conservation. Over the last two decades, multiple methods for surveying lion populations have been designed and tested. Each have strengths and weaknesses, with different applications, and varying levels of reliability, accuracy and precision. We conducted a PRISMA systematic review to identify and assess survey methods for estimating lion population abundance. We searched the Web of Science and Google Scholar for peer reviewed papers between January 1991 and December 2022. Sixty-five papers were included, with some using multiple methods or multiple study sites; when these were separated, 93 studies were identified. Seven broad population survey methods for lions were identified: call ups (34.8 % of studies), spoor counts (32.5 %), direct observations (15.7 %), direct observations with capture recapture elements (12.4 %), camera trap-based capture-recapture analysis (4.5 %), genetic surveys (3 %) and distance-based surveys (1.1 %). Our literature review suggests that the most reliable methods for determining lion density or abundance are direct observations and camera trap-based capture recapture surveys. Genetic surveys combined with spatially-explicit capture recapture analysis also hold significant potential. Due to their lack of reliability and tendency to over-estimate populations, call ups and spoor counts are not recommended for determining population abundance. We further recommend that harmonised methods be developed that can produce comparable and reliable estimates, which can be used to inform conservation decisions across the species range.

2.2 Introduction

To effectively monitor and conserve wild species, an accurate understanding of their population sizes, demographics, and temporal dynamics are required (Braczkowski *et al.,* 2020a; Maximillion *et al.,* 2020; Stander, 1998; Young-Overton *et al.,* 2014). In this context, accurate measures of population abundance and density can help with understanding how best to conserve a given population (Braczkowski *et al.,* 2020a; Jędrzejewski *et al.,* 2018). Tracking population density or abundance over time allows us to detect declines or improvements, and to deploy timely, effective, and targeted conservation interventions. Similarly, to be effective, conservation interventions, strategies, and national and international policy and action plans must be guided by reliable population estimates that are comparable among populations, and within populations over time (Braczkowski *et al.,* 2020a; Maximillion *et al.,* 2020).

The lion (*Panthera leo*) population in Africa, like those of many other large carnivores, is declining rapidly across much of its range and is currently listed as Vulnerable (Bauer *et al.,* 2015; Nicholson *et al.,* 2023.; Wolf & Ripple, 2017). These declines are mainly driven by prey loss, habitat loss, and direct persecution (Bauer *et al.,* 2020). As human populations and global resource needs continue to grow, the pressure on lion populations will inevitably increase, with remote and fragmented populations across the continent being particularly at risk (Bauer *et al.,* 2020; Wolf & Ripple, 2017). It is, therefore, essential to ensure effective monitoring of remaining populations to help identify those populations that require urgent conservation intervention. This requires rigorous monitoring and reliably determining abundance and density of lion populations, to allow for the interpretation of trends in lion populations (Young-Overton *et al.,* 2014).

Globally, a range of methods have been used to survey large carnivores (Barea-Azcón *et al.,* 2007; Wilson & Delahay, 2001). The most common are those that use field signs (e.g., scat, spoor, hair) to determine presence and estimate their relative or absolute abundance (Barea-Azcón *et al.,* 2007). Initial studies indicated a close fit between sign frequency and population density for several carnivore species (Barea-Azcón *et al.,* 2007; Stander, 1998), although concerns regarding the accuracy of these estimates have been long-standing (Barea-Azcón *et al.,* 2007). Spoor counts, or track counts, are often done following roads or set transects and have been used in terrain where substrate allows the clear identification of tracks (Midlane *et al.,* 2014; Stander, 1998). Snow counts involve using snow during winter seasons to cover existing tracks and then subsequently counting tracks in subsequent days to determine abundance (Kojola *et al.,* 2014). This method has been used widely for surveying wolves (*Canis lupus*) in Finland (Kojola *et al.,* 2014) and the interior of Alaska (Becker *et al.,* 1998), wild boars (*Sus scrofa*) in the Czech Republic (Plhal *et al.,* 2011) and Eurasian lynx (*Lynx lynx*) in Norway (Linnell *et al.,* 2007). In Africa, spoor counts have been used extensively to survey African wild dogs, (*Lycaon pictus*) (Stander, 1998), leopards (*Panthera pardus*) (Balme *et al.,* 2009) and lions (Stander, 1998). Another spoor-based method is total counts based on identification of individual pug marks (Sharma *et al.,* 2005), which has been used with Amur tigers (*Panthera tigris altaica*), in Northeast China (Alibhai *et al.,* 2023), leopards in Malaysia (Sanei *et al.,* 2011) and Mountain lions (*Felis concolor*) in California (Fitzhugh & Gorenzel, 1985). Other forms of indirect methods include genetic surveys, which often use scent detection dogs to increase sample size, have been used to count snow leopards (*Panthera uncia*) in Nepal (Karmacharya *et al.,* 2011) and in Kyrgyzstan and China (Long *et al.,* 2011; McCarthy *et al.,* 2008; Thompson *et al.,* 2012). Audio based counts have also been used extensively to survey carnivores (Wilson & Delahay, 2001). Howling response counts are used to estimate wolf pack size, composition and home range size, and are based on the replies to mimicked howling (Ausband *et al.,* 2014; Fuller & Sampson, 1988; Harrington & Mech, 1982). Similarly, roar counts, which record the number of roars produced in a given period, have also been used to survey lions (Rodgers, 1973). Call up surveys, sometimes referred to as call-in or playback surveys, differ from audio counts because they use calls of conspecifics, prey in distress, or competitors to draw individuals to a specific site so they can be visually counted. They have also been used to estimate abundance of spotted hyena (*Crocuta crocuta*) northern Botswana (Cozzi *et al.,* 2013), Etosha National Park in Namibia (Trinkel, 2009) and in Ethiopia's National Parks (Yirga *et al.,* 2021, 2014), and lions in the Masai Mara in Kenya (Ogutu & Dublin, 1998), Kafue National Park in Zambia (Midlane *et al.,* 2015) and northern Botswana (Cozzi *et al.,* 2013). Direct observation-based studies typically require some form of individual identification and have been used and adapted widely (Beukes *et al.,* 2017; Bouley *et al.,* 2018; Brink *et al.,* 2012). Although they are challenging to implement over large spatial scales (Brink *et al.,* 2012), they have been used to survey cheetahs (*Acinonyx jubatus*) and African wild dogs in Kruger National Park in South Africa where citizen science was used to gather photographs of individuals to determine an overall population estimate (Marnewick *et al.,* 2014). Total counts of known individuals have been used for African wild dogs (Nicholson *et al.,* 2020) and lions (Beukes *et al.,* 2017). For species that are individually recognisable from photographs, surveys using camera traps deployed in a pre-determined grid or along a transect can be implemented to obtain a population estimate by using a capture-recapture approach (Wilson & Delahay, 2001). This was pioneered with tigers using their unique pelage (Karanth, 1995; Karanth & Nichols, 2010), and has also been done for cheetahs (Brassine & Parker, 2015; Marnewick *et al.,* 2008), spotted and brown hyenas (*Hyaena brunnea*) (Vissia *et al.,* 2021), jaguars (*Panthera onca*) in the Brazilian Pantanal (Soisalo & Cavalcanti, 2006) and more recently, lions (Cusack *et al.,* 2015; Kane *et al.,* 2015) and leopards (Balme *et al.,* 2019; Pin *et al.,* 2022). Other methods tested to estimate abundance, but not widely used, include using predator to prey ratios, (tested on snow leopards in Kyrgystan and China (McCarthy *et al.,* 2008)), thermal imagery (tested on mountain lions in Florida (Havens & Sharp, 1998; Wilson & Delahay, 2001) and distance-based survey methods (Durant *et al.,* 2011; Wilson & Delahay, 2001).

To survey lions, various methods are used to determine population abundance, including direct observations that use individual identification with capture-recapture (Beukes *et al.,* 2017; Rosenblatt *et al.,* 2014) or without capture-recapture (Bouley *et al.,* 2018; Kissui & Packer, 2004), genetic based surveys (Tende *et al.,* 2010), spoor counts (also called spoor transects or track counts (Bauer *et al.,* 2014; Henschel *et al.,* 2010; Stander, 1998), call in surveys (also referred to as call up surveys) (Mohammed *et al.,* 2019; Ogutu & Dublin, 2002) and camera trap studies with capture-recapture analysis (Elliot & Gopalaswamy, 2017; Kane *et al.,* 2015; Strampelli *et al.,* 2022b; Western *et al.,* 2022). As species continue to decline, it is imperative that trends are reliably monitored to prioritise populations that require conservation action. However, there is still a lack of consensus regarding the suitability of each method and when it can be applied effectively (Belant *et al.,* 2019; Dröge *et al.,* 2020; Henschel *et al.,* 2020). Despite the widespread use of many of these methods, there has historically been some disagreement among practitioners regarding the appropriate choice, implementation, and interpretation of these survey methods (Braczkowski *et al.,* 2020a, 2020; Dröge *et al.,* 2020; Elliot *et al.,* 2020). This lack of consensus can hamper the ability to compare abundance estimates across sites and time, even when the same methods are used. Some of the most significant disparities that exist include the reliability of spoor surveys for determining population abundance (Belant *et al.,* 2019; Dröge *et al.,* 2020; Funston *et al.,* 2010; Midlane *et al.,* 2014; Stander, 1998; Winterbach *et al.,* 2016) and whether call up surveys can be used in areas where lions are hunted or persecuted (Kiffner *et al.,* 2009; Mwampeta *et al.,* 2021).

For a global conservation strategy to be developed and for Range States to adopt national strategies and prioritise conservation action, there needs to be an understanding of the number and density of lions within each population. It is also critically important to obtain robust confidence intervals for those figures to detect changes in population trends over time (Braczkowski *et al.,* 2020a). However, there is no universally accepted standard or norm in terms of lion survey methodology. Consequently, there is an urgent range-wide need to review methods of population estimation for lions in Africa and to recommend scientifically supported harmonised survey methods that are widely accepted and adopted. While doing this, we need to look beyond current practice to identify areas for opportunity and potential knowledge gaps, while considering methods under development, updated analytical techniques, and improved data collection methods for existing methodologies. Through a systematic literature review, we described and assessed the current state of knowledge regarding lion survey methodology. We addressed four questions: (1) What survey methods are being used to survey lions and for what purpose? (2) What are the strengths and weaknesses of methods used to survey lions? (3) What are some of the potential knowledge gaps that exist relating to lion survey methodology? Lastly, (4) based on the literature we reviewed, what methods are recommended to estimate lion abundance? In addition to these research questions, we aimed to provide a comprehensive comparison of existing methods for estimating lion abundance in Africa.

2.3 Materials and methods

In July 2023, we systematically searched for peer-reviewed, accredited scientific journal papers focussing on lion surveys in two comprehensive databases of scientific publications: the Web of Science (WoS) and Google Scholar. We excluded grey literature items, as conclusions may not be scientifically sound or may be inaccurate due to a lack of a peer-review process. In addition, there is no consistent means by which to assess the scientific rigor of these publications in grey literature, nor a systematic method for retrieving research items (Holland *et al.,* 2018). We followed the PRISMA method for conducting systematic literature reviews (Page *et al.,* 2021).

A preliminary search was conducted on the WoS to identify potential methods used to survey large carnivores (particularly lions) and the common wording for those methods. From there a full search was done of papers on the WoS and Google Scholar, for which we used the following search phrase:

ALL=("*Panthera leo*") AND (ALL=("camera trap") OR ALL=("call") OR ALL=("track") OR ALL=("individual identification") OR ALL=("spoor"))

We limited our search to papers published in the last three decades (between 1991 and the end of 2022) to capture the latest findings and methodologies used to survey lions. These parameters were strategically selected after conducting a preliminary scan of the literature. Results obtained from the WoS were included in our review, as well as the first 300 results from Google Scholar. We focused on the first 300 results, as the criteria (see below) for inclusion were no longer met past this point. In addition, we considered papers housed in the IUCN SSC Cat Specialist Group's African Lion Database (ALD) that met our inclusion criteria (African Lion Database, Unpublished Data. 2022). Based on approaches followed by similar review papers (Holland *et al.,* 2018), we only included publications that were in English.

For inclusion in this review, the article must have met the following criteria:

- One of the study species was the lion

- The study was carried out on wild lions in Africa
- A measure of abundance or density of lions was stated. An exception was made in the cases where authors were testing and developing methods to survey lions. For example, one study tested and developed indices for spoor counts at 18 sites (Funston *et al.,* 2010). Also, the case with Winterbach *et al.,* 2016.
- Only studies where the intention was to provide some abundance metric (e.g., population number, density, spoor density) were used.

Our searches returned a total of 505 papers (153 from WoS, 300 from Google Scholar, 52 from the ALD; Figure 2-1). We removed 30 duplicate papers from the Google Scholar results and 35 from the ALD library, resulting in 440 papers. We then systematically went through the title, abstract and methods of the remaining papers. In total, 379 (75 %) of the papers were removed as they did not meet our criteria for inclusion or were of tangential topics. This resulted in 61 records included in our review. Citation mining was then done on those 61 papers by manually reading the references and reviewing papers with titles indicating potential relevance to our review. An additional four papers that met our inclusion criteria were found. We reviewed the full manuscript to confirm an appropriate focus on survey methodologies to determine population or density estimations for lions in each study area. In total, 65 peer-reviewed publications dating from 1991 to December 2022 were included in this systematic review (Figure 2-1).

To provide a summary of selected papers, we determined if there were multiple surveys carried out within each of the 65 papers (i.e., a multiple study). We defined a multiple study when separate surveys were completed in different areas (for example; we regarded one paper as three independent surveys as call up surveys were carried out in three different areas, namely, Queen Elizabeth National Park, Murchison Falls Conservation Area, and Kidepo Valley National Park in Uganda (Omoya *et al.,* 2014)); or surveys that focused on one study area but carried out multiple methods (for example; one study in Zambia was regarded as two surveys as both call up and spoor surveys were carried out in Kafue National Park (Midlane *et al.,* 2015)). Each survey method–survey area combination was included as a unique entry. While reviewing the papers, considerable notes were taken regarding the strengths and weaknesses of each method that were detailed by the relevant paper authors, as well as potential opportunities to improve the method.

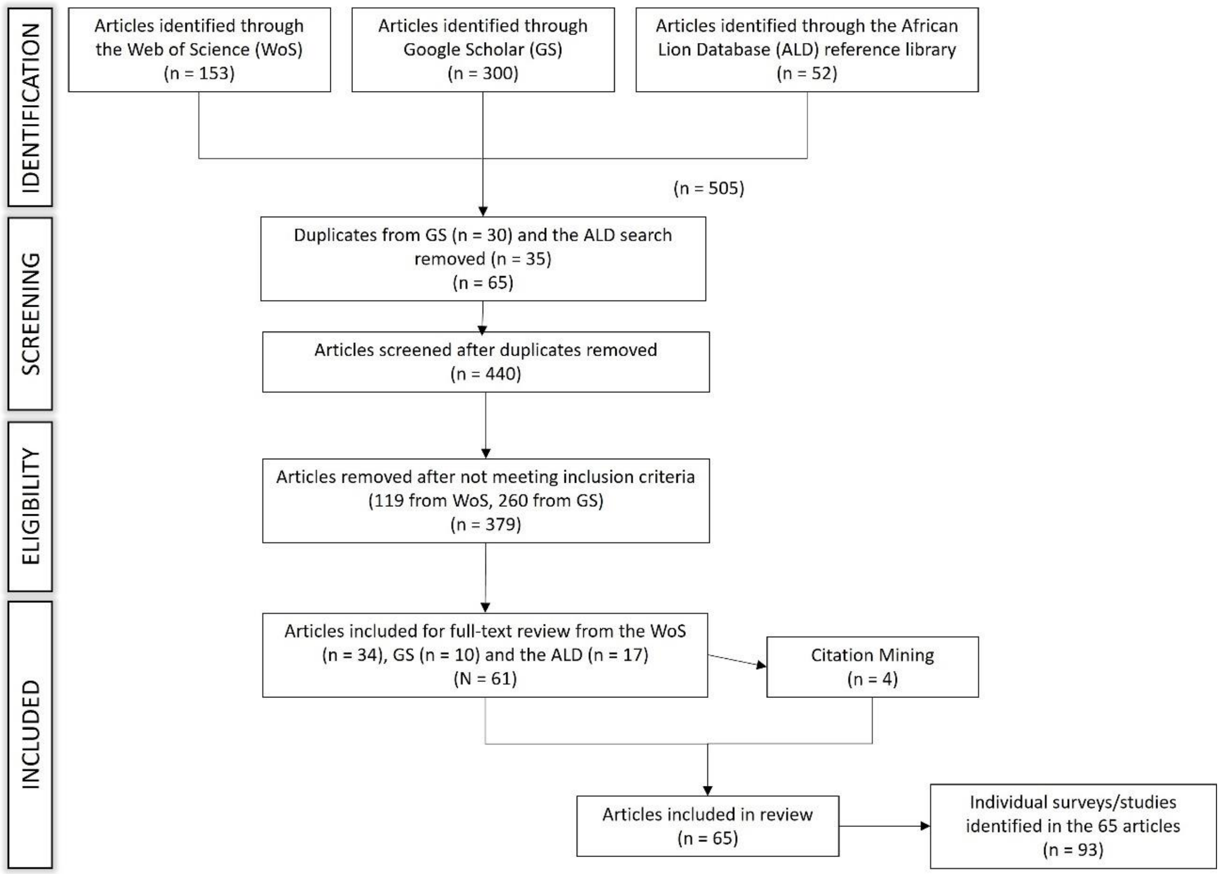

Figure 2-1. Flow chart of the article selection process for the systematic review of lion population survey methods.

Each article was reviewed in full by two of the authors (SN, EA or DM) and the necessary information extracted to enable us to address our four research questions (Table 2.1). For example, to determine what survey methods are used to survey lions and for what purpose, we looked at the objectives of the article as well as the general method used. To provide a summary of what purpose the methods were used for, we indicated whether a study was purely implementing the method, testing it, developing it, or testing and improving it (Table 2.1). We also utilised other information within the paper (e.g., data captured and analysis framework) to determine the survey method. If responses of the two reviewers differed, a third reviewer assessed the work, engaged in discussions and a consensus was reached. Information was extracted to allow a descriptive review and comparison of lion survey methods, rather than specifically testing methods against one another. This was used to address our research questions and provide a comparison of methods.

We used all information extracted from the papers to develop a comparison summary of lion survey methods. Studies which compared methods were used to rank methods according to their reliability, intensiveness and resource requirements. We detailed which research questions each method could address, whether they produced a reliable measure of abundance, the land use and habitat type they were best suited to, equipment required, ability to detect population trends and notes on their precision and bias. We ranked methods based on their invasiveness, ease and cost of implementation and the overall requirements. Finally, we also developed a generic flow diagram to help guide implementors in choosing the appropriate method based on their questions, area and funding.

Table 2.1. Summary of the information extracted by reviewers of each paper (n = 65 papers), linked to the four research questions: (1) What survey methods are being used to survey lions and for what purpose?; (2) What are the strengths and weaknesses of methods used to survey lions?; (3) What are some of the potential knowledge gaps that exist relating to lion survey methodology? and, (4) Based on the literature we reviewed, what methods are recommended to estimate lion abundance? Other relevant data were extracted from each paper to enable descriptive comparisons between studies.

INFORMATION EXTRACTED	DESCRIPTION	RESEARCH QUESTION
Publication year	Year the article was published.	1
Paper title and authors	Full title and list of authors.	
Study objectives	Objectives of the stated as stated by the authors.	1
Study category	"**Implementing"** - Studies that were purely carrying out study methods to determine a population number. **"Testing"-** studies that were determining the reliability or accuracy of a method. **"Testing and developing"** – studies that were a testing method as well as making changes in the methodologies in an effort to develop them further.	1
Method comparison	Making a note on whether lion survey methods were compared.	
Survey period	Start and end date of the field work.	
Study site details	Country, survey area, name, survey size (km^2), habitat type, substrate (if spoor surveys were done).	
Survey method	Call up, spoor survey, camera trap, distance-based surveys, faecal DNA, direct observations. Direct observations were split into those that used some element of capture recapture and those that did not.	1
Data collection method	Camera trapping, satellite collars, systematic surveys, intensive searches, etc.	
Data captured	Photos, individual IDs, spoor occurrence, faeces, sightings data, number of responses (for call up surveys), satellite tracking data, detections.	
Analysis framework implemented	Summarising the analysis approach taken.	
If detection was accounted for	How detection was accounted for.	
Population estimate	The reported population abundance estimated by the study and any confidence intervals or standard error provided.	
Lion density	The reported population density estimated by the study and any confidence intervals or standard error provided.	

Population trends	Reporting whether trends were assessed in the study or whether the authors of the studies indicated the method was suitable for detecting trends.	
Strengths of the method	Listing all strengths or advantages provided by the authors in the paper for the method.	2, 4
Weaknesses of the method	Listing all weaknesses or disadvantages provided by the authors in the paper for the method.	2, 4
Limitations in the methods implemented	Noting any limitations of the implemented survey methods for each survey as indicated by the authors.	
Notes on accuracy/precision	Any notes made on the accuracy or precision of the methods.	4
Suggestions on methodological improvement	Noting any statements made by the authors on potential ways to improve the method.	3
Future research needed	Noting any statements made by the authors on future research needed relevant to the methods.	3
Survey costs	Any costs related to implementing the method.	

2.4 Results

In total, 93 surveys from 65 peer-reviewed papers were included in this systematic literature review of lion survey studies. We classified each within one of seven broad methodological categories (Figure 2-2): Call up surveys (34.8 %, n = 31), spoor counts (32.6 %, n = 29), direct observation surveys with capture-recapture modelling (15.7 %, n = 14), direct observation surveys without a capture-recapture type framework (12.4 %, n = 11), camera trapping combined with capture-recapture modelling (4.5 %, n = 4), genetic surveys with capture-recapture modelling (3.4 %, n = 3) and distance based surveys (1.1 %, n = 1). Overall, two thirds of the studies used index-based methodologies (call up or spoor counts; 62.5 %; n = 60).

Most studies were conducted in Tanzania (17.2 % of studies; n = 17; Figure 2-3) and Kenya (11 %; n = 11). No published peer-reviewed studies were found from Angola, Chad, Democratic Republic of Congo, Gabon, Malawi, Rwanda, Somalia and South Sudan – all of which are lion range states. Most studies (67 %; n = 62) were considered implementation studies (Table 2.1, Figure 2-2, Figure 2-3). Seventeen studies (18.5 %) tested and developed ways to improve existing methods for surveying lions. Fourteen studies (15 %) tested survey methods. There were more papers published in the last decade than previously (72 %, n = 47, Figure 2-4, Figure 2-5). The field work required for observation-based studies were carried out over longer time periods than index-based methods (Figure 2-5). Publication of survey results often only occurred several years after the completion of the survey (Figure 2-5).

Several knowledge gaps were identified while conducting this review (Table 2.3). Most related to call up surveys, particularly around detection, survey design, or calibration. Inadequate overall study design and a lack of robust model design and validation were the biggest data gaps regarding camera trap surveys. Fewer gaps were identified for spoor counts (Table 2.3). We identified three knowledge gaps (Table 2.3) that span the lion survey topic in general – particularly the need to develop a "unified framework to assess lion densities" (Dröge *et al.,* 2020; Elliot & Gopalaswamy, 2017).

Based on the literature we searched, we summarise below the key advantages, disadvantages, knowledge gaps, reliability, and applicability of each of the methods to survey lions.

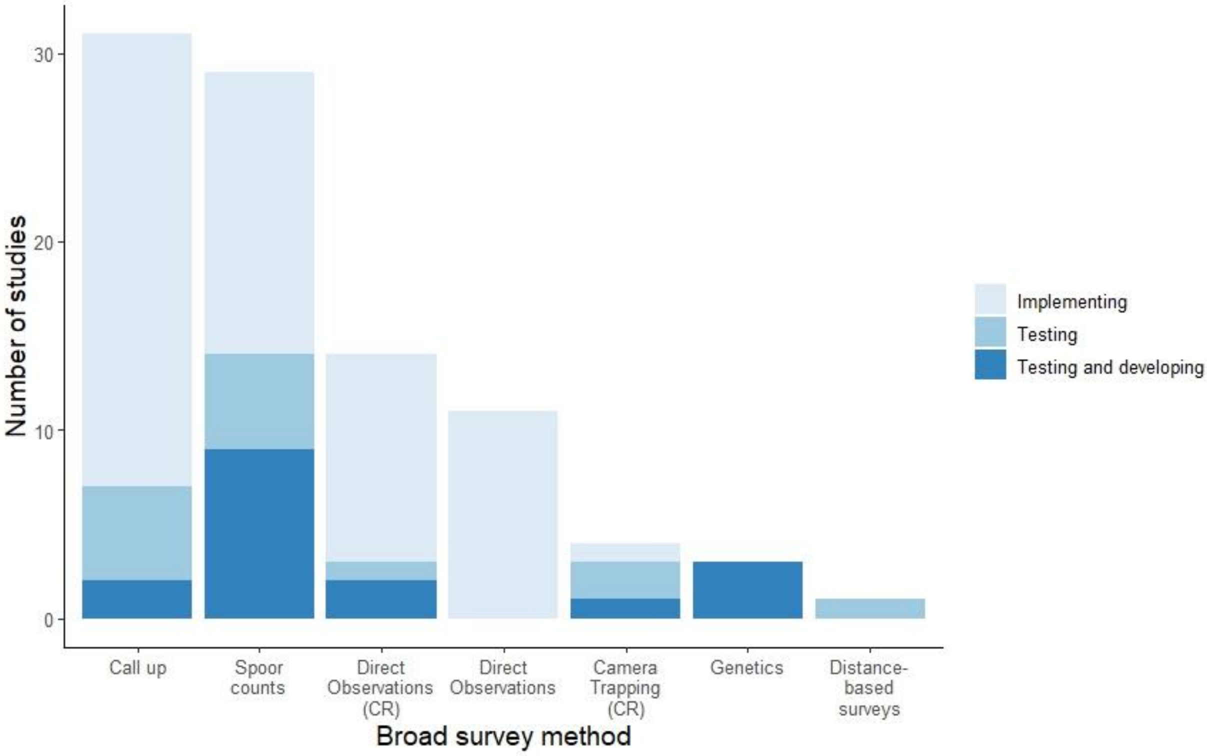

Figure 2-2. The lion survey methods carried out in the 65 peer-reviewed publications, and the study category of each of those studies (n = 93).

2.4.1 Call up surveys

The most published survey method is the call up survey (34.8 %, n = 31), which gained increased research interest in 2014 (Figure 2-4, Figure 2-5). This method of surveying lions (and hyenas) involves the structured and routine playback of a particular sound (e.g. prey distress calls) across a given area in an attempt to lure lions closer to the call up station (Midlane *et al.,* 2015), generally at night when lions are most active. The number of lion responses is used to determine their density in area. Key strengths of call up surveys include their comparatively high detection frequency (Midlane *et al.,* 2015; Supp Table 2.2), efficiency (Ogutu *et al.,* 2005), ease of execution, relatively low cost (Henschel *et al.,* 2014; Midlane *et al.,* 2015), and low effort (Table 2.2) (Bauer, 2007; Brink *et al.,* 2012; Henschel *et al.,* 2014; Mwampeta *et al.,* 2022; Ogutu *et al.,* 2005; Young-Overton *et al.,* 2014). In addition, call up surveys can be conducted in a range of landscapes independent of substrate and habitat (Cozzi *et al.,* 2013). Midlane *et al.,* (2015) estimated that additional cost of equipment required to add a call up component to an existing spoor survey was USD$ 1,145.

Several factors may reduce the reliability of estimates generated by call ups. If spotlights are used, the bright light can cause disturbance (Mwampeta *et al.,* 2022), discouraging individuals from emerging into the visual field. This risk can be partially mitigated by the use of red filters on spotlights, which have increased lion detection during surveys in the Serengeti National Park. In areas with moderate or high human activity, which may result in avoidance of humans, forward looking infrared (FLIR) thermal monocular spotlights may be more effective.

When call up surveys are carried out too frequently, lions may become habituated to the fact that, for example, there is no distressed prey animal present (Belant *et al.,* 2017; Mwampeta *et al.,* 2022; Ogutu *et al.,* 2005), resulting in decreased response rates and, therefore, a lower estimate (Belant *et al.,* 2017). Finally, call ups may not be suitable for low-density populations, or in areas where persecution levels are high, as response rates may be too low to calculate robust estimates (Ogutu & Dublin, 1998). Although there is debate in the literature on whether they are best suited here or not. In addition, the bright light can cause disturbance (Mwampeta *et al.,* 2022), and habituation may result in decreased response rates and, therefore, a lower estimate (Belant *et al.,* 2017). Notwithstanding this, various types of spotlights can have different levels of efficacy depending on the species, the population, and the area management regime, and researchers are encouraged to select the options that are most suitable for their environment and species (Mwampeta *et al.,* 2022). For example, spotlights with red filters are more effective in detecting and counting lions in Serengeti National Park (a non-hunted area) than FLIR (Mwampeta *et al.,* 2022). However, FLIR devices are recommended in areas where moderate or high human avoidance is exhibited by lions or hyenas (Mwampeta *et al.,* 2022).

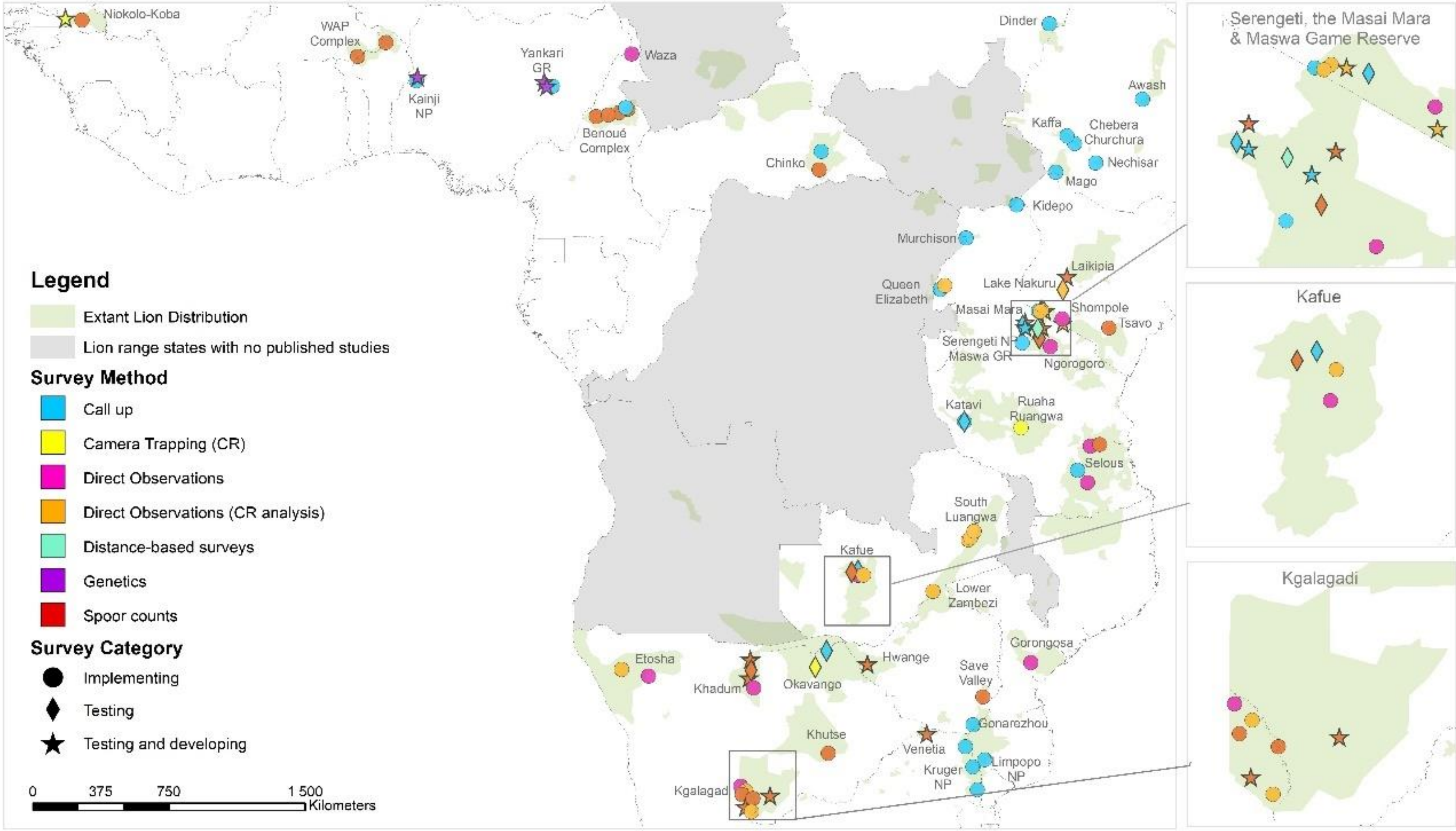

Figure 2-3 Study sites where methods to survey lions have been carried out. This literature review identified seven broad methods to survey lions and categorised them into studies that implemented them to determine a population estimate, or those that tested the methods (generally to determine their reliability or accuracy) or those that both tested and developed them. CR indicates Capture Recapture and the source for lion range: Nicholson et al. 2023.

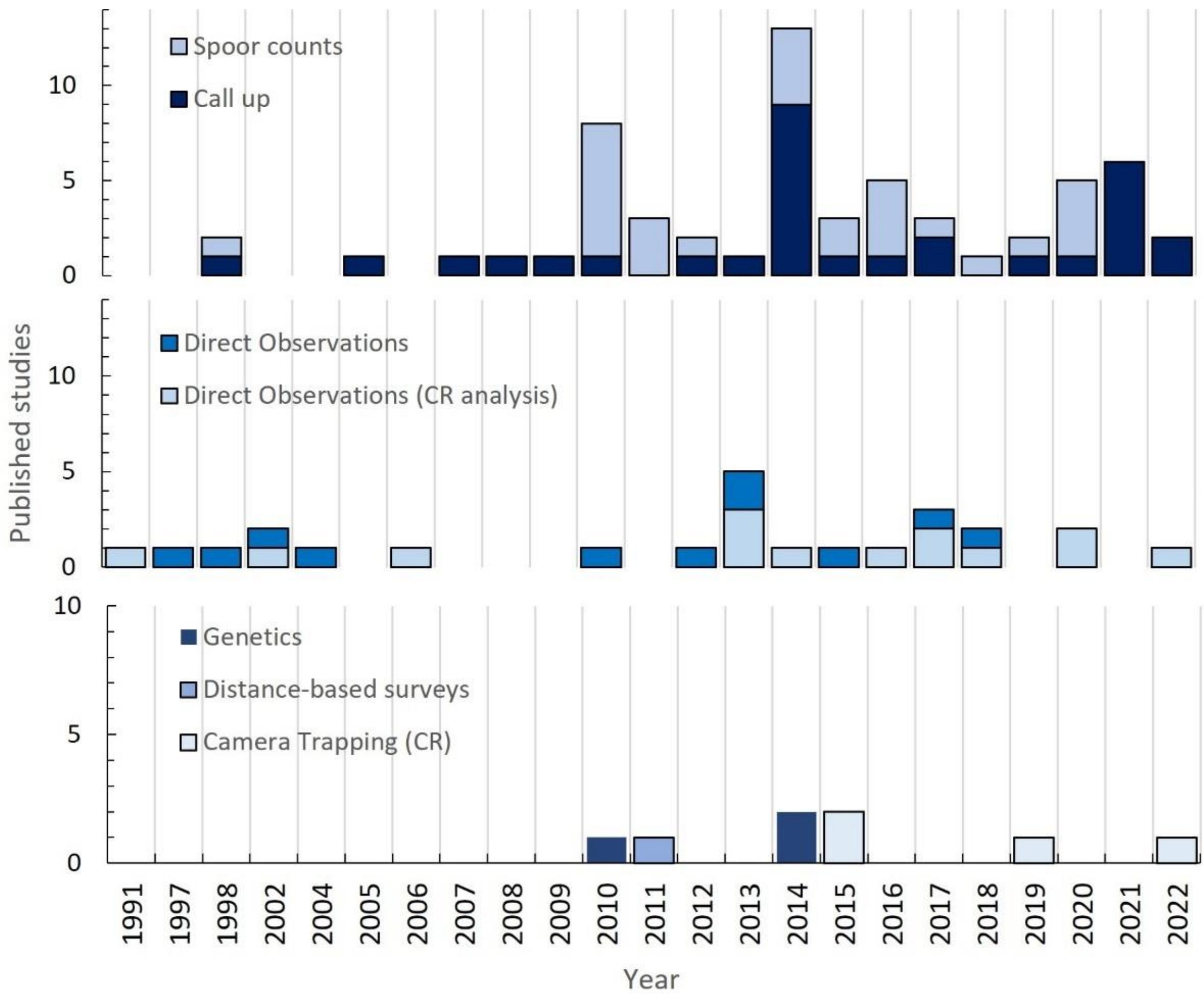

Figure 2-4 Lion survey method studies (n = 93) published between 1991 and 2022.

Our literature review indicated knowledge gaps or potential research needs (Table 2.3) for call up surveys including: calibration in West Africa (Bauer, 2007; Henschel *et al.,* 2014; Ogutu *et al.,* 2005), factors influencing detection across sites (Belant *et al.,* 2017; Kirsten *et al.,* 2017), determining optimal length between call ups (Belant *et al.,* 2017), and solutions to reducing habituation (Belant *et al.,* 2017).

This method is most suitable when resources (e.g., man-power, financial and equipment) are limited (Belant *et al.,* 2016; Brink *et al.,* 2012; Midlane *et al.,* 2015; Ogutu *et al.,* 2005). Call up surveys are also preferred in Central Africa were there are lower carnivore densities and poorer infrastructure (Bauer, 2007), and are also preferred in mesic savannahs (Young-Overton *et al.,* 2014). However, multiple studies demonstrate that this method is not accurate for determining population abundance (Belant *et al.,* 2019; Dröge *et al.,* 2020).

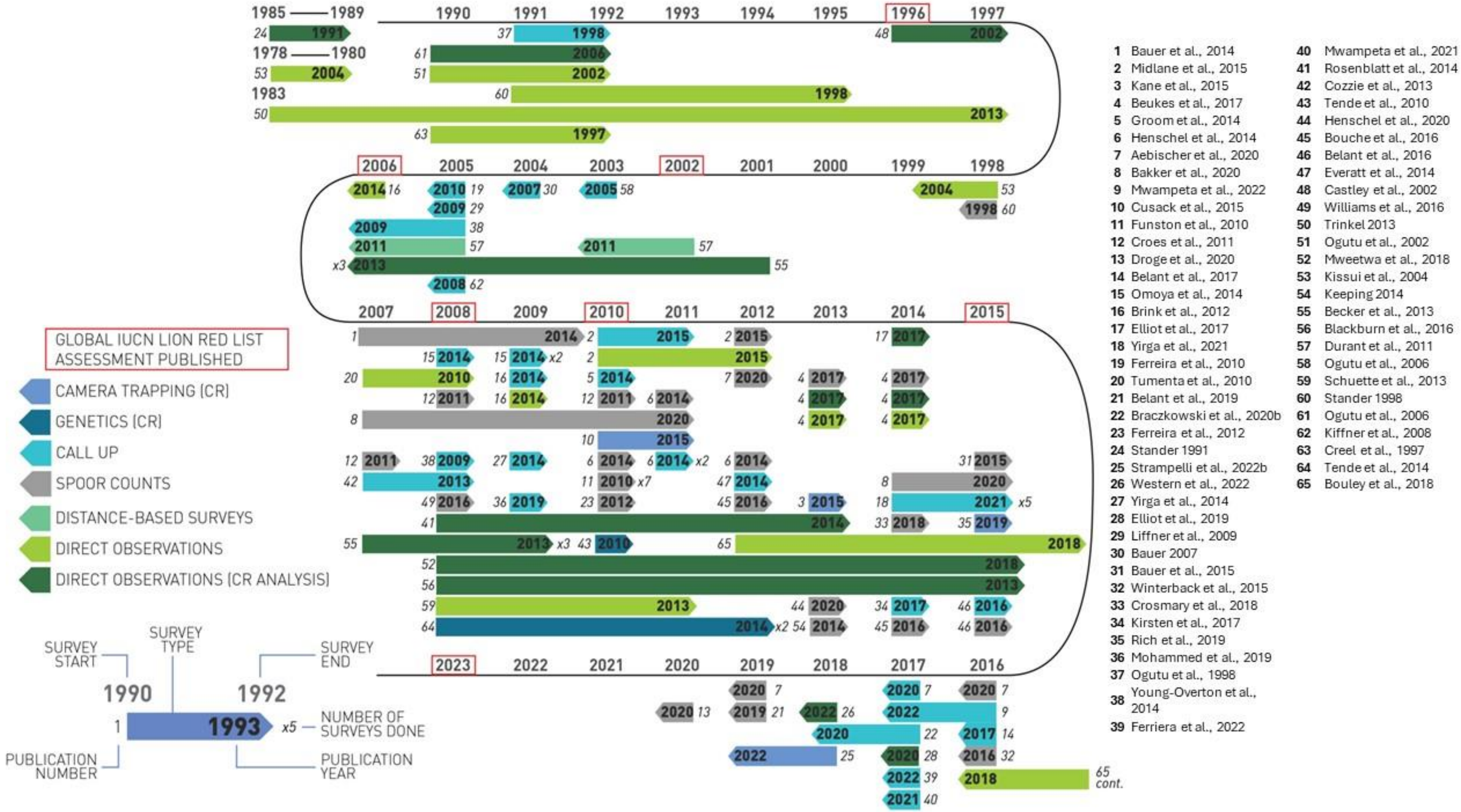

Figure 2-5. Field study period of the lion survey method studies (n = 93) published between January 1991 and December 2022 in 65 papers in this review.

2.4.2 Spoor counts

Spoor counts, or track surveys, were used by almost a third of the published studies (32.6 %, n = 29). These surveys involve using track frequency as an index of a species' density (Funston *et al.,* 2010; Winterbach *et al.,* 2016) based on a linear correlation between the true density of a species and the density of their tracks in some habitats (Winterbach *et al.,* 2016).

Spoor count strengths include that it is cost effective (Bakker *et al.,* 2020; Henschel *et al.,* 2020; Midlane *et al.,* 2015), easily repeated (Ferreira and Funston, 2010; Midlane *et al.,* 2015), can cover large spatial extents (Winterbach *et al.,* 2016), can be used to survey multiple carnivore species at once (Midlane *et al.,* 2015), and can be used where individuals are shy or heavily persecuted (Brink *et al.,* 2012). Density estimates resulting from populations that are less than 0.27 animals per 100 km^2 (<0.88 tracks/100 km^2) are not reliable (Winterbach *et al.,* 2016). Spoor count weaknesses are that it is not reliable for estimating abundance (Belant *et al.,* 2019; Dröge *et al.,* 2020), require an experienced tracker and an extensive road network (Kirsten *et al.,* 2017; Stander, 1998). Regarding their reliability and accuracy, recent studies have argued that this method of surveying lions is not reliable as it overstates precision with wide confidence intervals (Belant *et al.,* 2019; Beukes *et al.,* 2017; Dröge *et al.,* 2020).

A key weakness of spoor counts is that it requires an experienced tracker and an extensive road network (Kirsten *et al.,* 2017; Stander, 1998). This method is not suitable for all areas as it depends on the substrate (Beukes *et al.,* 2017; Winterbach *et al.,* 2016), and is not suitable in areas where there is high traffic where evidence of tracks is destroyed (Beukes *et al.,* 2017).

Recent studies have argued that this method of surveying lions is not reliable as it overstates precision and has wide confidence intervals (Belant *et al.,* 2019; Beukes *et al.,* 2017; Dröge *et al.,* 2020). Based on the literature, it is evident that this method is not reliable for estimating abundance (Belant *et al.,* 2019; Dröge *et al.,* 2020), and is only suitable for verifying the presence of lions within an area and to collect data to model lion distribution within an occupancy framework (Henschel *et al.,* 2016; Midlane *et al.,* 2014; Petracca *et al.,* 2020).

2.4.3 Direct observations (with and without capture recapture analysis)

Direct observation type surveys are also frequently used to survey lions (26.9 %, n = 25). These surveys can either be implemented with capture recapture modelling (15.7 %, n = 14) or without (12.4 %, n = 11). These forms of surveys involve identifying individual lions through opportunistic sightings (Beukes *et al.,* 2017; Braczkowski *et al.,* 2020b) or intensive monitoring (Blackburn *et al.,* 2016; Bouley *et al.,* 2018; Ogutu & Dublin, 2002), and rely on either the natural individual marking of individuals (e.g., whisker spot patterns or scars (Elliot & Gopalaswamy, 2017; Strampelli *et al.,* 2022b)) or through the direct marking of individuals (e.g., branding; (Stander, 1991)).

Direct observation surveys are generally the most robust and reliable method for defining population characteristics such as demographic composition (Beukes *et al.,* 2017; Rosenblatt *et al.,* 2014), can include citizen scientists (Braczkowski *et al.,* 2020a), and can be used for small populations (Elliot *et al.,* 2020). While this method is reliable for determining abundance (Beukes *et al.,* 2017), it tends to be fairly expensive because of the cost of equipment involved and can be relatively resource intensive (Beukes *et al.,* 2017; Braczkowski *et al.,* 2020b). This is likely because of the assumption that this method would require a lengthy amount of field time to obtain identification of all individuals within an area. Survey methods that utilise satellite tracking or radiotelemetry are also adapted to determine population sizes (Becker *et al.,* 2013; Mweetwa *et al.,* 2018). There are, however, techniques to combine statistical modelling with direct observation to obtain density estimates with moderate effort and cost. For example, a recent lion survey in Uganda's Queen Elizabeth National Park cost ~USD 3,690 for a 93-day long survey analysed using a spatial capture re-capture analysis based analytical framework (Braczkowski *et al.,* 2020a; 2020b).

This method has probably evolved the most relative to other lion survey methods, especially with regards to statistical analyses (Braczkowski *et al.,* 2020b, 2020a; Elliot *et al.,* 2020; Elliot & Gopalaswamy, 2017; Western *et al.,* 2022). Combining direct observations with SECR is more reliable than analytical methods previously used and generate highly robust animal densities (Braczkowski *et al.,* 2020b). This type of analysis has only been applied to lions in the last decade (Braczkowski *et al.,* 2020a; 2020b; Kane *et al.,* 2015). Intensive monitoring is often deployed by conservation management to identify individuals within the population to achieve a population estimate (Bouley *et al.,* 2018). These types of surveys provide additional information on the population, including demographic break-down, life histories, survival rates, and, if tracking collars are used, spatial use and home-ranges (Bouley *et al.,* 2018).

This method is best suited as part of long-term or intensive monitoring studies. It can be adapted to accommodate the resources available for the survey. In addition, these studies can be designed and implemented rapidly (Elliot *et al.,* 2020; Elliot & Gopalaswamy, 2017) or over longer time periods (Beukes *et al.,* 2017; Bouley *et al.,* 2018; Western *et al.,* 2022).

2.4.4 Camera trap-based capture-recapture surveys

Camera trap surveys combined with capture-recapture (CR) modelling is a new survey technique for lions, conducted in only four published studies (4.5 %), with the first published studies in 2015 (Figure 2-4, Figure 2-5; (Cusack *et al.,* 2015; Kane *et al.,* 2015)). The first study of this type was conducted in Niokolo-Koba National Park in Senegal and combined with mark-resight analysis (Kane *et al.,* 2015). Camera trap surveys were previously thought to be inefficient in estimating population density and abundance because individual lions can be difficult to distinguish in camera trap images (Beukes *et al.,* 2017). However, recent studies have found that this is not the case, as a result of advances in camera trap technologies including the increased quality and resolution of images and the use of a white flash (Cusack *et al.,* 2015; Strampelli *et al.,* 2022b).

The strengths of using camera trap surveys for lion density estimation is that the method is reliable, repeatable, relatively simple to implement, and does not require large teams (Cusack *et al.,* 2015; Kane *et al.,* 2015; Strampelli *et al.,* 2022b). The weakness of camera trapping is that it requires considerable time to deploy and check traps, capture large amounts of data in databases, and process photos (Strampelli *et al.,* 2022b) and can be costly. Individual identification, though possible, is still difficult, and requires experienced personnel. Finally, there is a risk that cameras get stolen, resulting in lost data, potential gaps in the survey, and lower sample size.

Camera trap surveys have not yet been carried out over large survey areas (Cusack *et al.,* 2015; Kane *et al.,* 2015; Rich *et al.,* 2019; Strampelli *et al.,* 2022b). Further studies are required to determine the feasibility of implementing this method at larger scales (Strampelli *et al.,* 2022b). Larger survey areas will potentially require wider spacing of trapping stations, designing models aimed at accurately identifying single-sided individuals and potentially rotating grids to allow greater area coverage (Strampelli *et al.,* 2022b). In addition to assessing the scalability of this method, aspects around model validation and survey design should also be assessed (Table 2.3; (Rich *et al.,* 2019; Strampelli *et al.,* 2022b)).

Strampelli *et al.,* (2022b) estimated that surveying an area of 5,000 km^2 with cameras would cost ~ USD 60,000 (including camera trap costs and accessory costs). This is estimated based on camera trap stations placed at 5 km intervals, requiring ~200 stations (400 cameras, if paired) at ~USD 150 per camera (https://www.cuddeback.com/shop) (Strampelli *et al.,* 2022b).

Artificial Intelligence software is now widely used to identify species within images, saving thousands of work hours (Green *et al.,* 2020; Mandisodza-Chikerema *et al.,* 2022), although the capability to identify to an individual level has yet to be developed. While the initial financial investment in camera trap surveys is high (e.g., purchasing cameras, camera mounts, batteries, SD cards), they can be used over many years to conduct repeat surveys or survey new areas, which reduces their overall cost per survey. In addition, they can be utilised to survey other species simultaneously, which, overall, increases their cost effectiveness.

This method is suited across all landscapes and where sufficient resources are available (particularly to cover the costs of equipment). As this method is indirect, it can be used effectively where lions are elusive.

2.4.5 Genetics with capture-recapture modelling

Genetic studies were carried out in three studies (3.4 %), although by the same author and restricted to two populations in Nigeria (Yankari Game Reserve and Kainji Lake National Park) (Tende *et al.,* 2014, 2010). This method involved analysing the Mitochondrial DNA of individuals using PCR methods gathered from lion faecal matter to determine a minimum population size (Tende *et al.,* 2014, 2010). The strengths of this method include that it is non-invasive and works well for secretive species, potentially those that are in highly persecuted environments (Tende *et al.,* 2010) (Table 2.2). An added benefit of this survey technique is that it offers insight into the health status of a population (e.g., inbreeding), which cannot be determined through conventional survey methods (Tende *et al.,* 2010). Weaknesses of this method include that it can be intensive to obtain sufficient samples, can be costly and requires specialists to analyse and interpret the results (Table 2.2). There is significant potential for applying SECR modelling with genetic survey data (Gopalaswamy *et al.,* 2012; Strampelli *et al.,* 2022b).

While the current literature does not provide much information regarding where this method is best suited, it likely to be applicable across a wide range of landscapes. This method is particularly applicable when various aspects relating to population health are required (Tende *et al.,* 2014, 2010) or when determining the minimum number of individuals in a population is required for management decisions.

2.4.6 Distance-based surveys

One paper (1.12 %) implemented distance-based surveys for counting lions (Durant *et al.,* 2011). Distance-based surveys involve recording all species and their numbers within a certain distance from a transect line (Durant *et al.,* 2011). Distance sampling can be used as a tool for rapid counts and monitoring of several species. The strengths of this method are that it is relatively cost effective and can be completed in a short study period (Durant *et al.,* 2011). The weaknesses are that there are several issues relating to detection (e.g., detection probability, imperfect detection, group size estimation) (Durant *et al.,* 2011) and wide confidence intervals that raises some concern over their precision (Durant *et al.,* 2011). These surveys are possibly only practical in habitats like the Serengeti where the area is flat, and it is relatively easy to see animals (such as desert or grasslands; Durant *et al.,* 2011). This method is thus best suited where resources are limited and where the habitats allow animals to be visually detected over long ranges, generally where vegetation is sparse.

Table 2.2. Reported weaknesses and strengths of survey methods taken from published studies found in this literature review (93 studies in 65 peer reviewed publications).

Method	Disadvantage/weakness of the method	Advantage/strength of the method
Call up surveys	• Cannot provide reliable estimates of population density [1]. • If used, "bright light emitted can disturb, cause avoidance and reduce animal detection"[2]. • Habituation of target species after multiple sessions results in poor estimates of precision or prevents any responses [3, 4]. • Not useful in areas where lions are hunted/persecuted as individuals may be too cautious to approach stations with human-activity [5,6].	• Comparatively high detection efficiency [7]. • Possible to simultaneously estimate lion and hyena density from a single survey [8,9]. • Survey duration is less than most other surveys (dependent on survey size) [10]. • Used across various landscapes independent of substrate and habitat and across large areas [1]. • Limited equipment, skills/training requirements [1,9]. • Easy to execute and low effort [7, 9]. • Low cost [7,11].
Spoor counts	• Cannot provide reliable estimates of population density [12,13,14]. • Requires experienced trackers [15,16]. • Track detection is more challenging when there is a high frequency of road use as tracks are destroyed [13]. • Large confidence intervals in population estimates [16]. • Imprecision precludes detecting trends over time [16]. • Estimates either overstate precision or are too imprecise to be meaningful [12]. • Track detection varies across substrates [13]. • Require much greater sampling effort to compensate for the lack of precision [13]. • Not suitable for low density populations. The validity of density estimates below 0.27 carnivores/100km^2 (<0.88 tracks/100km) is questionable [17].	• Multiple carnivore species can be surveyed simultaneously (e.g., spotted hyena, and possibly leopard, wild dogs, and cheetah) [18,19]. • Comparatively high detection efficiency [7]. • Low effort and cost [7]. • Relatively inexpensive method [16]. • Easy to implement, multi-scale and effective tool for carnivore population monitoring [7,19]. • Cover large spatial areas [19]. • Robust and repeatable technique for assessing large carnivore densities [7,16], distribution and population size.

Direct observation surveys (with and without capture recapture modelling)	• Registering individuals is resource and time intensive [13,15]. • May not be feasible in environments where low encounter rates or poor visibility restrict observations [13,15]. • Some difficulties in finding and monitoring low density, wide-ranging species [13,17].	• Most robust method for defining population characteristics [13]. • It can be used under a citizen-science approach, reducing the survey costs, making them considerably cheaper than traditional methods [20]. • Suitable for small sample sizes [21]. • They provide an appropriate standardised framework to monitor species that occur in diverse habitats, at varying densities and with changeable behaviour [21]. • Provide repeatable and inexpensive measures of some population parameters [22]. • If SECR models are applied, has been shown to provide reliable estimates of population density [21,23]. • Produce statistically rigorous and precise estimates of population [23].
Camera trapping surveys with CR analysis	• Initial financial layout is costly [24]. • Current drawback of the Random Encounter Models (REM) is its reliance on independent estimates of animal speed of movement and camera detection zone dimensions [25]. • Scaling the method to larger areas is likely to be costly and/or challenging [25]. • Deploying and checking cameras requires considerable time, as does the identification of individuals captured [24].	• Shown to provide reliable estimates of population density [25,24]. • Determine occupancy or density of multiple small- to wide-ranging species concurrently [25,26]. • REM may offer a promising and more cost-effective alternative to estimating animal density [25]. • Provides accurate and precise estimates of abundance [24,25].
Genetic surveys	• DNA can degrade resulting in low quantity and / or poor-quality DNA available for use [27]. • Amplification failures during PCR and false alleles can also affect population size estimates [27].	• Non-invasive sampling technique [27,28]. • Works well for secretive species and / or in dense habitats [27,28]. • Allows for genetic studies of wild animals without trapping them or observing them [27,28]. • Provides data on the health status of a population, e.g., inbreeding, which cannot be obtained easily using observation in the field [27,28]. • Has potential for application of SECR models.
Distance-based surveys	• Wide confidence intervals [29]. • Within lion range, they are only suitable in habitats similar to the Serengeti (flat and little vegetative cover). • Some issues with detection confidence [29].	• Relatively quick to implement [29]. • Cost effective [29]. • Applicable to most habitats with good visibility, such as short grass plains, grassland or desert [29]. • Can be used to effectively detect long-term trends [29].

[1] Cozzi *et al.,* 2013, [2] Mwampeta *et al.,* 2022; [3] Belant *et al.,* 2017; [4] Ogutu *et al.,* 1998; [5] Kiffner *et al.,* 2009; [6] Creel & Creel 1997; [7] Henschel *et al.,* 2014; [8] Bauer 2007; [9] Ogutu & Dublin 1998; [10] Belant *et al.,* 2016; [11] Brink *et al.,* 2012; [12] Droge *et al.,* 2020; [13] Beukes et al., 2017; [14] Belant *et al.,* 2019; [15] Midlane *et al.,* 2015; [16] Henschel *et al.,* 2020; [17] Winterbach *et al.,* 2016; [18] Midlane *et al.,* 2015; [19] Bakker *et al.,* 2020, [20] Braczkowski *et al.,* 2020b; [21] Elliot *et al.,* 2020; [22] Stander 1998; [23] Elliot & Gopalaswamy 2017; [24] Strampelli *et al.,* 2022; [25] Cusack *et al.,* 2015; [26] Rich *et al.,* 2019; [27] Tende *et al.,* 2010; [28] Tende *et al.,* 2014; [29] Durant *et al.,* 2011.

Table 2.3. Knowledge gaps identified in published studies found in this literature review for the recommended methods.

METHOD	KNOWLEDGE GAP AND IDENTIFIED RESEARCH NEEDS	REFERENCES
Camera trap surveys combined with capture-recapture modelling	Further develop Spatial Mark Resight (SMR) models (especially to "allow for the inclusion of finite-mixture covariates such as sex), for cases where identification rates are lower".	Strampelli *et al.,* 2022
	"Test the suitability of other models of xenon-flash camera traps for the individual identification of lions, as this may not be equal across models"	Strampelli *et al.,* 2022
	Further advance survey design advancements to improve precision of density estimates produced.	Strampelli *et al.,* 2022
	"Explore the scalability of this method to larger areas".	Strampelli *et al.,* 2022
	Explore how the dispersion of recaptures affects accuracy of estimates (this may provide additional insights into how to optimally space traps when movement patterns differ among species).	Rich *et al.,* 2019, Strampelli *et al.,* 2022
Observational studies	Continually develop SECR methods as they are a reliable method for surveying African carnivores.	Elliot & Gopalaswamy 2017
Genetic surveys	Evaluate and test the potential of SECR modelling.	Stampelli *et al.,* 2022 Gopalaswamy *et al.,* 2012
All	Develop a "handbook of best practices in monitoring populations of apex carnivores".	Droge *et al.,* 2020
	Develop "a "unified framework" to assess lion densities in key sites across their range to allow for accurate population assessments and trend analyses".	Elliot & Gopalaswamy 2017
	Conduct a cost benefit analysis of each method.	This review

2.4.7 Method comparison and summary

We summarised and compared the seven methods for surveying lions (Table 2.4) based on the 93 studies reviewed. A full descriptive narrative is available in Supplementary Table 2-1.

Seven papers (10.8 %) compared lion survey methods (Belant *et al.,* 2019, 2016; Beukes *et al.,* 2017; Bouley *et al.,* 2018; Groom *et al.,* 2014; Midlane *et al.,* 2015; Ogutu & Dublin, 1998). A comparison paper of call up and spoor surveys in northern Kafue National Park (Zambia) determined that spoor surveys were less resource intensive (Midlane *et al.,* 2015), with spoor surveys estimated to require less than half the number of survey days, 23 % less survey hours and 38 % less kilometres driven when compared to call up surveys (Midlane *et al.,* 2015). However, call up surveys were far more precise, and therefore this study recommended call up surveys over spoor counts (Midlane *et al.,* 2015). Another paper compared spoor counts, direct observations with capture recapture and total counts (direct observations) in the Kgalagadi Transfrontier Park (Beukes *et al.,* 2017). Spoor counts produced a population estimate of 242 individuals (95 % CI: 176 – 307), direct observations with capture recapture estimated 246 individuals (95 % CI: 237 – 256) and a total count of known animals identified 261 individuals (Beukes *et al.,* 2017). Minimum Known Alive calculations were found to significantly under-estimate the population (n = 145). Although spoor counts gave a similar estimate to direct observations with capture recapture, they were imprecise as indicated by wide confidence intervals (Beukes *et al.,* 2017). A comparison of total counts (through direct observations) and call up surveys in the Masai Mara National Reserve (Kenya) found that the estimates from both methods for lions was almost equal (Ogutu & Dublin, 1998). The total count identified 447 lions and the call ups estimated 450 (95 % CI: 436 – 464) (Ogutu & Dublin, 1998); the narrow confidence intervals imply reliability in the method as results were shown to have high precision and low bias (Ogutu & Dublin, 1998). In Gorongosa National Park (Mozambique), call up surveys proved to be ineffective because when implemented in areas where lions were known to be, none responded to any of the calling stations (Bouley *et al.,* 2018). However, direct observation through intensive monitoring determined a population of 104 individual lions (Bouley *et al.,* 2018).

In general, we found that all methods could answer research questions relating to lion presence within an area, but direct observations and camera trapping were the most suitable for estimating abundance (Beukes *et al.,* 2017; Bouley *et al.,* 2018; Kane *et al.,* 2015; Strampelli *et al.,* 2022b). It is possible that call up surveys can estimate population abundance, but results should be interpreted with caution as there is uncertainty regarding the reliability as confidence intervals vary from wide (Beukes *et al.,* 2017) to narrow (Ogutu & Dublin, 1998). Indirect survey methods, spoor, camera trapping and genetic surveys, are the least invasive and potentially more effective in areas where lions are less approachable. When it comes to ease of implementation, call up and spoor surveys ranked the least resource intensive (Bauer *et al.,* 2014; Henschel *et al.,* 2020; Midlane *et al.,* 2015, 2014) and camera trapping and genetic surveys the most resource intensive (Kane *et al.,* 2015; Strampelli *et al.,* 2022b; Tende *et al.,* 2014). Similarly, call up and spoor surveys are the least expensive (Midlane *et al.,* 2015), while direct observation and camera trapping surveys are the most expensive (Braczkowski *et al.,* 2020b). The most suitable methods to detect trends are direct observation studies (Bouley *et al.,* 2018; Mweetwa *et al.,* 2018; Rosenblatt *et al.,* 2014), distance-sampling (Durant *et al.,* 2011) and potentially camera trap studies (Kane *et al.,* 2015).

Table 2.4. Comparative summary of the preliminary lion survey methods according to the literature included in this systematic literature review. A descriptive narrative of how we compared methods, including their ranking, can be found in the supplementary material.

	CALL UPS	**SPOOR SURVEYS**	**DIRECT OBSERVATIONS (WITH OR WITHOUT CAPTURE RECAPTURE ANALYSIS)**	**CAMERA TRAP-BASED CAPTURE RECAPTURE SURVEYS**	**GENETIC SURVEYS WITH CAPTURE-RECAPTURE MODELLING**	**DISTANCE-BASED SURVEYS**
Key methodological papers	Ferreira & Funston 2010; Midlane *et al.,* 2015; Mwampeta *et al.,* 2022	Funston *et al.,* 2010; Keeping 2014; Midlane *et al.,* 2015; Winterbach *et al.,* 2016; Henschel *et al.,* 2020	Pennycuick & Rudnai 1970; Becker *et al.,* 2013; Rosenblatt *et al.,* 2014; Bouley *et al.,* 2018	Cusack *et al.,* 2015; Strampelli *et al.,* 2022	Tende *et al.,* 2014	Durant *et al.,* 2011
Research questions	Lion presence	Lion presence	Lion presence Lion density Population estimate Population trend Population structure	Lion presence Lion density Population estimate Population trend	Lion presence Genetic health Population estimate Genetic relatedness	Lion presence Population trend
Direct or indirect method	Direct	Indirect	Direct	Indirect	Indirect	Direct
Reliable measure of abundance	Yes	Yes	Yes	Yes	Yes	Yes
Reliability in estimating abundance	4	5 (least reliable)	2	1 (most reliable)	3	No information available
Detect trends	Yes	Yes	Yes	Yes	Yes	Yes
Precision and bias	High precision	Precision is overstated	Precise when used with capture-recapture	No information available	No information available	No information available
Confidence intervals	Poor assessment of	Wide confidence intervals. Poor	No information available	No information available	No information available	Wide confidence intervals

	variation around count (dependent on calibration effort)	assessment of variation around count				
Invasiveness	5	1 (least invasive)	6 (most invasive)	4	1 (least invasive)	3
Land use type	All land use types but less suitable in areas where lions are shy (e.g. hunting or remote areas)	All - especially suitable in areas where lions are particularly shy	Across all land use types	Across all land use types (camera theft needs to be considered in some areas)	Across all land use types	Across all land use types
Habitat type	Appropriate across all habitats	Ideally soft-substrate	Appropriate across all habitats	Appropriate across all habitats	Appropriate across all habitats	Habitats that allow good visibility
Ease of implementation	1 (easiest)	2	4	6 (hardest)	5	3
Cost of implementation	2 Cost of equipment required for the call-up survey was USD$ 1,145. The per-survey cost of additional equipment required for the call-up survey decreases with each new survey (Midlane *et al.,* 2015)	1 (cheapest)	6 (most expensive if satellite collars are required and extensive fieldwork) USD$ 3,690 on their 93-day SECR lion survey in Queen Elizabeth National Park (USD900 for vehicle and petrol costs, and USD$ 2,790 on food and lodging). Braczkowski *et al.,* 2020b	5 Surveying an area of 5,000km^2, with cameras placed at regular 5-km intervals (wider than in our study, but likely still suitable for lion), would require ~200 stations (400 cameras, if paired). At ~USD$ 150 per camera (https://www.cuddeback.com/shop), this would amount to ~ USD$ 60,000 of camera trap costs, in addition to significant accessory costs (for import fees, batteries, memory cards, and protective cases). Stampelli *et al.,* 2022	4	3
Time requirement	2	1 (shortest study period)	6	6 (longest study period)	4	3

Equipment	Vehicle, speakers, spotlight	Vehicle	Vehicle, photobook, Satellite/VHF collars (optional)	Vehicle, cameras, batteries, camera mounts, SD cards	Genetic sample kits, genetic laboratory, potentially sniffer dogs (not always required) to locate faecal matter	Vehicle, distance range finder
Minimum number of people required	2	2 (tracker and driver)	1	1	2	2
Key skills or expertise required	None	Experienced tracker	Potentially statistical analysis if incorporating capture recapture analysis	Experience in camera trap surveys and analysis	Genetic analysis or link to a genetic lab	Distance surveys and analysis
Key comparisons with other studies done	"Call ups are more precise than spoor counts, despite this method requiring less than half the number of survey days, 23 % fewer survey hours and 38 % fewer kilometres driven" (Midlane *et al.,* 2015)		"Intensive monitoring produced estimates with 3X to 7X greater precision than rapid indices of abundance". (Rosenblatt *et al.,* 2014)	"Estimates achieved through Random Encounter Modelling with camera traps were more precise (i.e., narrower confidence intervals) than those obtained for Serengeti lions using distance sampling, which also required a higher level of sampling effort." (Cusack *et al.,* 2015)	No comparisons to other studies done	"Distance-based transects provided estimates of density of carnivores with greater accuracy (density was underestimated by up to 65% in fixed-width transects) and precision (lower CVs were achieved in distance-based transects) than fixed-width transect" (Durant *et al.,* 2010)

2.5 Discussion

Over the past several decades, many studies have developed and evaluated methods for estimating density of lions in a variety of ecosystems (Braczkowski *et al.,* 2020a; Elliot *et al.,* 2020; Funston *et al.,* 2010; Stander, 1998). Broadly, methods to survey lions for abundance have included index-based methods, such as spoor counts (Funston *et al.,* 2010; Stander, 1998) and call-ups (Brink *et al.,* 2012; Midlane *et al.,* 2015), and capture-recapture frameworks that use camera traps (Braczkowski *et al.,* 2020a; Elliot & Gopalaswamy, 2017), direct observations (Elliot *et al.,* 2020; Elliot & Gopalaswamy, 2017), or genetic data (Tende *et al.,* 2010). Long-term direct monitoring of individuals (Elliot *et al.,* 2020; Mweetwa *et al.,* 2018) has also been employed by some longitudinal studies to monitor populations (Blackburn *et al.,* 2016; Brink *et al.,* 2012; Mweetwa *et al.,* 2018). These methods have evolved through time, making use of technological advances (e.g. improved camera traps) and more robust analytical approaches (e.g., SECR analyses).

The most robust, accurate, and precise methods for counting lions, and indeed most large carnivores, involve individual identification (Beukes *et al.,* 2017; Braczkowski *et al.,* 2020a; Dröge *et al.,* 2020; Strampelli *et al.,* 2022b; Tende *et al.,* 2014). These include direct and intensive monitoring, camera trapping, and genetic surveys. Identification of lions, which are not clearly marked with spots or stripes, can be challenging. Individual identification of lions began in the mid-1960's by George Schaller and Brian Bertram in the Serengeti, Tanzania (Rees, 2017). Whisker spot patterns were then also used to identify and count individual lions between 1968 and 1970 in Nairobi National Park, Kenya (Pennycuick & Rudnai, 1970; Rudnai, 1973). Although this method was only used in small, relatively habituated populations where identifying lions was less challenging than in many wild populations (Smuts, 1976). Some studies have used artificial marks to identify individuals. For example, branding was used in Kruger National Park, South Africa, in the mid-1970s (Bryden, 1976; Smuts, 1976; Smuts *et al.,* 1977) and in the Kalahari Gemsbok National Park, South Africa (Mills *et al.,* 1978). The earliest published method in our review (1991) assessed the demography of lions in Etosha National Park (Namibia) using direct observations analysed in a capture-recapture framework between 1985 and 1989 (Stander, 1991). More recently, advances in the resolution and clarity of camera trap images have allowed scientists to identify individuals using whisker spots, scars, ear notches, and other marks (Braczkowski *et al.,* 2020a). Though many of these change over time, they are unlikely to change dramatically within a single survey period. Camera trap surveys have been used to estimate lion densities in Tanzania, Uganda and Zimbabwe (Cusack *et al.,* 2015; Kane *et al.,* 2015; Strampelli *et al.,* 2022b). The first published studies for camera trap surveys combined with SECR modelling for surveying lions were published in 2015, with the added benefit that this is an effective way to survey multiple species simultaneously (Kane *et al.,* 2015; Rich *et al.,* 2019; Strampelli *et al.,* 2022b). Individual identification is further enhanced using Artificial Intelligence (AI). Machine learning algorithms, such as those designed by WildBook, Tech4Conservation, and the African Carnivore Book can now distinguish individuals with increasing accuracy (Verschueren *et al.,* 2023). Between 2008 and 2014, the use of DNA in lion faecal matter to identify individual lions was used to determine the minimum number of lions in a population (Tende *et al.,* 2014, 2010). While this method has not been used widely for lions, it has been used with detection dogs to determine population numbers of cheetahs in Western Zambia (Becker *et al.,* 2017), where 27 scat samples were found to provide a population estimate of 8-14 individuals (Becker *et al.,* 2017). This method holds potential to be used more widely for lions, especially within an SECR framework, and has been used for other carnivores (Karmacharya *et al.,* 2011; Long *et al.,* 2011; McCarthy *et al.,* 2008; Thompson *et al.,* 2012).

Due to the intensive input of time and resources required to calculate reliable population estimates using many of the individual identification methods, especially over large systems, spoor counts and call up surveys were developed (Ogutu & Dublin, 1998; Stander, 1998). Due to their broad applicability and relatively low cost, spoor counts have been a popular method used to survey lions in many areas across the species' range (Funston *et al.,* 2010; Stander, 1998). Initially, spoor counts were frequently used and implemented in southern Africa (Funston *et al.,* 2010; Stander, 1998; Winterbach *et al.,* 2016), while call up surveys were used in East Africa (Kiffner *et al.,* 2009, 2008; Ogutu *et al.,* 2005; Ogutu & Dublin, 1998). However, recent research suggests that this method produces high variation in abundance estimates with wide confidence intervals, making it difficult to detect even large changes in population (Dröge *et al.,* 2020). Call up surveys have also been used for decades across a variety of habitats, but also carry serious biases relating to individual responsiveness, and the possibility of undercounting shy individuals in areas with lions that are wary because of human persecution (Midlane *et al.,* 2015).

As technology and analytical techniques have evolved and these index-based methods have been repeatedly tested, it has become apparent that they are not reliable for estimating density and abundance (Belant *et al.,* 2019; Dröge *et al.,* 2020). For example, a simulation study published in 2020 found that spoor surveys generate estimates that either overstate precision or are too imprecise to be of any value (Dröge *et al.,* 2020). As a result, these methods are no longer recommended for counting lions (Dröge *et al.,* 2020). Nevertheless, they remain valuable tools for confirming lion presence in study areas, to understand space use and human impacts in an occupancy framework, and to map lion distributions (Henschel *et al.,* 2016; Petracca *et al.,* 2020). We caution the utility of estimating lion population size from methods that are proven to be unreliable for estimating abundance, especially to inform conservation and management decisions. This would particularly apply to estimates derived from questionnaire or interview type surveys (Dröge *et al.,* 2020; Mesochina *et al.,* 2010a, 2010b; Riggio *et al.,* 2013). The latter method requires collecting information on lion observations to determine frequency of occurrence and applying it to an equation that accounts for variables to estimate a population size of lions (Jacobson *et al.,* 2013; Mesochina *et al.,* 2010b, 2010a; Riggio *et al.,* 2013). This method has a strong likelihood of overestimating numbers and is scientifically questionable (Riggio *et al.,* 2013). Additionally, spoor surveys have also been shown to produce questionable estimates that are not reliable (Belant *et al.,* 2019; Dröge *et al.,* 2020; Midlane *et al.,* 2015).

Other methods have been implemented to survey lions, but not extensively tested for robustness. Roar counts were tested in the Selous Game Reserve in 1974, but no further studies utilised this method (Rodgers, 1973). While lions do reply to playbacks of conspecifics, this is not as predictable as seen with wolves and not all pride members vocalise in response to calls. In 2011, in the Serengeti National Park (Tanzania), distance-based surveys successfully demonstrated that trends in lion abundance could be understood (Durant *et al.,* 2011). However, this approach can only be implemented in systems such as the Serengeti where the landscape and sparse vegetative cover allow animals to be seen easily over relatively large distances.

We identified several key knowledge gaps that exist across the seven survey methods we identified. Broadly, these gaps included the need to account for detection probability and understand its impact on lions in different contexts, clarifying the efficacy and reliability of equipment used (Mwampeta *et al.,* 2022), the need to develop a robust a-priori survey design for each survey and to investigate opportunities for improvement, and implementing and refining analytical model design and validation techniques (Belant *et al.,* 2016; Strampelli *et al.,* 2022b). Additionally, there is limited information regarding the cost of these methods. A cost analysis comparing the different suitable methods would be beneficial, as this kind of information is limited in the literature (Midlane *et al.,* 2015) and would reveal the true financial cost of each survey method which would give practitioners with limited resources important information (Midlane *et al.,* 2015).

It appears that lion populations in East and southern Africa are surveyed more than those in Central or West Africa. This supports the findings of other studies that found biases towards large carnivore surveys in the same regions (Strampelli *et al.,* 2022a). Published lion population/abundance surveys are not available for Angola, Chad, Democratic Republic of the Congo (DRC), Malawi, Rwanda, Somalia and South Sudan. As most of the small populations in Malawi and Rwanda are recent reintroductions into fully fenced and intensively monitored reserves, urgent surveys may not be a priority. However, large expanses of potential lion range in Chad, DRC, and South Sudan have never been formally surveyed, and considerable uncertainty exists regarding lion status there. This is potentially because of long periods of political unrest and insecurity in these countries (Angelo & McGuinness, 2012; Ploch, 2010; van Damme & de Cordier, 2017). Surveys in these areas should be prioritised (African Lion Database, Unpublished Data. 2022). Similar data gaps have been found for other carnivores where there is a strong negative bias for carnivore research (Strampelli *et al.,* 2022a). Notably, survey results (population numbers) are often only published years after survey work has been completed (Figure 2-5). This is potentially problematic as decisions made with available (published) information, which are likely to be outdated by the time they are published, could result in conservation action or management decisions being made based on information that might no longer be correct.

Due to the globalisation of conservation and science and the need to understand and compare lion population status across their range, there is a growing consensus that standardised survey methodologies for the counting of lions is urgently needed. Standardised survey methodologies will greatly enhance our capacity to assess the need for conservation intervention, to measure the impacts of ongoing conservation efforts across their range, and to direct conservation funding and other resources to the most critical locations.

One of the challenges in implementing survey methods is that the most appropriate methodology is not always selected, and guidelines for standardised implementation are not available. While some studies use the same method, they may not always follow the exact same methodological implementation, and this renders the results incomparable across both space and time. For example, not taking sampling or observer bias into account during study design and during implementation could result in limited replication of the study in subsequent years, thus preventing temporal comparison of results. This, combined with the range of survey methods available and the sometimes-contradicting information, highlights the need for standardised guidelines on surveying lions (Dröge *et al.,* 2020; Elliot & Gopalaswamy, 2017). To better track population trends over time, standardised methodology should be repeated at set intervals. This has been valuable for monitoring local populations, instrumental in identifying declines (Bauer *et al.,* 2015) and has led to policy change at the local and national level (Becker *et al.,* 2013). Directly coordinated and comparable estimates obtained over space and time using standardised and rigorous methodology will allow for easier identification of range-wide population trends. This will also provide a reliable source for deciding where to direct limited resources to lion populations that are most at risk, and to compare the effectiveness of conservation interventions.

A decision tool, or framework, should be developed that will guide researchers and protected area managers on how best to select the most appropriate method based on their research objectives and the resources available to them (e.g., funding, human capital, and time availability). Based on the literature within our review, we provide a preliminary guidance tool to demonstrate how a decision tool could assist in selecting the most suitable methodology (Figure 2-6). For example, if population abundance needs to be determined, call up and spoor surveys should probably not be used, but direct observation-based surveys, distance-based surveys, camera trapping with capture-recapture, and genetic studies would be more suitable lion survey methods. Whether there are sufficient resources available will also factor into decision making (Figure 2-6). There is an urgent need for greater consensus on methods and to develop a unified framework for deciding when to employ which methods. While we have attempted to do that based on the information in this review, a more robust tool with input from survey experts would be beneficial. In addition, including elements on the cost of conducting surveys or monitoring per square kilometre would be immensely valuable.

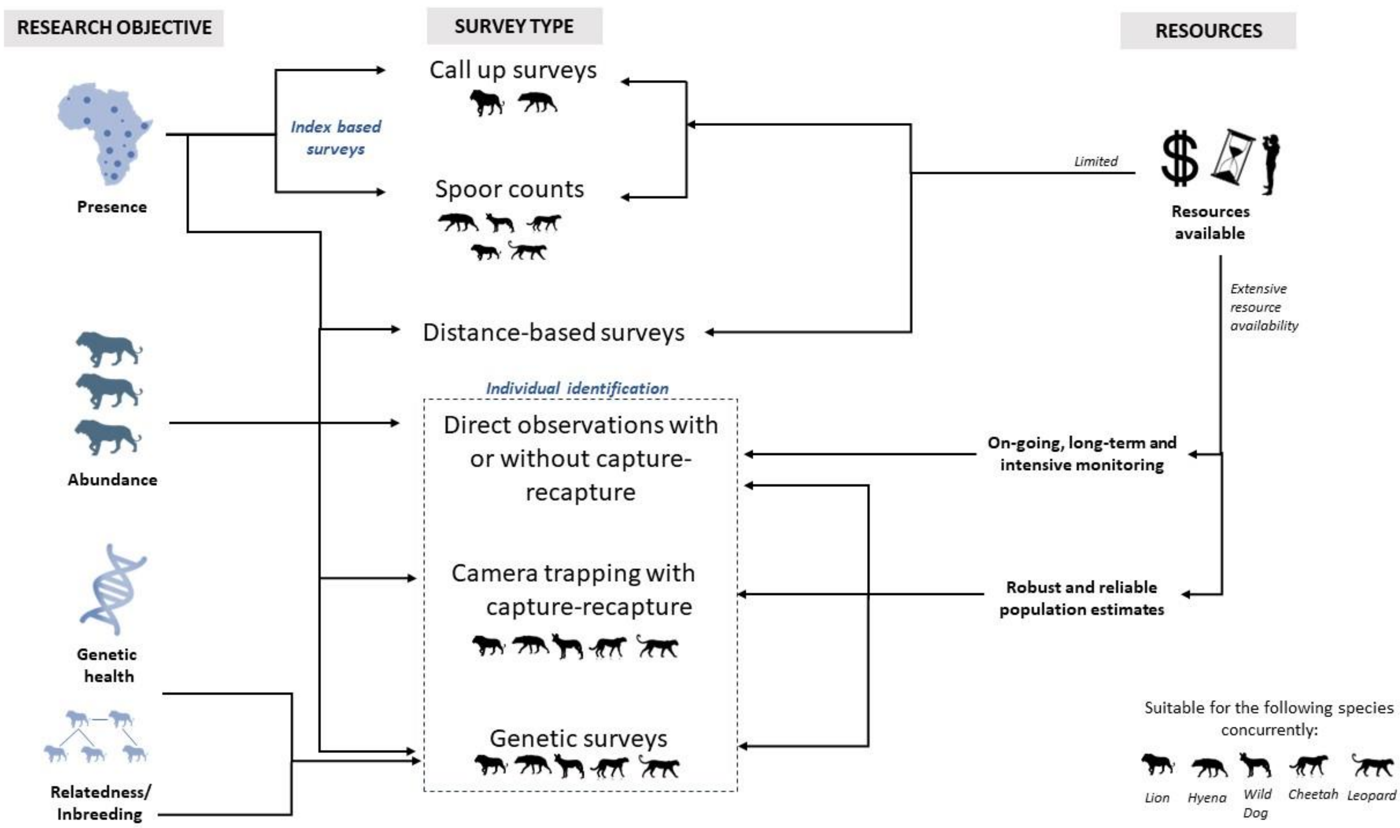

Figure 2-6 High-level overview of the methods used to survey lions relative to research primary research objective.

The methods discussed within this review, as well as their strengths, weaknesses, and reliability are broadly applicable to other large carnivores globally (Balme *et al.,* 2009; Becker *et al.,* 2017; Gompper *et al.,* 1973; Gopalaswamy *et al.,* 2012; Karanth, 1995; Karanth & Nichols, 2010;

Marnewick *et al.,* 2008; Wilson & Delahay, 2001). Just as various methods were employed and refined for surveying lions, researchers studying other species should adapt and develop survey methods that are tailored to the specific ecological and behavioural characteristics of the target species. Many of these methods were originally developed and refined to count elusive species like tigers and jaguars (Gopalaswamy *et al.,* 2012; Karanth & Nichols, 2010). Few large carnivores, other than lions, can be monitored through direct or intensive survey methods. This has been attempted for some species, such as leopards (Balme *et al.,* 2019). While these have provided insights into population demography, survivorship, reproductive success, and other valuable information, they are only applicable over a relatively small area. Camera traps and genetic sampling hold the most promise for surveying large carnivores, and some small carnivores with distinguishable markings (Bahaa-el-din *et al.,* 2016). These non-invasive techniques allow us to count even the most elusive carnivores (Bahaa-el-din *et al.,* 2016). However, when surveying for multiple species, particularly using camera traps, it is critical to understand how one species impacts the presence of others. For example, African wild dogs avoid areas of high lion activity. If the area surveyed is too small or biased towards areas of known lion activity, this could lead to misleading results indicating low African wild dog density (Dröge *et al.,* 2017). Carnivores also operate at different spatial scales. Surveys intended for wide ranging species like lions or wild dogs may create data gaps for species with smaller home ranges that ultimately preclude density analysis for the smaller species because of a lack of recaptures, a key requirement for capture-recapture frameworks. Nevertheless, camera trap and genetic surveys are powerful tools for gathering data on multiple species at once, thereby maximising the impact of conservation resources.

2.6 Conclusions

Our findings highlight the need for minimum standards for harmonised survey methods, including consensus on the prohibitive limitations of some older methods. This would ensure that population estimates are reliable and comparable. We also encourage that surveys be carried out where data gaps exist across lion range in Africa to provide a clearer understanding of the status of lions throughout Africa. Based on the literature, we determine that reliable estimates of lions can only be estimated through direct observation (both with and without capture recapture frameworks) surveys and camera trap-based capture-recapture surveys.

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2.8 Supplementary material

Supplementary Table 2-1. Several weaknesses were identified for each method.

METHOD	WEAKNESS/DISADVANTAGES OF THE METHOD TO SURVEY LIONS	KEY REFERENCES
Call up	"Limited utility for surveying other carnivore species due to changing response rates of spotted hyaena in areas of high lion response rates".	Midlane *et al.,* 2015
	"Bright light emitted can disturb, cause avoidance and reduce animal detection".	Mwampeta *et al.,* 2022
	"Lion response can decline with multiple exposures. The disadvantage of using multiple sessions has been habituation by target species, resulting in poor estimates of precision".	Belant *et al.,* 2017
	Not useful in areas where lions are hunted/persecuted.	Kiffner *et al.,* 2009
	Under lower densities this technique may not be functional.	Ogutu & Dublin 1998
	Behavioural responses are flexible and therefore subject to influences of several intrinsic and extrinsic factors.	Young-Overton *et al.,* 2014
	Response rates of lions and spotted hyaenas to distress calls may be lower if prey is more accessible during droughts.	Ferreira & Viljoen 2022
Spoor	"May be less useful in areas where carnivores are heavily persecuted, as these animals are less likely to travel on roads".	Midlane *et al.,* 2015; Yirga *et al.,* 2021
	Requires highly experienced trackers and fresh tracks.	Midlane *et al.,* 2015; Henschel *et al.,* 2020
	"Track detection is more challenging when high frequency of road use by tourists destroys evidence of lion tracks. These sources of error, the consequences often resulting in outlier estimates, restrict the robust use of track indices to determine trends in the population".	Beukes *et al.,* 2017
	"Track detection varies across substrates – there are a number of roads in the study area where the road substrate has been transformed from sand into gravel, making tracks more difficult to detect".	Beukes *et al.,* 2017
	Large discrepancies "in track index estimates imposes large sampling effort to derive robust estimates from which trends can be detected, particularly in the dune savanna habitat".	Beukes *et al.,* 2017
	"Require much greater sampling effort in order to compensate for the lack of precision. The large sampling effort required could render a method such as track indices impracticable, as resource constraints often restrain research design and could bias results".	Beukes *et al.,* 2017
	"Estimates either overstate precision or are too imprecise to be meaningful".	Belant *et al.,* 2019; Droge *et al.,* 2020
	"Evident that neither a capturing of the true population size ~95% of the time nor a HRCIW of <50% occurs with this method".	Droge *et al.,* 2020
	"Do not provide reliable estimates to monitor populations".	Droge *et al.,* 2020
	"Method frequently produced population estimates that differed more than fivefold, despite no change in the true population size".	Droge *et al.,* 2020
	Do not adhere to IUCN criteria.	Droge *et al.,* 2020
	The validity of density estimates below 0.27 carnivores/100km^2 (<0.88 tracks/100km) is questionable.	Winterbach *et al.,* 2016
	Estimates and trends obtained from track surveys in low density populations should be interpreted with caution.	Winterbach *et al.,* 2016
	"Large confidence intervals in population estimates and consequent imprecision in detecting trends over time".	Henschel *et al.,* 2020

Camera trapping	Methods for estimating density remain largely focused on marked species.	Cusack *et al.,* 2015
	Current drawback of the REM is its reliance on independent estimates of animal speed of movement and camera detection zone dimensions.	Cusack *et al.,* 2015
	Scaling the method to larger areas is likely to be costly and/or "challenging to implement over particularly vast areas, particularly given the ongoing shortage in conservation funding for African PAs".	Strampelli *et al.,* 2022
	"Unlikely that many large PAs will have a sufficiently developed road network to allow for the access of all areas by road, considerably increasing the logistical requirements of the fieldwork".	Strampelli *et al.,* 2022
	"Deploying and checking such a large number of cameras would also require considerable time, as would the identification of a considerably greater number of individuals".	Strampelli *et al.,* 2022
	"The use of camera trap photographs for individual identification proves inadequate for lions. Lions have few obvious features from which to identify individuals".	Beukes *et al.,* 2017
Individual identification/intensive monitoring	"Registering individuals, particularly at low population densities, takes large amounts of resources and time".	Beukes *et al.,* 2017
	"Conducting mark-recapture through individual identification may not be feasible in environments where low encounter rates or poor visibility restrict observations".	Beukes *et al.,* 2017
	"Individual identification and enumeration through mark-recapture in this manner may only be feasible in similar arid environments with low vegetation density".	Beukes *et al.,* 2017
	"Mark-recapture is a relatively intensive technique, with large resource requirements".	Beukes *et al.,* 2017
Distance-based Surveys	Wide confidence intervals.	Durant *et al.,* 2011
Faecal DNA	DNA might be degraded resulting in low quantity and ⁄ or poor quality DNA available for use. This can lead to scoring errors such as false alleles (when an allele appears to have more or fewer repeats than it truly has) and 'allelic dropout' where only one allele of a heterozygous is often detected, thereby producing false homozygotes leading to genotyping errors.	Tende *et al.,* 2010
	Amplification failures during PCR and false alleles can also affect population size estimates.	Tende *et al.,* 2010

Supplementary Table 2-2. Several advantage/strengths were identified for each method.

METHOD	ADVANTAGE/STRENGTH OF THE METHOD TO SURVEY LIONS	KEY REFERENCES
Call up	More precise than spoor counts, "despite this method requiring less than half the number of survey days, 23% fewer survey hours and 38% fewer kilometres driven".	Midlane *et al.,* 2015; Belant *et al.,* 2016
	Comparatively high detection efficiency.	Henschel *et al.,* 2014
	Efficient and effective.	Ogutu *et al.,* 2005; Bauer 2007; Bauer *et al.,* 2015
	Given that lion and hyaena responses are positively correlated, it is possible to simultaneously estimate lion and hyaena density from a single survey.	Ogutu & Dublin 1998
	May be used as a rapid, easy to execute, relatively inexpensive.	Ogutu & Dublin 1998
	Preferred survey technique for lions in mesic savannah.	Young-Overton *et al.,* 2014
	A potentially less biased method to assess distribution and density of elusive carnivores on a broad scale.	Cozzi *et al.,* 2013
	Limited equipment, time (multiple calling stations can be conducted in a night).	Cozzi *et al.,* 2013
	Limited skills/training requirements.	Cozzi *et al.,* 2013
	Can be conducted in various landscapes independent of substrate and habitat and across large areas. They are effective in savanna and forested systems.	Cozzi *et al.,* 2013; Belant *et al.,* 2016
	Calling stations have been used to investigate spatial and temporal variation in density and distribution across heterogeneous landscapes and habitats.	Cozzi *et al.,* 2013
	Repeated call-in surveys "can be conducted in a shorter time period than some other methods (e.g., remote cameras)".	Belant *et al.,* 2016; Cozzi *et al.,* 2013
	Low cost.	Ogutu *et al.,* 2005; Henschel *et al.,* 2014; Cozzi *et al.,* 2013
	Moonlight does not seem to have an effect on response to playback sounds.	Kiffner *et al.,* 2008
	Low effort.	Henschel *et al.,* 2014
Spoor	"Multiple carnivore species can be surveyed simultaneously, including spotted hyaena, and possibly leopard and cheetah".	Midlane *et al.,* 2015
	"Comparatively high detection efficiency, and low effort and cost".	Henschel *et al.,* 2014; Bakker *et al.,* 2020
	Cost effective.	Funston *et al.,* 2010; Brink *et al.,* 2012; Henschel *et al.,* 2014; Winterbach *et al.,* 2016; Bakker *et al.,* 2020; Droge *et al.,* 2020; Henschel *et al.,* 2020
	"Easy to implement, multi-scale and effective tool for the carnivore population monitoring".	Bakker *et al.,* 2020
	"Easily repeated, and can provide reliable estimates of the population size together with a measure of precision".	Funston *et al.,* 2010
	"Can be used to census shy animals such as those hunted individuals".	Brink *et al.,* 2012
	Cover large spatial extents.	Winterbach *et al.,* 2016; Belant *et al.,* 2019
	"Robust and repeatable technique for assessing large carnivore densities, distribution and population size".	Henschel *et al.,* 2020
	"Cost, effort and feasibility are major concerns in any population survey effort; spoor transects may be less expensive and simpler to carry out than sight–resight techniques and are at present one of the few methods to reliably document persecuted carnivores".	Henschel *et al.,* 2020
	"Transect data can also be incorporated into occupancy models that explicitly account for the spatial dependence of adjacent transect segments, permitting the estimation of species occurrence while accommodating imperfect detection".	Henschel *et al.,* 2020

	“A simple, standardised, repeatable and relatively inexpensive method for estimating African carnivore densities in large areas”.	Henschel *et al.,* 2020
	Accumulate unbiased observations quickly, in environments where animal tracks are readily visible.	Keeping 2014
Camera trapping	Determine occupancy for other species concurrently.	Kane *et al.,* 2015
	“The SMR model demonstrated here provides a versatile and relatively easily implemented monitoring strategy and provides useful estimates of an elusive, low density population”.	Kane *et al.,* 2015
	“Bayesian inference is not constrained by asymptotic assumptions and allows for unbiased and precise estimates even with small sample sizes and low detection rates”.	Kane *et al.,* 2015
	Cost-effective way of gathering information on multiple species.	Cusack *et al.,* 2015
	When relying on natural marks, we expect that many practitioners will also have difficulty distinguishing between these unresolved classifications and face similar limitations. Thus, we encourage the development of a likelihood-based SMR model where detections of unknown status could be grouped together potentially as an overall correction factor for detection.	Rich *et al.,* 2019
	A single camera trap survey can be used to estimate the densities of multiple small- to wide-ranging species.	Rich *et al.,* 2019
Individual identification/intensive monitoring	Most robust method for defining population characteristics.	Beukes *et al.,* 2017
	“SECR methods integrate the individual identity and landscape use of African lions in the density estimation process while explicitly accounting for search effort”.	Braczkowski *et al.,* 2020
	“It can be used under a citizen-science approach. This could make the costs of such surveys considerably lower than traditional methods”.	Braczkowski *et al.,* 2020
	Can be used for small sample sizes.	Elliot *et al.,* 2020
	“They provide an appropriate standardised framework to monitor species that occur in diverse habitats, at varying densities” and with changeable behaviour.	Elliot *et al.,* 2020
	Some difficulties in finding and monitoring low density, wide-ranging, and declining species. “This uncertainty, however, was much less than that of other methods commonly used for large carnivores”.	Rosenblatt *et al.,* 2014
	“Intensive monitoring produced estimates with 3X to 7X greater precision than rapid indices of abundance”.	Rosenblatt *et al.,* 2014
	Provide repeatable and inexpensive measures of some population parameters.	Stander 1998
Faecal DNA	Non-invasive sampling technique.	Tende *et al.,* 2010
	Works well for secretive species and ⁄ or in dense habitats.	Tende *et al.,* 2010
	Allows for genetic studies of wild animals without trapping them or even observing them.	Tende *et al.,* 2010
	Non-invasive sampling techniques can increase sample sizes, hence enhancing estimation of important population parameters.	Tende *et al.,* 2010
	Genetic sampling often provides data on the health status of a population, like inbreeding, which cannot be obtained easily using observation in the field.	Tende *et al.,* 2010
Distance-based surveys	Can be completed within 3 days.	Durant *et al.,* 2011
	Relatively cost effective.	Durant *et al.,* 2011
	Applicable to other habitats with similar visibility, such as grassland or desert.	Durant *et al.,* 2011
	Combining rare species with similar sized, but more commonly observed, species aids calculation of the detection function, making the method potentially useful for other habitats where visibility is reduced and detection lower.	Durant *et al.,* 2011

Supplementary material – Descriptive narrative for Table 2.4:

Research questions

This section was completed by looking through the study objectives of each of the 65 papers and determining their key research questions.

Direct or indirect method

A method was determined to be direct if there was direct involvement of researchers with lions. An indirect method would be one where the researchers have no physical interaction with the species at all.

Level of invasiveness

This was determined by reviewing the methods of each paper and determining an overall score for each method.

We viewed spoor surveys and genetic sampling as the least invasive methods as the researchers only look for and record tracks/spoors (Stander, 1998; Winterbach *et al.,* 2016) or gather faecal matter from lion (Tende *et al.,* 2014, 2010); neither requiring direct contact with lions. We then proposed that Distance-based sampling was also fairly less invasive but there is minimal contact with lions (Durant *et al.,* 2011). While researchers have no interaction with lions while carrying out camera trapping studies, the cameras themselves do still have some level of interaction with lions, particularly when using white-flash models (Strampelli *et al.,* 2022). Call up surveys were also determined to be relatively invasive as the researchers are influencing the species behaviour through the use of routine (and sometimes regular) call up stations (Belant *et al.,* 2017) and the spotlight, particularly without a red filter, can cause significant disturbance (Mwampeta *et al.,* 2022). Individual identification was determined to be the most invasive because researchers need to locate individuals and get relatively close to them in order to capture individual identifications and in some cases, radio or satellite collars are used (Beukes *et al.,* 2017; Bouley *et al.,* 2018; Braczkowski *et al.,* 2020; Midlane *et al.,* 2015). Satellite tracking and radiotelemetry are certainly the most invasive uses as it requires individuals to be immobilised to fit and remove tracking collars (unless an automatic drop-off device is used) (10). This method requires the most physical interaction with the species and there are risks to the lions when collars are fitted.

Land use type

This was determined by following the suggestions of researchers and paper authors regarding the land use type to deploy these methods which was generally detailed in the study area section of the paper.

Habitat type

This was determined by following the suggestions of researchers and paper authors (of the 65 papers) regarding the habitat use where this method is most suitably deployed. For example, (Young-Overton *et al.,* (2014), suggests that call-ups are the most suitable survey technique for lions in mesic savannah.

Population density suitability

This was also determined by following the suggestions given in the 65 papers. However, this information was not always presented.

Ease of implementation

Methods were ranked in order of easiest to implement (ranking a one) to hardest to implement (ranking as 6). We determined these scores based on what the literature in our review indicated.

We suggest that call up surveys are arguably to easiest to implement as limited specialised equipment is needed and require less skill than other methods (Midlane *et al.,* 2015; Ogutu & Dublin, 1998). Although call ups do require more detailed study design (e.g. calibration, number of stations, etc.). We then suggest that following call up surveys, spoor surveys are also fairly easy to implement based on the similar reasons as spoor surveys (Midlane *et al.,* 2015; Mohammed *et al.,* 2019). Spoor surveys are also among the easiest methods to implement as there is very little equipment required, they can be done over a short period of time and are not resource intensive (Funston *et al.,* 2010; Henschel *et al.,* 2020; Keeping, 2014; Stander, 1998; Winterbach *et al.,* 2016). However, they do require some skill to reliably and accurately identify spoor (Henschel *et al.,* 2020; Stander, 1998). Distance-based sampling, with relatively quick study periods, does potentially require some training and experience to carry out than other methods (Durant *et al.,* 2011). Direct observations through individual identification can be relatively easy to implement but does require significant time to individually identify each lion within the study population (Beukes *et al.,* 2017; Braczkowski *et al.,* 2020; Ogutu & Dublin, 2002). In addition to being costly, it can be both time and resource consuming. If satellite collars or radiotelemetry methods are used then it can challenging to implement (Rosenblatt *et al.,* 2014; Schuette *et al.,* 2013).

Firstly, collars are very expensive, procedures often require a veterinarian or particular set of expertise to dart individuals which can also be costly. These types of studies often require a longer study period than the previously mentioned methods. Genetic surveys, while not invasive and indirect, require the use of a specialised lab to analyse the material (although this could be outsourced). The costs involved can be heavy if areas require many samples. There may also be the added challenge of locating lion scats unless researchers are following individuals and waiting for the appropriate sample to be available, however, this was not clearly stated in the literature. We assume that camera trapping is also not particularly easy to implement as there needs to be significant study design to effectively carry out such a survey and it is essential that it is well designed (Kane *et al.,* 2015; Strampelli *et al.,* 2022). This expertise might not always be available. In addition, the initial financial layout for cameras would be quite high. Camera trapping would require a longer period of time to adequately carry out (especially when compared to spoor and call up surveys). Lastly, cleaning and analysing the data would also require expertise and would take longer than other methods.

Cost of implementation

Methods were ranked in order of the cheapest (scoring a one) to the most expensive (scoring a seven) to implement. We considered the time it would take to carry out the survey, the resources required, and the equipment needed.

We determined that spoor surveys are the cheapest to implement as there is little required in terms of equipment, it can be carried out rapidly and with a relatively small team (Henschel *et al.,* 2020; Midlane *et al.,* 2015, 2014). Based on Midlane *et al.,* (2015) who concluded that call ups were more expensive than spoor surveys, we ranked them second. Individual identification can be relatively time consuming and would require more exploration around the study area in an attempt to identify all lions. We ranked Distance-based sampling fourth as some equipment (such as a rangefinder) is required, larger teams and travelling is required. Due to the costs of genetic analysis and transporting samples from the study site to the respective laboratory, we ranked genetic studies as five. Following genetic studies, we determined that camera trapping studies were ranked the most expensive studies to carry out due to the initial expense of camera traps, memory cards and batteries. This kind of study would also require significant time in the field setting up the traps, downloading photos and replacing memory cards as well as actually analysing the data. Although it must be noted that subsequent studies would be significantly cheaper seen as the initial equipment has been purchased. Lastly, studies involving satellite devices or radiotelemetry are ranked sixth as this kind of equipment is very expensive.

Time requirement

By examining the study periods of each of the studies in the 65 papers included in this review, we were able to rank the methods in terms of quickest to carry out (ranking as one) to the longest to carry out (ranking seven).

We determined that spoor surveys and call ups with very quick to carry out (Henschel *et al.,* 2020; Midlane *et al.,* 2015, 2014), followed by distance-sampling surveys (Durant *et al.,* 2011). Genetic surveys were ranked fourth as time is needed to gather samples, send to the lab and then analyse at a laboratory. Direct observation studies ranked fifth and as they often require long periods of intensive monitoring (Braczkowski *et al.,* 2020). Lastly, we determine that camera trapping studies are the longest to carry out because both the field work and the study analysis phase are both intensive (Strampelli *et al.,* 2022).

Equipment

This was complied based on information provided in the methodological sections in the peer-reviewed papers.

Key comparisons with other studies done

Here, we make reference to comparisons made with other studies. We only included those studies which directly compared methods such as Midlane *et al.,* (2015), Bouley *et al.,* (2018), *Beukes et al.,* 2017.

Detect trends

We simply made a note on whether this methodology is able to detect trends in population over time based on the literature.

Reliability in estimating abundance

We stated whether the method was reliable for estimating lion populations based on the literature. Numerous studies indicate that spoor surveys are not reliable for estimating population abundance (Belant *et al.,* 2019; Midlane *et al.,* 2015, 2014). Direct observation studies with capture recapture, intensive monitoring studies and camera trap surveys do provide reliable measures of abundance (Beukes *et al.,* 2017; Bouley *et al.,* 2018; Kane *et al.,* 2015; Ogutu & Dublin, 1998; Strampelli *et al.,* 2022). We were only able to assess spoor counts, call ups, direct observations and camera trapping. According to Midlane *et al.,* (2015), call up surveys are more precise when compared to spoor counts. Therefore, we stated that of the three methods, spoor surveys were the least reliable followed by call-ups. Based on the literature, we know that camera trapping is more reliable than these two methods but there is no evidence to confirm whether Distance-based sampling, genetic sampling, individual identification or methods using satellite collars are more reliable when compared to other methods.

Precision and bias

There was limited available literature regarding which methods are more accurate than another when it came to determining precision, bias and accuracy of each method. However, we summarised what was available.

Confidence intervals

Here, we made comment of notes provided by authors regarding the confidence intervals of the results when using the respective study method.

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CHAPTER 3

Red List Assessments as critical tools for conservation: Updating the Global status of the Lion, *Panthera leo* in Africa

Please note that this chapter is an overview, placed in the context of this PhD thesis, based on the recent Red list assessment for lion: Nicholson, S., Bauer, B., Strampelli, S., Sogbohossou, E., Ikanda, D., Tumenta, P., Venkataraman, M., Chapron, G., & Loveridge, A. 2023. Global Lion (*Panthera leo*) Red List Assessment. Available at: https://www.iucnredlist.org/species/15951/231696234

3.1 Abstract

Red List assessments for species are critical for conservation as they provide a systematic and standardised evaluation of the extinction risk faced by various organisms globally, serving as a crucial tool for prioritising conservation efforts. Red List assessments aid in identifying species that are at high risk of extinction and assist with guiding conservation strategies and policies to mitigate threats and ensure the preservation of biodiversity on a global, regional and local scale. As a globally important species, lions are assessed globally every four to five years but were last assessed in 2016. The recent IUCN Red List assessment was completed for the species this year (2023). Key threats to the species were identified as: habitat loss, reduction in suitable prey, indirect poaching, and targeted poaching for parts. Extant lion range is considerably fragmented and is presently estimated to be ~1,571,296 km^2. This is an estimated 36 % range decline since 2002 (three lion generations), when range was estimated to be ~2,460,986 km^2. This decline, which is likely to continue, reflects a combination of recent known and inferred decline, as well as improved knowledge. Based on this significant decline in range, which is synonymous with a decline in population size and abundance, a 36 % decline in population numbers for the lions was suspected. Therefore, lions globally met the requirements for a Vulnerable listing (Red List criteria A2abcd). Based on ongoing threats to the species, along with my co-assessors, I recommended that the lion is a species under observation, that its threats and pressures are closely monitored, and that reassessment is done after a minimum of three years or as soon as more information emerges. This Red List assessments provides a standardised and globally recognised framework for gauging the extinction risk faced by lions, informing policymakers, conservationists, and researchers about the urgent needs and priorities for lion conservation. By offering a comprehensive overview of the species' status and trends, Red List assessments play a pivotal role in shaping targeted and effective strategies, ensuring the long-term survival of lions and other species in their ecosystems.

3.2 Introduction

Global biodiversity is presently experiencing a primarily human-driven extinction crisis (Nazarevich, 2015; Davis *et al.,* 2018; Ceballos *et al.,* 2020; Torres-Romero *et al.,* 2020; Rull, 2022). Our planet is experiencing unprecedented rates of accelerated biodiversity loss and existing threats are continuing to place unnatural pressure on remaining species (Andermann *et al.,* 2020; Compson *et al.,* 2020; Cowie *et al.,* 2022). Human activity has been considered as the main driver leading to animal population reduction and range contractions of many mammal species (Wolf & Ripple, 2017; Andermann *et al.,* 2020). Human population size has been able to predict past extinctions with 96 % accuracy (Andermann *et al.,* 2020). With increasing human populations, it is expected that human-driven threats like poaching, habitat conversion, increasing livestock density, human-wildlife conflict will increase (Pimm *et al.,* 2014; Andermann *et al.,* 2020; Ceballos *et al.,* 2020; Torres-Romero *et al.,* 2020). The biodiversity crisis is irreversible and remains one of the most serious environmental threats facing the planet (Ceballos *et al.,* 2020). The complex web which all species form a part of, and the ecosystem services they deliver, is eroded when species within the web disappear (Ceballos *et al.,* 2020). For example, bee pollinators play essential roles in crop production and productivity and are responsible for the persistence of many plant species, improving the quality of the environments they occur in (Wahengbam *et al.,* 2019; Kratschmer *et al.,* 2021). Globally, bumble bee species are in severe decline, with some going extinct altogether, due to habitat loss, pesticide use and changes in climate (Wahengbam *et al.,* 2019). This ongoing decline threatens countless plant species, and its ripple effect of their decline extends to other species dependent on these plants, disrupting the delicate ecosystem balance (Wahengbam *et al.,* 2019; Kratschmer *et al.,* 2021). This exemplifies how the erosion of individual species can have cascading effects on the entire web of life and the species within it, including our own (Wahengbam *et al.,* 2019; Kratschmer *et al.,* 2021).

In the face of an increasing global human population (Gu *et al.,* 2021) and limited resources (Lindsey *et al.,* 2018), prioritising investments in preventing the extinction of species at risk becomes a pragmatic necessity (Bottrill *et al.,* 2008; Hayward & Castley, 2018). A "Triage Approach" is often adopted and, in a conservation context, "is the process of prioritising the allocation of limited resources to maximise conservation returns, relative to the conservation goals, under a constrained budget" (Bottrill *et al.,* 2008). This approach accounts for financial outputs, as well as the benefits and the likelihood of success (Bottrill *et al.,* 2008; Hayward & Castley, 2018). This strategic allocation of limited resources contributes to the preservation of biodiversity hotspots, ecological niches, and keystone species critical for ecosystem stability (Bottrill *et al.,* 2008; Hayward & Castley, 2018). Now, more than ever, it is vital to develop tools and indicators to monitor the status of species for effective triage conservation action (Joseph *et al.,* 2009; Torres-Romero *et al.,* 2020; Kratschmer *et al.,* 2021).

The IUCN Red List of Threatened Species (hereafter Red List) was created in 1964 and is the most comprehensive resource regarding the global conservation status of life on earth including plants, animals and habitats (Rodrigues *et al.,* 2006). To date, 150,300 species have been assessed for the Red List, 28 % of which are threatened with extinction, including 41 % of amphibians, 37 % of sharks and rays, 36 % of reef building corals, 34 % of conifers, 27 % of mammals and 13 % of birds (IUCN 2023). Red List assessments are globally important resources for conservation (Rodrigues *et al.,* 2006; Maes *et al.,* 2015; Bachman *et al.,* 2019; Marneweck *et al.,* 2021) and provide a comprehensive and standardised method for evaluating the extinction risk faced by a species (Maes *et al.,* 2015; IUCN Standards and Petitions Committee, 2022). This standardised approach, which makes use of rigorous criteria, provides a clear understanding of the vulnerability of a species, considering factors such as threats, habitat loss, population trends and size and distribution (Maes *et al.,* 2015; Winker *et al.,* 2020; IUCN Standards and Petitions Committee, 2022).

Determining a species listing (Extinct, Critically Endangered, Endangered, Vulnerable, Least Concern or Data Deficient) involves a systematic and rigorous process conducted by species experts (IUCN Standards and Petitions Committee, 2022). The team of experts (assessors) under the auspices of the relevant IUCN Species Survival Commission Specialist Groups, use the IUCN Red List process to determine the species' extinction risk. These criteria include assessing the rate of population decline, the size or trends of the current population, the overall distribution of the species, and the degree of population fragmentation (IUCN Standards and Petitions Committee, 2022). Additionally, the criteria account for the probability of extinction over a specified timeframe and can make use of modelling techniques (Durant *et al.,* 2017; IUCN Standards and Petitions Committee, 2022). The data used in assessments are gathered from a range of sources, including scientific studies, field surveys, and expert assessments. Using the data, the assessors then apply strict criteria to best determine the conservation status of the species (IUCN Standards and Petitions Committee, 2022).

The Red Lists' objective and systematic approach allows for the identification of species that are at high risk of extinction and, as a result, Red Lists serve an important role when prioritising conservation efforts on a global, regional and local scale (Bachman *et al.,* 2019; Winker *et al.,* 2020). While there is an opportunity to raise an appeal if there are any issues with the assessment (IUCN, 2016, 2021), the outcome of the assessment (i.e., a listing) is generally adopted and accepted by Range States, conservation bodies and high-level international conventions (IUCN, 2016, 2021). Red List assessments are also important when developing targeted conservation strategies and policies, aiding in the allocation of resources to address the most urgent threats and significant areas of concern (Maes *et al.,* 2015). Effective conservation action at a species level can be guided by Red List assessments and they are vital in conservation planning and action for species and habitats (Hoffmann *et al.,* 2008). At a socio-political level, assessments foster collective global commitment as the process itself is undertaken and recognised by all Range States, promoting a united effort in addressing conservation challenges and implementing necessary measures (Hoffmann *et al.,* 2008; Kratschmer *et al.,* 2021). Furthermore, information from the Red List is used to create the Red List Index (RLI), which tracks the overall trends in the projected overall extinction risk to groups of species (Butchart *et al.,* 2007). The RLI is an essential tool or indicator for measuring progress towards the international target of reducing biodiversity loss (Butchart *et al.,* 2006, 2007, CBD 2023).

In addition to providing scientifically important and reliable information about the status, Red List assessments are essential tools for intergovernmental organisations such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on the Conservation of Migratory Species of Wild Animals (CMS), to establish regulations and guidelines for the conservation and management of wildlife species. For CITES, assessments offer valuable information that can be used in regulating international trade (Bauer *et al.,* 2018a). As international trade is a major threat to biodiversity worldwide (Challender *et al.,* 2015; Williams *et al.,* 2017), CITES ensures that the levels of legal trade do not threaten a species further. Species that are threatened by forms of trade are afforded some protection under CITES and are listed under Appendix I, II or III to which signatory countries must abide and which can include trade bans or controls (Abensperg-Traun, 2009; Challender *et al.,* 2015; Bauer *et al.,* 2018a; Hellinx, 2020). The data and information that are used to guide these listings comes from a myriad of sources, including the Red List assessment. For example, trade in species that are threatened with extinction is prohibited and are generally listed as "Appendix I" (Abensperg-Traun, 2009). CMS (or the Bonn Convention) is "a global international treaty concerned exclusively with the conservation of migratory species and the habitats on which they depend" (Hykle, 2002). For CMS, Red List assessments provide some of the necessary information required to make decisions around transboundary populations (Hellinx, 2020), which is applicable to many carnivore species including lion (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*) and African wild dogs (*Lycaon pictus*). The United States Fish and Wildlife Service (USFWS) utilises the IUCN Red List as a crucial tool in the implementation of the Endangered Species Act (ESA) which is one of the most prominent and legislatively important acts and can have global conservation implications (Harris *et al.,* 2012). In fact, although not without its' problems, the ESA has been hailed as one of the world's most effective biodiversity protection laws (Harris *et al.,* 2012). Red List assessments provide scientifically sound information on species that is used in USFWS's decisions and actions which fall under the ESA (Haig *et al.,* 2006; Harris *et al.,* 2012). In addition, assessments are a critical scientific foundation that guides the USFWS in making informed decisions about listings, delisting or reclassifying particular species under the ESA (Haig *et al.,* 2006). The ESA regulates trade into the United States of globally threatened species, as assessed under the Red List, including lions (Harris *et al.,* 2012). Species that have a higher listing on the USFWS ESA have increased legal protection, stricter trade and hunting regulations, more recovery planning, increased funding and generally increased conservation efforts (Miller *et al.,* 2002; Haig *et al.,* 2006; Harris *et al.,* 2012). Reliable and robust information pertaining to species conservation forms the foundation for evidence-based policies. This enables intergovernmental organisations, such as CITES and CMS, and legislative frameworks, such as the USFWS ESA, to make decisions relating to conservation action and resource allocation and prioritise and implement targeted measures for conservation (Hykle, 2002; Miller *et al.,* 2002; Haig *et al.,* 2006; Harris *et al.,* 2012).

Carnivores occur naturally at low densities, have large spatial requirements, and experience high levels of conflict with humans, resulting in them being among the taxa that are the most threatened with extinction (Obbard *et al.,* 2010; Ripple *et al.,* 2014, 2014b; Wolf & Ripple, 2017; Fernández-Sepúlveda & Martín, 2022). These traits increase their risk of local level extirpations and population declines resulting from anthropogenic impacts (Wolf & Ripple, 2017; Fernández-Sepúlveda & Martín, 2022). Although intact carnivore guilds once occupied 96 % of the world's terrestrial area, this area has declined to just 34 % (Wolf & Ripple, 2017). On the IUCN Red List, carnivores are more threatened with extinction (26.9 % are considered Endangered) than other group of other mammalian taxa and have a higher proportion of species with declining populations (Fernández-Sepúlveda & Martín, 2022). A study by Fernández-Spúlveda (2022) assessing the conservation of the world's carnivores according to the Red List, found that species within the Eupleridae (Malagasy carnivores), Ursidae (bears), Felidae (cats), and Otariidae (eared seals) had the poorest state of conservation. The second largest carnivore family, Felidae, were identified as the third most threatened among the carnivores, with 18 of the 38 species being listed as either Endangered or Vulnerable and 76.3 % of the Felid species experiencing global population declines (Fernández-Sepúlveda & Martín, 2022). While all species declines are concerning, declines in carnivores are especially alarming for several reasons (Wolf & Ripple, 2017; Fernández-Sepúlveda & Martín, 2022). Firstly, carnivores play important roles in the ecosystems in which they occur as they are of a high trophic level (Ripple *et al.,* 2001; Wolf & Ripple, 2017). Their declines or extinction would result in ecosystem wide impacts through the alteration of trophic cascades (Ripple *et al.,* 2001; Ripple *et al.,* 2010; Ripple *et al.,* 2014). Their declines also have an impact on human well-being (Fernández-Sepúlveda & Martín, 2022). As many carnivore species act as a drawcard for tourism offering financial gain, their absence would have an economic impact at a local and national level (Macdonald & Sillero, 2002).

The lion, once widespread across Africa, has experienced dramatic declines in both population size and distribution range over the last several decades (Loveridge *et al.,* 2022). While most large carnivores have experienced similar declines, the impact on Africa's lion has been particularly severe (Wolf & Ripple, 2017; Loveridge *et al.,* 2022). The lion was first assessed by the IUCN in 1996 and was listed as Vulnerable due to significant population declines (Nowell & Jackson, 1996). Since then, six assessments (2002, 2004, 2008, 2012, 2015 and 2016) have been undertaken, all with a Vulnerable listing (Nowell & Jackson, 1996; Nowell & Bauer, 2004; Bauer, Nowell & Packer, 2008; Bauer *et al.,* 2016). Lions were first included under the USFWS ESA as a threatened species in 2015, meaning they would be formally protected under the act (Booth *et al.,* 2020). This listing required the USFWS to make a positive finding that the importation of lion trophies from African Range States would not be of detriment to the survival of the species (Booth *et al.,* 2020). Under CITES, lions are listed under Appendix II as the species is not threatened with extinction but may become so if trade is unregulated (Bauer *et al.,* 2018a). Lions are also presently listed as Appendix II under CMS, meaning that they would benefit from transboundary protection.

As lions are considered a high-profile and important species by the conservation community and society at large (Macdonald & Sillero, 2002; Macdonald *et al.,* 2015), it is imperative that the assessments are conducted regularly to ensure they are relevant and based on the best available data. As the last assessment was last completed in 2016 (Bauer *et al.,* 2015, 2016), seven years ago, it was essential that it was updated to ensure that the lion's current Red List status was reflective of the reality on the ground. Determining their conservation status fits in with the broad aim of this PhD thesis, and, as such, it was incorporated as one of the tangible outcomes of this dissertation. The Red List assessment was completed under my lead, and under the auspices of the IUCN Species Survival Commission's Cat Specialist Group. In this Chapter, I describe the process undertaken by the assessment team, summarise the results contained within the assessment as published by the IUCN, and discuss the implications of the red-list outcome in the context of this thesis. The full assessment can be found online on the IUCN Red List website and in the supplementary files of this chapter.

3.3 Methods

The lion is an iconic member of the Felidae family, but despite being considered well-studied, significant uncertainty exists, making assessing the conservation status of this species a challenge.

3.3.1 Notable differences between the 2016 and 2023 Red List assessments

The previous Red List assessment was based on time trend analysis of available census data for 47 relatively well monitored lion subpopulations across Africa (Bauer *et al.,* 2015, 2016). The trends calculated for these subpopulations were applied to the species as a whole, as well as regionally to determine an overall status for the species (Bauer *et al.,* 2016).

For this assessment, the lack of reliable population data that are comparable for the species across time posed a challenge (See chapter 2 of this thesis). Although these data are more numerous for lions than for other big *Panthera* cats, there is still considerable uncertainty inherent in the data because of varying survey methods used and accuracy of the results (Bauer *et al.,* 2015). Currently, reliable and comparable population data that exist are biased towards well-monitored populations (Nicholson *et al.,* 2023). These populations often have some element of protection, generally have effective management and have limited anthropogenic pressures and this could bias observed trends to a more optimistic state (Bauer *et al.,* 2015). Due to insufficient confidence in continent-wide population estimates across a range of sites, and bias towards well-protected sites, we were unable to assess the lion on changes in population size, using population numbers. Therefore, the assessment used the change in lion distribution range in this assessment as a proxy for overall decline in population (Riggio *et al.,* 2013; Nicholson *et al.,* 2023).

Another notable difference with this assessment was the inclusion of all small, fenced reserves, particularly those in southern Africa. In South Africa, there are 50 small, fenced reserves that are represented as one subpopulation that is referred to as South Africa's Managed Metapopulation (J. Selier, pers. comm. 2022). The South African Managed Metapopulation and other fenced areas are considered 'lightly managed' as defined in the IUCN guidelines (IUCN Standards and Petitions Committee 2022) and can be considered "wild". As such, there was no basis on which to exclude them from the assessment, providing they were within the species historic distribution range, the reintroduction had taken place at ≥5 years prior and offspring had been produced.

3.3.2 Mapping current lion distribution

To determine lion distribution range, the best available data were used for mapping the distribution range of the species. This was done by using the IUCN SSC Cat Specialist Group's African Lion Database (ALD) with the contribution of data from more than 300 data providers. The ALD is a project that aims to consolidate population and distribution data for the species across their African range. Preliminary distribution range maps were created in ArcGIS Desktop and a collaborative approach was taken by sharing these with the relevant country experts for input. Several iterations were done of the distribution range maps until a completed map was finalised. To create the maps for this assessment, I made use of the "Guidelines for Using the IUCN Red List Categories and Criteria" (IUCN Standards and Petitions Committee, 2022) and the IUCN "Mapping Standards and Data Quality for the IUCN Red List Spatial Data" (IUCN Standards and Petitions Committee, 2021). To account for the recent loss of habitat in areas where data are lacking, we overlayed the continental lion distribution range with a cropland layer obtained from the ESA WorldCover V2 2021 product (ESA 2022). Areas of at least 100 km^2 of continuous range that consisted of over 50 % cropland were reclassified from "Extant" to "Possibly Extinct", as it is extremely unlikely that such areas still sustain resident lion populations.

3.3.3 Determining change in lion distribution range over time

Once the final distribution map of current lion distribution was completed, we calculated the area of the species' total distribution range. As an estimate figure for lion distribution range in 2002 (the starting year of this assessment) was not available, we had to extrapolate this from available data (IUCN, 2006a, 2006b). The distribution range figure for 2005 was used from the lion conservation strategies for East and southern Africa (IUCN, 2006a) and for West and Central Africa (IUCN, 2006b). I first calculated the range lost between two available data points (2005 and 2023) to determine the annual loss of range. Using these estimates, I was able to use this annual loss of range to extrapolate a distribution range figure for 2002. Using the total range figure for 2002, I was able to calculate the percentage of total distribution range lost over three lion generations.

ArcGIS Desktop (Version 10.6; Environmental Systems Research Institute: Redlands, CA, USA, 2018) was used and all shapefiles were projected to the "Africa Albers Equal Area Conic" projection and was used for all calculations and mapping.

3.3.4 Applying change in lion distribution over time to the Red List criteria

To determine the suitable listing for lions under criteria A (Population reduction, Figure 3-1) the assessment used the change in distribution as a proxy for change in population size, assuming they are synonymous. Riggio *et al.,* (2013) showed that declines in lion habitat result in declines in lion numbers, supporting the reasoning of the assessment that lion distribution range decline can be used as a suitable proxy for lion population decline and is an appropriate measure for our assessment.

A. Population size reduction. Population reduction (measured over the longer of 10 years or 3 generations) based on any of A1 to A4

	Critically Endangered	Endangered	Vulnerable
A1	≥ 90%	≥ 70%	≥ 50%
A2, A3 & A4	≥ 80%	≥ 50%	≥ 30%

A1 Population reduction observed, estimated, inferred, or suspected in the past where the causes of the reduction are clearly reversible AND understood AND have ceased. A2 Population reduction observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood OR may not be reversible. A3 Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) *[(a) cannot be used for A3]*. A4 An observed, estimated, inferred, projected or suspected population reduction where the time period must include both the past and the future (up to a max. of 100 years in future), and where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.	*based on any of the following:*	(a) direct observation *[except A3]* (b) an index of abundance appropriate to the taxon (c) a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality (d) actual or potential levels of exploitation (e) effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.

Figure 3-1. Summary of the population size reduction criteria (Criteria A) used to evaluate the lion according to the IUCN Red List Categories (IUCN Standards and Petitions Committee, 2008).

The IUCN Red List Criteria define three generations as the relevant time span for trend assessment. The generation length of Lions is estimated to be 6.98 years (Pacifici *et al.,* 2013). As such, three generations would require the species to be assessed over 21 years (2002 – 2023).

3.3.5 The assessment team and publication

The assessment team included myself as lead assessor (IUCN SSC Cat Specialist Group (hereafter CatSG) and manager of the IUCN SSC Cat Specialist Group's African Lion Database), Dr Hans Bauer, (CatSG, Oxford's Wildlife Conservation Research Unit), Dr Paolo Strampelli (Panthera), Dr Etotepe Sogbohossou (CatSG, Abomey-Calavi University, Benin & Senghor University, Egypt), Dr Dennis Ikanda (CatSG, WWF-Tanzania), Dr Pricelia Tumenta (CatSG, Dschang University, Cameroon), Dr Meena Venkataraman (CatSG, Carnivore Conservation & Research – India), Dr Guillaume Chapron (Swedish University of Agricultural Sciences) and Dr Andrew Loveridge (CatSG, Oxford University – Wildlife Conservation Research Unit). I worked closely with Tabea Lanz who is the IUCN CatSG Red List coordinator and with the chairs of the CatSG.

The Red List assessment was accepted by the IUCN Red List Authority in early 2023 and was published in December 2023.

3.4 Summary of results provided in the 2023 Red List assessment for lion

The latest assessment of the African lion (*Panthera leo*) for the IUCN Red List of Threatened Species indicates that the global conservation status of the species remains as Vulnerable.

Lions occur in ~6 % of historical distribution range, and current range analysis revealed that extant lion range is ~1,571,296 km² (Figure 3-2). In 2002, it was extrapolated that lion range was estimated to be 2,460,986 km^2. A range decline of 36 % was calculated from ~24,609,86 km^2 in 2002

(~21 years: 2002-2023). Therefore, a population decline of 36 % was, thereby, suspected. Therefore, lions remained listed as Vulnerable under criteria A2abcd (Figure 3-1).

Due to significant habitat loss and fragmentation, the global lion population is highly fragmented (Loveridge *et al.,* 2022) with isolated and small populations occurring (e.g., Kainji Lake in Nigeria, Niokola-Koba in Senegal, Waza National Park in Cameroon). As anticipated, half of lion range was estimated to be within southern Africa (51.27 %) and East Africa (33.84 %). Both West and Central Africa have the smallest lion extant range, constituting of only 3.31 % and 11.57 %, respectively. Only 37.5 % of total extant range for the species falls within formal protected areas (defined as category one to four in the World Database of Protected Areas).

3.5 Discussion

The global lion population is declining rapidly across its distribution because of indirect threats such as habitat loss and encroachment and more direct threats such as targeted killing for parts and poaching (Bauer *et al.,* 2020). Despite a decline in range and a suspected decline in population, lions remain listed as Vulnerable (Nicholson *et al.,* 2023a). The latest Red List assessment provides enhanced knowledge of the status of the species including data gaps, threats, geographic distribution and changes in range.

As with the previous assessment and associated studies (Packer *et al.,* 2013; Bauer *et al.,* 2015, 2016), a stark difference in the perceived trends and status of the species was evident across its distribution range. The last remaining lion stronghold in West Africa persists, where more than 90 % of the mature individuals in West Africa remain in the W-Arly-Penjari Complex (a transboundary area in Benin, Burkina Faso and Niger), and there is still evidence of population declines (Bauer *et al.,* 2018; Nicholson *et al.,* 2023). The West African lion subpopulation was assessed as Regionally Critically Endangered C2a(ii) as more than 90 % of mature adults were in one subpopulation (Henschel *et al.,* 2014, 2015). However, in southern Africa, lions show a general increasing or stable trend. In South Africa, populations of lions are still increasing with many populations at carrying capacity or above (Packer *et al.,* 2013; Bauer *et al.,* 2015). The regional Red List assessment for lions in South Africa, Swaziland and Lesotho lists lions regionally as Least Concern due to an increasing population trend (Miller *et al.,* 2016). While these regional assessments are in the process of being updated, initial assessment of the data indicates that these regional listings will possibly remain as Least Concern (Miller *et al.,* 2016; Nicholson *et al.,* 2023a). While the lion population in India has yet to be assessed, population trends are positive (Gujarat Forest Department 2020) and the remaining population in the Gir landscape is safe from anthropogenic pressures.

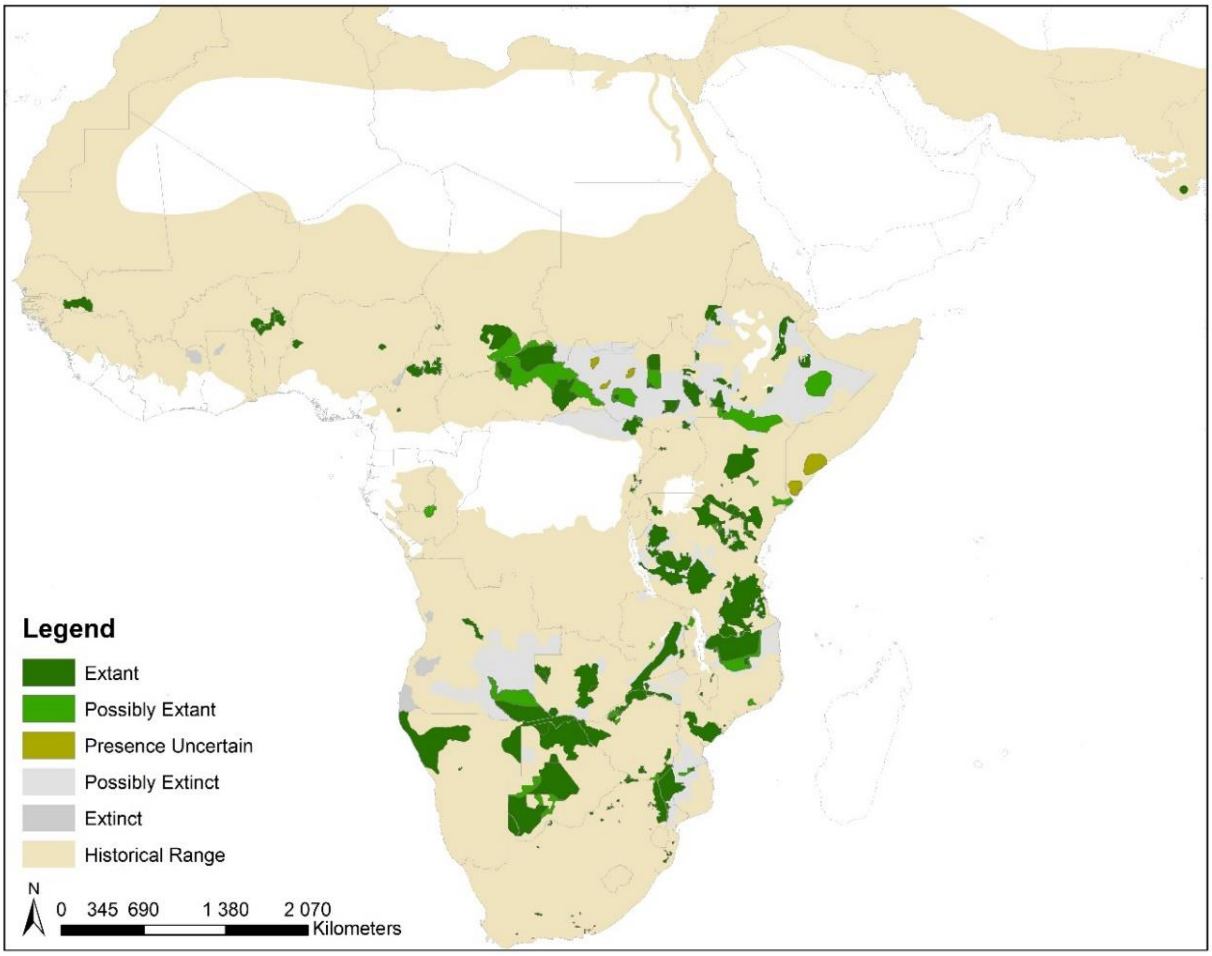

Figure 3-2. Present lion distribution as mapped in the global Red List assessment for *Panthera leo* (Nicholson *et al.,* 2023a).

Despite the species still being relatively well-studied (Riggio *et al.,* 2013; Bauer *et al.,* 2018c; Nicholson *et al.,* 2023b), considerable knowledge gaps remain, some of which were identified in this assessment (Nicholson *et al.,* 2023a). Some of the areas currently mapped as "Possibly Extinct" could contain relict lion subpopulations and should be prioritised for field surveys (Bauer *et al.,* 2018b; Nicholson *et al.,* 2023a). This includes large areas in South Sudan, Central African Republic, and Somalia where surveys aimed at establishing lion presence or absence should be a priority. Population numbers or reliable density estimates for many areas across Africa are either lacking or require updating. This data gap includes areas in Tanzania (e.g. Katavi National Parks last lion survey was done in 2009 (Kiffner *et al.,* 2009)), Nigeria (last surveys done in 2010 and 2014 (Tende *et al.,* 2014)), Democratic Republic of the Congo and Botswana (for example, the last survey for Central Kalahari was done before 2003 (Macfarlane, 2004)). There is an urgent need for reliable and robust population numbers for populations in Africa that are repeated across time (Elliot & Gopalaswamy, 2017;

Braczkowski *et al.,* 2020). It is essential that surveys are carried out and the findings are made available and included in future Red List assessments that allow for more reliable assessments of trends for the entire species distribution range and not just a subset of the population (Nicholson *et al.,* 2023a). Lion conservation strategies, policies and conservation action are guided by the population estimates and findings in the Red List assessment (Braczkowski *et al.,* 2020). Ensuring these population data are available is the basis for more robust future Red List assessments of the lion. In this current assessment, reliable population numbers were found to be heavily biased to well monitored populations (Nicholson *et al.,* 2023a). These populations generally have more resources to manage them efficiently and safeguard them from unnatural threats, such as poaching (Nicholson *et al.,* 2023a). Conservation managers, funders and researchers need to ensure that populations that generally have less management and resources should be prioritised for survey work, as they are at higher extinction risk or population declines (Lindsey *et al.,* 2018; Robson *et al.,* 2022).

Presently much of West Africa is under pressure from violent extremism which hinders conservation and park management effectiveness and increases anthropogenic pressures like poaching (Lhoest *et al.,* 2022). Recent surveys in the W-Arly-Penjari complex, particularly in Benin and Niger, were hindered by unsafe working conditions and as a result updated information on wildlife populations in the complex are further threatened (Lhoest *et al.,* 2022; Nicholson *et al.,* 2023a).

This assessment process faced a few challenges, particularly as reliable and repeatable population survey data across Africa were lacking, it is strongly recommended that these be addressed before the next Red List assessment. This would require developing and implementing standardised survey methods to ensure results from surveys are reliable, robust and can be compared across survey periods (Elliot & Gopalaswamy, 2017; Braczkowski *et al.,* 2020). Surveys that are carried out with reliable methods (ideally using surveys that require some form of individual identification rather than index-based methods (Elliot & Gopalaswamy, 2017; Dröge *et al.,* 2020)) should be used as the standard for data used for Red List assessments, especially spatially-explicit capture recapture methods which allow the reliable monitoring of population change over time (Braczkowski *et al.,* 2020). Unreliable methods (e.g. index-based methods (Dröge *et al.,* 2020), and expert opinion-based estimates, can lead to inestimable uncertainties or under/overestimating populations (Braczkowski *et al.,* 2020). This can lead to an over-investment in populations that may require more effort than another population that is declining significantly (Elliot & Gopalaswamy, 2017; Braczkowski *et al.,* 2020) and this could lead to unforeseen population losses. Due to the dichotomy observed in population status across Africa, it is recommended that the species regional listings are updated (particularly for India, and West and Central Africa) and that the lion is assessed at a subspecies level.

The latter would require two assessments: *P. leo leo* (lions in Central and West Africa and including the Asian population) and *P. leo melanochaita* (southern and East Africa) (Bertola *et al.,* 2015, 2016, 2021, 2022). Regional assessments are vital as they provide localised assessments of species' extinction risks (IUCN Standards and Petitions Committee, 2022). They offer a nuanced understanding of the specific threats faced by lions in distinct geographic areas, helping tailor conservation strategies to regional needs that are likely more manageable to implement. During the assessment, several populations of concern were identified that require close monitoring because of increasing human-driven threats. Anthropogenic pressures on lions are concerning for many populations, including: 1) the WAP complex (the last remaining stronghold of lions in West) which is threatened by a violent extremist groups (Lhoest *et al.,* 2022); 2) populations in Mozambique where the targeted poaching of lions for parts is increasing (Everatt *et al.,* 2014; Everatt *et al.,* 2019), and 3) the widespread increase in poaching for bushmeat which threatens both the natural prey base and lions (Becker *et al.,* 2013; Wolf & Ripple, 2016; Loveridge *et al.,* 2020). It is recommended that the impact of these threats on populations be monitored and mitigated, and these areas receive some of the focus from funding sources to enable targeted conservation action.

Despite the general decline in lion distribution range, lions retain their Vulnerable listing. While "Vulnerable" does not imply imminent extinction (IUCN Standards and Petitions Committee, 2008), it signals a critical need for sustained conservation measures to ensure the long-term survival of lions. The declining global lion population not only signifies a troublesome state of the species, but carries broader ecological, economic, and cultural implications. Lions, as apex predators, play a pivotal role in ecosystem balance by regulating prey populations, thereby influencing vegetation, and contributing to biodiversity conservation (Rosenblatt *et al.,* 2014; Aebischer *et al.,* 2020). Economically, countries relying on lion-based tourism face challenges, as fewer lions could result in reduced tourism and, therefore, less foreign expenditure in the area (van der Meer *et al.,* 2016). Culturally, lions hold symbolic significance for many cultures, and their decline may impact traditions and spiritual beliefs (Ikanda & Packer, 2008).

While present population trends (inferred, suspected, or observed) did not meet the criteria for an Endangered listing, for which declines of more than 50 % would have to have been observed/suspected (IUCN Standards and Petitions Committee, 2022), it is concerning that the fragile state of populations may see lions regarded as Endangered in the future (Nicholson *et al.,* 2023b). This is especially so given the evidence of ongoing and increasing threats to lions across much of their fragmented range (Bauer *et al.,* 2020; Nicholson *et al.,* 2023a, 2023b). Therefore, based on this assessment, it is recommended that the lion is regarded as a species under observation and that its status and trends of threats are closely monitored (Nicholson *et al.,* 2023a). Continued monitoring as well as filling knowledge and data gaps with reliable data and information will contribute to refining conservation strategies, improving data reliability, and addressing emerging threats to lion populations.

While the Red List is used widely (Hoffmann *et al.,* 2008; Harfoot *et al.,* 2021; Kratschmer *et al.,* 2021), it is important to acknowledge that there is some criticism regarding its value, especially when used in isolation, for priority setting and resource allocation (Palacio *et al.,* 2023). Presently, the Red List is heavily biased, both in a taxonomic and geographic sense and towards the subset of known biodiversity (Hoffmann *et al.,* 2008; Stuart *et al.,* 2010; Bachman *et al.,* 2019; Palacio *et al.,* 2023). This bias, combined with several limitations of the Red List (including outdated threat categories and incorporation of more modern quantitative methods), can be misused in priority setting which can result in incorrect resource allocation (Palacio *et al.,* 2023). Therefore, it is essential that the Red List is not used in isolation when priority planning for conservation or when making inferences about a system in its entirety (Stuart *et al.,* 2010; Palacio *et al.,* 2023). It is important to recognise that, when used correctly, and combined with other datasets and tools, the Red List can contribute to effective conservation action and priority setting (Hoffmann *et al.,* 2008; Kratschmer *et al.,* 2021). Other important tools and studies that can be considered in the case of lions, is information regarding their fragility (Nicholson *et al.,* 2023b), funding availabilities or deficits (Lindsey *et al.,* 2017, 2018), full assessments of the anthropogenic landscape (IUCN 2006a, b, see Chapter 5) and local level policy or regulation impacts such as trophy hunting (IUCN, 2006a, 2006b; Edwards *et al.,* 2014; Trouwborst, 2015; Creel *et al.,* 2016; Trouwborst *et al.,* 2017; Bauer *et al.,* 2018a; Hodgetts *et al.,* 2018; Mweetwa *et al.,* 2018).

Amidst our present biodiversity crisis (Rull, 2022), lion populations face escalating anthropogenic pressures resulting in population declines with some approaching local extinctions (Wolf & Ripple, 2017; Nicholson *et al.,* 2023a). Effectively halting population declines through conservation action requires strategic resource allocation guided by reliable tools, such as the IUCN Red List (Bottrill *et al.,* 2008). Red List assessments play a crucial role in this process, providing a standardised framework rooted in scientific data (Hoffmann *et al.,* 2008). This information forms the basis for informed decision-making, ensuring conservation efforts are strategically aligned with the most urgent needs of endangered species (Bottrill *et al.,* 2008; Hoffmann *et al.,* 2008; Betts *et al.,* 2020). The Red List's categorisation for lion as Vulnerable, based on their extinction risk, is particularly instrumental in guiding policymakers, intergovernmental organisations (CITES and CMS) and conservationists. This, emphasising the practical importance of these assessments in shaping targeted and effective conservation strategies for lions and other species.

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3.7 Published Red List Assessment

Source: Nicholson, S., Bauer, H., Strampelli, P., Sogbohossou, E., Ikanda, D., Tumenta, P.F., Venktraman, M., Chapron, G. & Loveridge, A. 2023. Panthera leo. The IUCN Red List of Threatened Species 2023: e.T15951A231696234. Available at: https://www.iucnredlist.org/species/15951/231696234. Accessed on 2023/12/19.

Lion (*Panthera leo*)

Global Lion (*Panthera leo*) Red List Assessment.

3.7.1 Taxonomic Notes

Taxonomy currently used by the IUCN SSC Cat Specialist Group (see Kitchener *et al.,* 2017):

- *Panthera leo leo*—Central Africa, West Africa and Asia
- *Panthera leo melanochaita*—Southern and East Africa

Lions were previously described as two subspecies: the African lion (*Panthera leo leo*) and the Asiatic lion (*Panthera leo persica*). However, this has subsequently changed.

Recent studies (Bertola *et al.,* 2015, 2016, 2022) indicate that lions in Western and Central Africa are more closely related to lions found in India than they are to those found in Southern and East Africa. This is likely the result of lions being reduced to local refugia during the more recent part of the Pleistocene climatic cycles (Bertola *et al.,* 2011, 2016). Divergence times estimated from genetic data match large-scale changes in habitat, including expansion and contraction of forested areas, possibly reducing connectivity and isolating lion subpopulations (Bertola *et al.,* 2016). This temporary isolation may have led to divergence of subpopulations, which can still be observed today. Historical connectivity between lion subpopulations in West or Central African and subpopulations in India explain the close evolutionary relationships between these subpopulations, even though a series of bottlenecks have led the Indian subpopulation to differentiate quickly as a result of increased genetic drift (Bertola *et al.,* 2015, 2016). Based on recent genetic studies, the two subspecies of lions overlap in a contact zone in Ethiopia which possibly extends into Sudan and South Sudan (Bertola *et al.,* 2015, 2016, 2021, 2022).

3.7.2 Justification

The lion is assessed as Vulnerable under criterion A2abcd based on an estimated 36 % decline in the species' range over three generations (approximately 21 years) and therefore a similar population reduction is suspected.

Despite the lion being well-studied, uncertainty remains a challenge in assessing this species (refer to the section on this topic under Population below for more detail). In recent years, considerable conservation effort has led to stable lion populations in some areas and even species recovery in others (e.g., reintroductions into the Zambezi Delta in Mozambique, Akagera in Rwanda, and Zakouma National Park in Chad). However, over the last 21 years, declines in certain populations have also occurred (e.g., Limpopo National Park, Etosha National Park, and Niassa Game Reserve) with some areas experiencing local extinctions (e.g., Quirimbus National Park in Mozambique, Yankari Game Reserve in Nigeria (P. Funston pers. comm. 2023) and Toro-Semuliki Wildlife Reserve in Uganda). The present assessment is guided by the best available data and methods. Uncertainty is a common problem in the assessment of long-lived species where trends are assessed over a time span that either includes historical periods where some survey techniques were not yet available, or future periods that are inherently unpredictable.

Extant lion range in 2023 is estimated to be ~1,571,296 km², only 6 % of its historical range. This is an estimated 36 % range decline since 2002 (three lion generations), where range was estimated to be 2,460,986 km². This decline, which is likely to continue, reflects a combination of recent known and inferred decline, as well as improved knowledge.

A population of between 22,000 and 25,000 adult and subadult lions in Africa (African Lion Database, unpub. data 2023) and ~670 adult and subadult lions in India (Gujarat Forest Department 2020) was estimated for this assessment. This is an estimated decline from ~33,000 lions in 2006 (IUCN 2006 a, b), an estimated 30 % decline in 17 years (i.e., less than three generations). The former figure shares a common background with Bauer *et al.,* (2018), and the latter informed estimate in 2013 (Riggio *et al.,* 2013) show that these numbers are similar but with different reference years. These numbers all have extensive caveats, enormous uncertainty, and were partly based on differing methodologies; they cannot be used for a direct calculation of population trends, but they are consistent with the estimated range decline of 36 %. Riggio *et al.,* (2013) showed that declines in savanna habitat translate into declines in lion numbers. Lindsey *et al.,* (2017) showed that lion densities vary substantially across their range, and that lions occur at levels below 50 % of carrying capacity in two thirds of the sites they analysed. However, these sites were spread all over the African continent, and the range decline is also across the continent, so we have no reason to reject lion range decline as a direct proxy for lion population decline. This supporting evidence suggests that range declines equate proportionately to lion population declines, and that range is an appropriate measure for our assessment. Therefore, this suspected decline of 36 % in population is justified.

The previous Red List Assessment (Bauer *et al.,* 2015) used a representative subset of estimates to infer a global population decline of 43 %, albeit with regional variation. That same dataset was used in the same year with the same result, but with a much-improved methodology that involved Bayesian modelling to predict the probability of population decline (Bauer *et al.,* 2015). This assessment used the same improved methodology to demonstrate the plausibility of our assessment (see the Population section for more details). In summary, using Bayesian modelling, we estimated lion populations in Africa to have a 41 % probability of declining by one third (33 %) within three lion generations (including past, present, and future), while this risk is estimated at 2 % in India (Table 1 in the Supplementary Information). This supports a ≥30 % reduction threshold for a Vulnerable listing for lion. The probability of a 33 % decline within three generations is estimated to be 74 % in West Africa, 36 % in East Africa, 33 % in Central Africa, and 20 % in southern Africa (Table 1 in the Supplementary Information). However, while it demonstrates strong support for a Vulnerable listing, it cannot be used as a formal method to which we assess the species as this method is not fully consistent with the IUCN Red List Guidelines.

There are high threat levels across the species' broad geographic range, with 12 recent extirpations and two suspected extirpations recorded (Table 2). However, it is encouraging to note that the number of extirpations has not increased since the previous (2015) assessment. The most important driver of lion decline is habitat loss (Bauer *et al.,* 2020). Prey base depletion is also a significant driver and is partly linked to habitat loss, but more importantly to poaching and the bushmeat trade (Becker *et al.,* 2013). Human–lion conflict, which results in the indiscriminate killing of lions in defence of human life and livestock, is another major threat to the species (Sibanda *et al.,* 2021). The trade in bones and other body parts for traditional medicine, both within Africa and in Asia (Williams *et al.,* 2017, Mole and Newton 2020, Coals *et al.,* 2022) is an emerging threat. Furthermore, although trophy hunting can contribute positively to lion conservation, improvements in management practices of this practice have been recommended (Edwards *et al.,* 2014, Dickman *et al.,* 2019), as when poorly regulated, it also contributes to population declines (Packer *et al.,* 2009, Croes *et al.,* 2011, Rosenblatt *et al.,* 2014, Loveridge *et al.,* 2023). Poorly regulated trophy hunting has been previously highlighted as a threat to lions, however, attempts have been made to mitigate through the implementation of science-based management practices. Populations that are trophy hunted should be effectively monitored to ensure that there are no negative population impacts. The impact of violent extremism in several parts of lion ranges in Africa (Lhoest *et al.,* 2022) is likely to further drive the declining nature of lions in these regions. The increasing number of lions poached for their body parts in Mozambique (African Lion Database, unpub. data 2023; Mole and Newton 2020) is of concern, but this presently appears to be confined to this region (Coals *et al.,* 2020), however, illegal trade is reported in at least six African countries (see CITES CoP 17 Prop. 4).

Given the evidence of ongoing and increasing threats to lions across much of their fragmented range, we recommend that the lion is a species under observation and its threat status is closely monitored, with a reassessment after a minimum three-year period or as soon as new information emerges.

This decline in both population and range, which is likely to continue, reflects a combination of recent known and inferred decline, as well as improved knowledge. This meets the requirements for listing as Vulnerable (A2abcd).

3.7.3 Geographic Range Information

Lions are the carnivores that have undergone the largest range contraction, with about 85 % of lion range lost since CE 1500 (Morrison *et al.,* 2007). Outside sub-Saharan Africa, the lion formerly ranged from North Africa through Southwest Asia (where it disappeared from most countries within the last 150 years), west into Europe (where it became extinct almost 2,000 years ago), and east into India (Nowell & Jackson 1996). Today, the only remainder of this once widespread northern population is a single isolated subpopulation in the 1,400 km² Gir Forest National Park and Wildlife Sanctuary and the surrounding landscape in India. Lions are extinct in North Africa, having perhaps survived in the High Atlas Mountains up to the 1940s (Nowell & Jackson 1996, West and Packer 2013).

Lion distribution was assessed using the lion distribution map created and maintained by the IUCN SSC Cat Specialist Group's African Lion Database (ALD). The ALD is used to provide a continually updated assessment of the abundance and distribution of lions in Africa. Based on the data in the ALD, regional maps were generated, and adjustments made based on feedback from country experts. Where new data were lacking, the 2015 Red List Assessment and the IUCN Cat Specialist Group's Guidelines for the Conservation of lions in Africa (IUCN SSC Cat Specialist Group 2018) were used as both have been through a peer-review process. Repeated observation data from areas previously considered as out-of-range were obtained. These areas do not necessarily indicate range expansion since the last assessment, but rather more accurate data. Such areas include: Luando area in Angola (J. Anderson pers. comm. 2019), the Mpem and Djem area in Cameroon (Bauer *et al.,* 2019), the northern boundary of Central Kalahari Game Reserve in Botswana (A. Loveridge pers. comm. 2022), additional wildlife management areas in the Okavango (A. Stein pers. comm. 2022; A. Albertson pers. comm. 2019), Southern National Park in South Sudan (M. Moeller pers. comm. 2022), Zeraf area in South Sudan (R. Gony pers. comm. 2023), Erindi Private Game Reserve in Namibia; (Erindi PGR, unpub.

data 2020), various hunting concessions in Mozambique (e.g., in Tete Province; R. Lovemore pers. comm. 2022; Rio Save Safaris Lda, unpub. data 2022) and Chad (African Parks, unpub. data. 2022) and several game reserves in South Africa (SANBI, unpub. data. 2022). However, some areas do reflect an increase in range due to the successful reintroductions of lions into fenced areas (e.g., fenced reserves in South Africa, Liwonde and Majete in Malawi, Akagera in Rwanda).

Several amendments were made to this assessment's distribution map that were not accurately captured in the previous assessment. These are as follows:

- The Benoué Complex in Cameroon was previously incorrectly mapped. This has been corrected to include the surrounding concessions that are included in the complex and are known lion range.
- Bubye Valley Conservancy in Zimbabwe was previously incorrectly mapped (in terms of size and location) and this has been corrected.
- An expansive range in the Northern Cape Province in South Africa was removed as it was depicted as lion range, but was inaccurate as no known lion population has existed there.
- Coutada 9 in Mozambique was included as it was previously not mapped.
- Revision of range in Ethiopia following Yirga *et al.,* (2021) and Gebretensae and Kebede (2022).

Furthermore, some of the mapped subpopulations are in areas where armed conflict may have had an impact on lion persistence (e.g., Central African Republic and South Sudan). Until proof to the contrary and based on the lack of recent data to confirm lion presence, we therefore classified such areas as "Possibly Extinct" but maintained Protected Areas as lion range (including many large hunting concessions, such as in the Central African Republic). Some of the areas currently mapped as "Possibly Extinct" could contain relict lion subpopulations and should be prioritised for field surveys (e.g., large areas in South Sudan, Central African Republic, and Somalia) aimed at establishing lion status.

Finally, to account for recent loss of habitat in areas where data are lacking, continental lion range was overlaid with a cropland layer obtained from the ESA WorldCover V2 2021 product (https://esa-worldcover.org/en). Areas of at least 100 km² of continuous range that consisted of over 50 % cropland were reclassified from "Extant" to "Possibly Extinct", as it is unlikely that such areas still sustain resident lion populations.

Lions are difficult to survey, and knowledge of lion numbers and distribution is limited. Therefore, lion researchers have worked with two metrics: known or extant lion range, where lion presence has been confirmed, and possible or possibly extant lion range, where lion presence is suspected. Lions were once widely distributed across Africa and Asia, but populations have become reduced and isolated, and they are now extirpated from large portions of their historic range. In Supporting Online Information Table 3 we present the range figures from 2002, 2005, 2016, and 2023. We estimate extant lion range in 2023 to be ~1,571,296 km², or 6 % of historical range. This is a 33 % decline from 2005, and a decline of 36 % over three lion generations. This range reduction reflects a combination of recent known and inferred decline, as well as improved knowledge.

In West Africa, lions are largely confined to small populations (<50 individuals) in Niokolo-Koba (Senegal), and Yankari and Kainji Lake National Parks (Nigeria) with the largest population (estimated 187 lions) in the W-Arly-Penjari Complex (Benin, Burkina Faso, and Niger). In Central Africa, lions are found within the Bénoué Complex and Waza National Park in Cameroon. Dispersed individuals have been found south of Bénoué, around Mpem and Djem National Park, and in Sena Oura National Park in Chad. Zakouma National Park and the surrounding areas have the largest population of lions in Chad. There is more uncertainty around the exact presence of lions in both the Central African Republic and South Sudan. In the Central African Republic, they are found in some of the national parks, including Bamingui-Bangoran National Park, Andre Felix National Park, Yata-Ngaya Faunal Reserve, and the Chinko Conservation Area (CCA). The latter is believed to have the largest population, estimated at ~150 lions (T. Aebischer pers. comm. 2023). Based on conservation projects in the area, it can be assumed that the CCA is the only place in eastern Central African Republic where the Northern lion population is increasing, in all other areas it is likely stable or more likely decreasing, locally even dramatically (T. Aebischer pers. comm. 2023). In South Sudan there are small populations throughout the country confirmed in Southern National Park, Badingilo National Park, Zaref Game Reserve, and Boma National Park. In the Democratic Republic of the Congo, there are two populations, one in Garamba National Park and the surrounding hunting complex (and extending into Lantoto in South Sudan) and Virunga National Park.

In East Africa, lions are found in several areas in Ethiopia—although there is considerable uncertainty regarding their extent. Populations of lions occur in Uganda (including Queen Elizabeth National Park, Murchison National Park and Kidepo Valley). In Rwanda, one small, reintroduced population (<50 individuals) is found in Akagera National Park. Lions have significantly larger distributions in both Kenya and Tanzania, where they are found in most National Parks, protected areas, and hunting concessions. However, range in Tanzania has been reduced due to the increasing conversion of habitat into agricultural land. Field surveys for many areas of Tanzania are also still lacking. In Somalia there have been some reports of lion presence, but there is no tangible evidence to support this, thus this range is assigned to the uncertain category.

In southern Africa, lions occur in multiple fenced reserves in Malawi, where they have been reintroduced (each population <50 lions). In Zambia, lions are found in Kafue, Liuwa Plains National Park, Sioma Ngwezi National Park and within the South Luangwa Valley. Lions are believed to have been recently extirpated from Northern Zambia. Within Namibia, lions are found in Etosha National Park, up the Skeleton Coast, and the Kunene and Caprivi regions. South Africa's largest lion populations are in the Transfrontier parks of Kruger and Kalahari Gemsbok National Park, as well as a large managed metapopulation network of fenced reserves. In Botswana, they are found in the Central Kalahari and the Okavango-Delta region. The largest population in Zimbabwe occurs in the Hwange ecosystem. In addition, lions also occur in Gonarezhou National Park and the surrounding areas (including Savé Valley Conservancy and in Bubye Valley Conservancy, a large fenced protected area). Lions also occur in northern Zimbabwe in the Zambezi Valley protected area complex bordering Zambia and protected areas south of Lake Kariba. In Mozambique, lions have been extirpated from much of their range (including Quirimbus National Park and the Tete Province). The largest population (>800 lions) within the country occurs in Niassa Reserve. In addition, lions occur in the Zambezi Delta, extending north towards Coutada 9, Limpopo National Park, Lebombo Conservancy, Zinave National Park, and a restricted area south of the Tete Province.

The global population of lions is highly fragmented (Loveridge *et al.,* 2022). This is especially true in West Africa were the seven subpopulations (Niokola-Koba, WAP, Yankari Game Reserve, Kainji Lake, Waza National Park, Benoué Complex and Mpem and Djem) are all considered to be isolated from one another. In Central and East Africa, various populations are also fragmented.

3.7.4 Population Information

Abundance

For this assessment, we do not aim to provide a new estimate of total lion numbers. Determining a population number for lions is incredibly challenging as most populations have yet to be surveyed and population numbers that may exist are based on guesses or extrapolations. In addition, some surveys are outdated. For this assessment, to determine a global population number, we used the latest population estimates published in the Guidelines for the Conservation of Lions in Africa (GCLA, Bauer *et al.,* 2018), and where possible, updated those figures from the IUCN SSC Cat Specialist Group's African Lion Database (ALD) where more recent surveys have been completed. Caution must be exercised when using these figures and inferring trends based on these data presented in the GCLA due to various data limitations. Considering the difficulty in interpreting lion numbers and the availability of an alternative, we decided not to base this assessment on total population numbers. Though our knowledge of the lion distribution has improved with time, it is still limited at the national, regional, and range-wide scales because reliable data on lion population trends are missing from large portions of their range, particularly those in West and Central Africa.

The estimate Lion population size in Africa isIn this assessment, we estimate the total number of adult and subadult Lions to be ~between 22,000 and 25,000 Lions in Africa 23,000 including subadult and adult lions (Bauer et al.,, 2018, African Lion Database. Unpublished Data. 2023; Supplementary Table 4) and ~670 subadult and adult Lions in India (Gujarat Forest Department 2020). However, this estimate should be used with caution as there is significant uncertainty around population estimates. For this assessment, we were unable to estimate the number of mature individuals. This is largely due to the levels of uncertainty in population estimates (see discussion below). In addition, the proportion of mature individuals can differ from one population to the next. This makes estimating the mature population challenging and potentially unreliable. This emphasises the need for standardized means to estimate and report Lion population data.

The largest proportion of Africa's Lions are found in Southern Africa 47.55%, with 46.54% in East Africa, 4.82% Central African and 1.07% in West Africa. Between 2006 and 2018, the Lion population in Africa was estimated to have declined by 25% over 12 years from 33,292 to 25,105 (Bauer et al., 2018). In this assessment we estimate a decline of 8% from ~25,105 in 2018 to ~23,000 in 2023. Although in the past decade, Lion populations seem to be increasing in many of their Southern African ranges, there are indications of a general population decline across its total range with the biggest assumed declines in West and Central Africa. Several subpopulations have been stable, among them the only remaining subpopulation in Asia (surviving in the Gir Forest area of Gujarat, India) and several subpopulations in southern Africa—especially those in fenced, well-protected reserves. Subpopulations appear to be stable where management is sufficiently funded with fencing being one of several effective conservation management techniques (Packer *et al.,* 2013, Lindsey *et al.,* 2018, di Minin *et al.,* 2021). However, many lion subpopulations occur in areas where management budgets insufficient (Lindsey *et al.,* 2018, Robson *et al.,* 2022), leading to local declines and even extinction (e.g., West Africa; Henschel *et al.,* 2014). Little is known about lion subpopulations in Angola, Central African Republic, Democratic Republic of the Congo, Nigeria, Somalia, and South Sudan, but these are assumed to be declining based on the limited data available from these areas and the conservation challenges in these areas (e.g., political instability).

While lions qualify as Vulnerable, it is of great concern that parts of the African population is inferred to have declined at a rate that meets the category for Endangered – particularly in West Africa. Since the sample subpopulations were all monitored, an even greater average rate of decline is likely for unmonitored subpopulations across much of Africa, since lack of monitoring could suggest lack of conservation and mitigation effort.

Bayesian Modelling

A Bayesian state space model to estimate the growth rate-λ of each subpopulation was completed following the methods in Bauer *et al.,* (2015). While this model demonstrates strong support for a Vulnerable listing, it cannot be used as a formal method to which we assess the species as this method is not fully consistent with the IUCN Red List Guidelines.

Data from relatively well-studied lion subpopulations were used with additional unpublished data provided by contributors (Supplementary Information Table 4 online). Population estimates were obtained by commonly used scientific research methods including total counts, individual identification, total or sample inventory using calling stations, radio telemetry, photographic databases, and density estimates based on direct observations (Supplementary Information Table 5 and 6 online). Population estimates were excluded for sites based on extrapolation of densities from other areas, or informed estimates by researchers. The minimum number of surveys per site over the assessment period was two, but some sites were monitored more regularly.

The IUCN Red List Criteria define three generations (or ten years, whatever is longer) as the relevant time span for trend assessment. A lion generation length of 6.98 years (three generations = 21 years) was used for the modelling (Pacifici *et al.,* 2013). Subpopulations were first categorised individually and then according to region. The mean of the regional values was used to determine a continental result for Africa and India (Supplementary Information Table 1 and 6 online). However, because the two continental results were significantly different, their mean could not be used to estimate a global probability of population trend.

To assess population trends a Bayesian hierarchical state space model was used to estimate the growth rate-λ of each population (Bauer *et al.,* 2015). Fifty-six unweighted posterior density distributions of growth rate (one per population) were summed across three sets to provide geographic conservation-relevant estimates of demographic trends. The four African regions defined by the IUCN regional lion conservation strategies constituted four sets (Bauer *et al.,* 2015). The projected probability of decline over T years by 33 % and 50 % (see supplementary material online for formulas and Bauer *et al.,* 2015) for each population was estimated (Supplementary Information Tables 1 and 2 online) without making inferences on true population size N, with T equal to 7 (one generation), 14 (two generations) and 21 years (three generations).

The summed posterior densities of growth rates for regional groups showed that, the West African populations were sharply declining λ = 0.87 ± 0.25 (Supplementary Figure S1 online), Central African populations were slightly increasing λ = 1.02 ± 0.18 (Supplementary Figure S2 online) while East African populations were stable λ = 1 ± 0.15 (Supplementary Figure S3 online). Southern African populations were by contrast, increasing λ = 1.07 ± 0.17 (Supplementary Figure S4 online).

The models estimated that the West African group had the highest probability of declining by one third in three lion generations of 0.74, followed by the Central African group (0.33), the East African group (0.36) and the southern African group (0.20; Supporting Information Table 1 online). At a continental African level, the lion population has a 41 % probability of declining by 33 % (one third) within three lion generations, while we estimate that probability to be 2 % in India.

Models estimate the probability of meeting the thresholds for lower or higher categories (Near Threatened or Endangered) is lower than 41 % and thus lions do not qualify for these categories. The threshold for Endangered under Criterion A is a 50 % population size decline over three generations. The probability of such a decline is estimated to be 72 % in West Africa, 29 % in Central Africa, 30 % in East Africa, 17 % in southern Africa and 2 % in India (Table 1). Therefore, only West Africa would qualify as Endangered. The lion subpopulation in West Africa has been classified as Regionally Critically Endangered under criterion C2a(ii) in 2014 (Henschel *et al.,* 2014), which is supported in the current analysis. It is vital that more lion areas are surveyed rigorously, and that urgent conservation priority should be placed on West Africa. Based on our analysis, lions qualify as Vulnerable, but it is of great concern that parts of the African population is inferred to have declined at a rate that meets the category of Endangered. Since the sample subpopulations were all monitored, an even greater average rate of decline is likely for unmonitored subpopulations across much of Africa, since lack of monitoring could suggest lack of conservation effort. Finally, trends inferred are from a small proportion of lion populations, given so few populations are subject to regular surveys; there is therefore a chance that they may not be representative of most populations, for which data is lacking (see Figure S6 in the Supplementary Information online).

Approach to uncertainty and data limitations

Due to insufficient confidence in earlier or recent species population estimates, they cannot be employed to estimate overall, real-time trends, as such, groupings of scientific time series site estimates have been used as a proxy. Although these data are more numerous for lions than for other big Panthera cats, there is still considerable uncertainty inherent in both the data (Bauer *et al.,* 2015) and the treatment of it to estimate species population trend.

The difficulties in comparing survey data are recognised. In some cases, survey methods varied between years, and for some surveys accuracy may have been low, but the complete data set shows an obvious trend that is unlikely to be an artefact of methodological insufficiencies. There is inherent bias when using survey data as these often come from well-monitored areas with some element of protection and limited anthropogenic threat pressure (Packer *et al.,* 2013, Bauer *et al.,* 2015). This could bias overall results to a more optimistic state as declining populations do not necessarily have supporting data due to limited monitoring on the ground (See Figure S6 in Supplementary information online). For example, the data available for the Burkina Faso component of the W-Arly-Penjari Complex indicates a steady, but slow, increase in population size between 2012 and 2015. However, due to the recent and ongoing violent extremist presence in the area (Lhoest *et al.,* 2022), protected area management is no longer present – offering little protection to species. This is very likely to have resulted in population declines of all wildlife, including lions (as explained in the Threat Section below). However, due to the simple fact that conducting rigorous surveys on the ground is near impossible, population data to support the well-based assumption that this subpopulation is declining are not available. As a result, it is assumed that a more optimistic view on regional trends is presented here (Bauer *et al.,* 2015). Robust and regular surveys must be carried out in future that promote more reliable assessments of trends.

Fenced Reserves

Another aspect of the assessment that needs to be documented is our treatment of small, fenced reserves in southern Africa (specifically South Africa, Zimbabwe, and Malawi). Most of the population increases have occurred in these areas where management practices include translocations and reintroductions. It must be noted that South African Reserves that have a contracepted population have not been included in our estimates. In South Africa, there are 50 small, fenced reserves that are represented as one subpopulation that we refer to as South Africa's Managed Metapopulation (J. Selier pers. comm. 2022). Such management decisions should consider the 'type, scale, frequency, and effects of the suite of management interventions' and could be taxon specific (Hayward *et al.,* 2015). Management of lions in the concerned areas aims to mimic natural processes and to retain adaptive potential and follows a nationally coordinated meta-population management approach (Mallon and Stanley Price 2013, Hayward *et al.,* 2015). It is further recognised that fences have been documented as effective tools in lion conservation (Packer *et al.,* 2013). Thus, these populations are 'lightly managed' as defined in the IUCN Red List Guidelines (IUCN Standards and Petitions Committee 2022) and that they can therefore be considered "wild" and are therefore included in the assessment.

3.7.5 Habitat and Ecology Information

The African lion has a broad habitat tolerance, absent only from tropical rainforest and the interior of the Sahara Desert (Nowell & Jackson 1996). There are records of lion at elevations of more than 4,000 m asl in the Bale Mountains in Ethiopia and on Mount Kilimanjaro in Tanzania; (West and Packer 2013). Although lions drink regularly when water is available, they can obtain their moisture requirements from prey and even plants (such as the Tsama Melon in the Kalahari Desert), and thus can survive in very arid environments.

Lions are the most social of the cats, with related females remaining together in prides, and related and unrelated males forming coalitions competing for tenure over prides. Prides can vary in size and up to 30 individuals have been observed in larger ecosystems, although the average pride size (including males and females) is four to six adults (Smuts 1976). In the Kgalagadi Transfrontier Park (South Africa/Botswana) it was found that the average pride size was 11.3 ± 1.1 individuals for prides in the park; similar in size to other areas (11.8 individuals in Kruger National Park, 12.5 in Etosha National Park (Funston 2011)).

Lions tend to live at higher densities than most other felids, but with a wide variation from 1.5 adults per 100 km² in southern African semi-desert to 55/100 km² in parts of the Serengeti (Sunquist & Sunquist 2002). Pride ranges can vary widely even in the same region: e.g., from 266–4,532 km² in the Kgalagadi Transfrontier Park of South Africa (Funston 2001). Across regions, lion home ranges can also vary significantly. For example, lion home ranges in Tarangire National Park in Tanzania can range between 52–616 km² (Laizer *et al.,* 2014). In contrast, in more arid environments such as Etosha National Park, home ranges up to 2,075 km² have been recorded (Stander 1991).

Medium- to large-sized ungulates (including antelopes, zebra, and wildebeest) make up large portions of lion's prey base (Hayward & Kerley 2005), but lions will take almost any animal, from rodents to rhinos. Out of the five preferred prey species in southern Africa (Hayward *et al.,* 2007), three historically never occurred in West and Central Africa and giraffe (*Giraffa camelopardalis*) are rare in that region, leaving only buffalo (*Syncerus caffer*) but even that species is notably smaller there. Instead, medium sized species such as Kob (*Kobus kob*) are the preferred prey in West and Central Africa (Bodendorfer *et al.,* 2006, Bauer *et al.,* 2008, Tumenta *et al.,* 2013). Some lion populations have adapted to specialise in unique prey species within their own environments, such as Elephants (*Loxodonta africana*) in the Chobe (Power & Compion 2009) and in Hwange (Loveridge *et al.,* 2006), and Cape Fur Seals (*Artocephalus pusillus*) on the Skeleton Coast in Namibia (Stander 2019). Lions will also scavenge, displacing other predators (such as the Spotted Hyaena (*Crocuta crocuta*) and Cheetah (*Acinonyx jubatus*) from their kills.

In India, Asiatic lions prefer the most mesic and thick canopy forest vegetation available to them in the dry deciduous forests of Gir (Jhala *et al.,* 2009). The Gir National Park and Wildlife Sanctuary is surrounded by cultivated areas and inhabited by the pastoralist Maldharis and their livestock (Meena *et al.,* 2014). Domestic cattle have historically been a major part of the Asiatic lion's diet, although the Chital Deer (*Axis axis*) is the most common prey species. Mean pride size, measured by the number of adult females, tends to be smaller than for African lions: most Gir prides range between two and eleven adult females (Jhala *et al.,* 2009).

3.7.6 Threats Information

The main threats to lions include continued habitat loss and conversion of safe space. This has led to several subpopulations becoming small and isolated (Bauer *et al.,* 2008, 2020). Other significant threats include indiscriminate killing (primarily due to retaliatory or pre-emptive killing to protect human life and livestock), and prey base depletion (Wolf and Ripple 2016). In recent years the targeted poaching for parts (Everatt *et al.,* 2019, African Lion Database, unpub. data 2023) and violent extremism/warfare (Lhoest *et al.,* 2022) have emerged as significant threats to the species. Furthermore, while trophy hunting has a net positive impact in some areas, it may, at times, contributed to local population declines in Botswana, Namibia, Tanzania, Zimbabwe (Packer *et al.,* 2009, 2011, 2013), Cameroon (Croes *et al.,* 2011) and Zambia (Rosenblatt *et al.,* 2014). In general, there seem to be an increasing number of lions poached through snaring and targeted poaching in many areas across the species range (e.g., the Greater Kruger, Zambeze Delta, Niassa Reserve, Waza National Park, and WAP complex (African Lion Database, unpub. data. 2023)).

Conflict

The economic impact of stock raiding can be significant. Patterson *et al.,* (2004) estimated that each lion costs ranchers in Kenya living alongside Tsavo East National Park USD 290 per year in livestock losses. Likewise, annual losses of cattle to lions in areas adjacent to Waza National Park in Cameroon comprised only about 3.1 % of all livestock losses but were estimated to represent more than 22 % of financial losses, amounting to about USD 370 per owner (Bauer, 2003). Generally, economic losses caused by lions are among some of the highest reported in East Africa when compared with other wildlife species (Muriuki *et al.,* 2017). Consequently, lions are persecuted intensely in livestock areas across Africa; their scavenging behaviour makes them particularly vulnerable to poisoned carcasses put out to eliminate predators. Little actual information exists on the number of lions killed as problem animals by local people, even though this is considered the primary threat to their survival outside protected areas. However, some case studies exist. For example, Hazzah *et al.,* (2014) estimated that on average, 12.5 lions were killed per year between 2003 and 2008 by residents of Olgulului Group Range in Kenya. Implementation of appropriate livestock management measures, coupled with problem animal control measures and mechanisms for compensating livestock losses, are some of the primary responses to resolving human-lion conflict (Hazzah *et al.,* 2014). For example, Sibanda *et al.,* (2021) studied lion conflict in three communal areas in northwestern Zimbabwe (~3,306 km^2) and recorded 46 lions killed between 2008 and 2017. Following the implementation of livestock protection strategies, livestock losses generally decreased, and the number of lions killed per year declined by 41 % (Sibanda *et al.,* 2021).

Prey depletion

Prey depletion is generally defined as the substantial decline in prey abundance, and its effect on the survival and reproduction of lions is still fairly under-studied (Vinks *et al.,* 2021). Generally, prey depletion reduces an area's carrying capacity, which therefore reduces lion density without necessarily reducing their survival rates (Vinks *et al.,* 2021). Lion population density across the species' range is known to track the biomass of principle lion prey species; large wild herbivores (Hayward *et al.,* 2007, van Orsdol 1984). The latter are increasingly under threat from an unsustainable and increasingly commercialised bushmeat trade, leading to collapses in prey populations across large parts of savanna Africa (Lindsey *et al.,* 2013). Regional lion population trends reported in this assessment, are closely mirrored by time series data on main Lion prey species from 78 herbivore populations monitored between 1970 and 2005 in West, Eastern and southern Africa; while herbivore population sizes increased by 24 % in southern Africa, they declined by 52 % in Eastern Africa and by 85 % in West (Ripple *et al.,* 2015). It is likely that these declines have been even more dramatic since the publication of this study, although precise data is lacking.

Bycatch in snares

Wire snare poaching is widespread throughout much of the species' range. Snares are generally set in an effort for to capture species for bushmeat, although lions are not commonly targeted. However, lions are often captured in snares intended for other species (Becker *et al.,* 2013, Everatt *et al.,* 2015, Bauer *et al.,* 2020). This threat has the potential to result in severe population declines of all large carnivores if not mitigated accordingly. For example, Becker *et al.,* (2013) found that ~11.5 % of the adult and subadult lion population and 20 % of the adult (>4 years) males within the population were snared at some point (82 % were treated and recovered).

Use of lion bones and body parts and derivatives for traditional medicine

While there has historically been some level of illegal trade and use of lion bones and body parts for traditional medicine, this threat has escalated in recent years and has emerged in several countries within the species range (Williams *et al.,* 2017, Everatt *et al.,* 2019, Coals *et al.,* 2022). More information on this threat can be found under the Use and Trade section above.

Trophy hunting

Trophy hunting is carried out in several sub-Saharan African countries and is considered an important management tool for conserving wild land, providing financial resources for lion conservation for both governments and local communities (Holechek and Valdez 2018). However, there is concern that management regimes have not always been sufficient to deter unsustainable offtakes (Packer *et al.,* 2006). A sustainable offtake level of one male lion per 2,000 km^2 has been recommended (Packer *et al.,* 2011), but offtake has been higher in many areas, which suggests that it is potentially a threat (Lindsey *et al.,* 2013b) to continued survival of lions in these areas. Trophy hunting can thus be a tool for conservation but also a threat, depending on how it is regulated and managed (Loveridge *et al.,* 2007, 2023; Packer *et al.,* 2011). Hunter *et al.,* (2013) cautioned that regulatory measures which reduce the profitability of lion trophy hunting could have widespread negative impacts on wildlife-based land use, anti-poaching, and tolerance of lions outside protected areas.

Violent extremism and warfare

There are often unforeseen and dramatic consequences and severe environmental impacts resulting from violent extremism adjacent to protected areas (Bouley *et al.,* 2018, Lhoest *et al.,* 2022). Several protected areas (e.g., W-Arly-Pendjari complex, Niassa) within lion range are under pressure from rebel groups or violent extremist organisations. Unsafe areas resulting from such threats, makes conservation action and protected area management challenging. Protected areas which are occupied by such groups generally lack park management, see increased and unmanaged livestock invasion, suffer habitat loss due to increased crop planting and experience increased bushmeat poaching.

This threat needs to be particularly highlighted in the W-Arly-Pendjari complex (Burkina Faso, Niger and Benin). The W-Arly-Pendjari complex has the last remaining stronghold for lions in West and Central Africa. With the WAP being under severe threat from extremist groups in Niger and Burkina Faso, it places significant threat on this vital remaining population of lions. Supporting this claim is the fact that aerial survey reports in W Park in Burkina Faso, which is currently occupied by extremist groups, indicate that the area is devoid of any large mammalian wildlife (Ouindeyama *et al.,* 2021, Lhoest *et al.,* 2022). While lions may still occur throughout the complex, if the situation in the complex remains unchanged, this population may likely become significantly reduced, if not extinct altogether.

Other

We expect that climate change will likely have a negative impact on the species; however, the extent of this impact is largely unknown.

The lack of sufficient funding to support protected areas with lions poses a significant challenge to their successful conservation (Lindsey *et al.,* 2018). It has been estimated that protected areas with lions require between USD 1,000 to USD 2,000/km² annually to be managed effectively, yet receive, on average, USD 200/km² annually (Lindsey *et al.,* 2018). Nearly all protected areas in Africa with lions are inadequately funded, with deficits totally USD 0.9 to USD 2.1 billion.

3.7.7 Use and Trade Information

Use of lion bones and body parts and derivatives for traditional medicine

Illegal trade in lion body parts for medicinal purposes is considered a threat to African lion subpopulations (according to the regional lion conservation strategies, which call on countries to prohibit (IUCN 2006a) and control (IUCN 2006b) trade in lion bone and other parts and products) as well as to the small subpopulation in India's Gir Forest (M. Ventraman pers. comm. 2014). Traditional medicinal practices in Africa and Asia are perceived to be the main uses that lion body parts and bones are required (Williams *et al.,* 2017). Specific parts such as skin, claws, teeth, and bones are the most in demand parts (Williams *et al.,* 2017, African Lion Database, unpub. data 2023). However, other parts such as tails, reproductive parts and internal organs are also harvested (African Lion Database, unpub. data 2023).

While there has historically been some level of illegal trade and use of lion bones and body parts for traditional medicine, this threat has escalated in recent years and has emerged in several countries within the species range (Williams *et al.,* 2017; Everatt *et al.,* 2019; Coals *et al.,* 2020, 2022). In Mozambique the targeted poaching of lions and suspected poaching incidences are high, accounting for 74 % and 48 % of anthropogenic lion mortalities in Niassa and Limpopo National Park respectively, with evidence of domestic, regional, and international trade of lion parts and derivatives (Everatt *et al.,* 2019, Mole & Newton 2020). In South Africa, lions within captive facilities are intentionally killed (generally poisoned) for body parts, presumably to sell to international markets.

The increase in the number of lions killed in Mozambique for their parts is of particular concern (African Lion Database, unpub. data 2023) and may cause the lion subpopulations within the country to decline. However, there is currently little evidence of this threat being a major concern in other areas across their range.

3.7.7.1 Conservation Actions Information

Since 1975 *Panthera leo* has been included in CITES Appendix II, and the Endangered Asiatic lion subspecies *P. leo persica* in CITES Appendix I.

In Africa, lions are present in numerous large and well-managed protected areas (Nicolson *et al.,* in prep., Lindsey *et al.,* 2018, Loveridge *et al.,* 2022), and remain one of the most popular animals on the must-see lists of tourists and visitors to Africa (Nzomo *et al.,* 2020). Most range states in East and southern Africa have an infrastructure which supports wildlife tourism, and in this way, lions generate significant cash revenue for park management and local communities and provide a strong incentive for wildland conservation.

Regional conservation strategies have been developed for lions in West and Central Africa (IUCN 2006a, Funston *et al.,* 2023) and Eastern and southern Africa (IUCN 2006b). However, these are almost 20 years old and need to be reviewed and potentially updated. By setting out common priorities to guide action on both national, community and landscape levels, the regional conservation strategies have the potential for broad and significant improvement of lion status and management (IUCN 2006a, b; IUCN SSC Cat Specialist Group 2007, 2018; Bauer *et al.,* 2020). While all these documents show awareness of the threats and recognition of solutions, the continued decline in lion range and numbers show that political priority and funding are not sufficient (Lindsey *et al.,* 2018, Packer *et al.,* 2013).

Key conservation efforts should include effective protected area management including funding (Lindsey *et al.,* 2018, 2021; Bauer *et al.,* 2020; Robson *et al.,* 2022), mitigating anthropogenic causes of mortality such as lion-human conflict (Bauer *et al.,* 2020, Sibanda *et al.,* 2021) and snaring (Becker *et al.,* 2013), and reducing or mitigating the negative effects of armed conflict (Bauer *et al.,* 2020, Lhoest *et al.,* 2022).

With the lion currently listed as Critically Endangered in West Africa and with declining populations within the region, urgent conservation action is required to prevent local extinctions of this subspecies within the region.

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CHAPTER 4

Socio-political and ecological fragility of threatened, free-ranging African lion populations

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4.1 Abstract

Lions are one of the world's most iconic species but are threatened with extinction. Developing effective range-wide conservation plans are crucial but hampered by the relative lack of knowledge on specific threats facing each population and the socio-political context for conservation. Here, we present a range-wide examination of the relative fragility of lion populations, examining socio-political factors alongside ecological ones. We found Ethiopia's Maze National Park had the most ecologically fragile geographic population while Kavango-Zambezi was the least. At a country level, lion populations had highest ecological fragility in Cameroon and Malawi. When we examined socio-political fragility, Somalia was the most fragile lion range country, followed by South Sudan. When socio-political and ecological fragility were combined, lion populations in Maze National Park and Bush-Bush (Somalia) and more broadly, Somalian and Malawian lion populations were the most fragile. These insights should help inform more nuanced and appropriately targeted lion conservation plans.

4.2 Introduction

The African lion (*Panthera leo*) is one of the world's most iconic and charismatic species (Macdonald *et al.,* 2015) and much of the global public imbues them with a high existence value and is passionate about their conservation (Macdonald *et al.,* 2016). Even in those places where lions pose a very real threat to peoples' livelihoods and sometimes their lives, they often have high cultural value amongst local communities, particularly traditional pastoralists (Goldman *et al.,* 2010). As apex predators, lions also have substantial ecological value, and the removal of top carnivores from ecosystems can have significant and long-lasting negative ecological impacts (Ripple *et al.,* 2014). In addition to their cultural and ecological significance, lions have high economic value, and are one of the top attractions for both photographic tourists and trophy hunters to the countries where they remain (Lindsey *et al.,* 2012).

Despite their ecological, economic and existence value, lions have undergone striking declines in both geographic range and population size over recent decades. The latest range-wide estimates from 2023 estimate a remaining population of approximately 20,00-25,000 African lions (Nicholson *et al.,* 2023). Alarmingly, lions are considered to have been extirpated from at least 92 % of their historic range-wide distribution (Bauer *et al.,* 2016; Nicholson *et al.,* 2023). Lions are currently listed as Vulnerable based on an estimated 36 % decline in the species range in the last 21 years (Nicholson *et al.,* 2023). As lions depend upon their habitat, it is therefore suspected that a similar population reduction has occurred (Nicholson *et al.,* 2023). This listing suggests a high risk of extinction in the wild

(Bauer *et al.,* 2016; Nicholson *et al.,* 2023). However, there is a marked dichotomy in population trends between countries and regions - in four southern African countries (Botswana, Namibia, South Africa and Zimbabwe) lion populations increased by 12 % between 1993 and 2014, but in the remainder of African range, sample lion populations declined by 60 % (Bauer *et al.,* 2016). Lions in West and Central Africa, meanwhile, have undergone particularly severe declines (estimated to be 66 % (Bauer *et al.,* 2016)) and West African lions meet the criteria of being Critically Endangered, with fewer than 250 mature lions remaining (Henschel *et al.,* 2014).

The specific threats causing these declines vary substantially across lion range countries and regions. For example, in Eastern and southern Africa, the most severe threats to lions include poaching of prey for bushmeat, indiscriminate killing (usually due to conflict with livestock-keepers), and small population size (Henschel *et al.,* 2010; IUCN, 2006a; Lindsey *et al.,* 2013a). Meanwhile, in West and Central Africa the three primary threats are prey depletion, small population size and livestock encroachment (Henschel *et al.,* 2014; IUCN, 2006b). Protected areas are vital strongholds for lions (Riggio *et al.,* 2013), but are not always effective in conserving them. For example, bushmeat poaching with snares most likely led to local extinctions of lions in Nsumbu National Park in Zambia (Dröge. pers. comm. 2022) while populations in Limpopo National Park in Mozambique have been driven to near extinction by increasing poaching for lion parts (Everatt *et al.,* 2019). A substantial portion of lion range also falls outside of protected areas, exposing lions to higher risks of conflict, habitat loss, prey loss and other threats (Bauer *et al.,* 2020, 2016, 2015).

Although in some cases the direct cause of death of an individual lion may be easy to identify e.g., poisoning, the underlying drivers of that poisoning can be more difficult to understand. Human-lion conflict is described as a multi-dimensional and 'wicked problem,' with no easy solution and requiring multidisciplinary and interdisciplinary research to understand (Beck *et al.,* 2019; Montgomery *et al.,* 2018). However, human-lion conflict is not the only threat in which understanding the underlying drivers of a specific threat is important (Bauer *et al.,* 2020). Conservation threats in general are driven and affected by a multitude of wider-scale socio-political factors (Bauer *et al.,* 2020; Dickman *et al.,* 2015; Kuiper *et al.,* 2018; Negret *et al.,* 2017). Key factors include poverty, governance (particularly corruption), wildlife policies, human pressures, and the extent of armed conflict (Dickman *et al.,* 2015; Henschel *et al.,* 2014; IUCN, 2006b; Kuiper *et al.,* 2018), yet they are rarely explicitly considered in conservation planning. The IUCN called for this broader perspective to be considered in lion conservation over 15 years ago (IUCN, 2006b), yet it is often still ignored in conservation assessments (Dickman *et al.,* 2015). We argue the time has come to finally include and compare the socio-political contexts in which remaining lion populations survive. Assessing socio-political alongside ecological pressures is essential to understand threats and to develop effective conservation strategies and priorities.

Here, using recent, available data for extant free-ranging African lion populations, we examine their ecological and socio-political fragility at both a national and geographic population scale. Fragility is defined as a species or ecosystem that are vulnerable to damage/harm or even extinction (Nilsson and Grelsson, 1995). This approach provides a novel tool for understanding the fragility of lion populations and range countries and will inform decision-makers regarding choices around lion conservation, such as funding strategies and priorities for action. For instance, different lion populations could be compared to better understand ecological factors that may affect population persistence as well as the socio-political factors that may enable successful conservation action. This model also has applicability for many other taxa, as remaining wildlife populations are subject to increasing anthropogenic threats from both an ecological and socio-political perspective.

Our analyses indicated 62 free-ranging geographic lion populations remain across 25 range countries. When transboundary populations were split according to national boundaries, we identified 84 national lion populations. Maze National Park in Ethiopia was identified as the most ecologically fragile population at both a geographic and national level. This can largely be attributed to intense edge effects from high densities of both cattle and people. When assessing at the national level, Cameroonian and Malawian lion populations were most ecologically fragile due to their small populations and isolation from other lion populations. Somalia was the most fragile lion range country from a socio-political perspective. Maze National Park and Bush-Bush (Somalia) were found to be the most fragile overall when ecological and socio-political fragility scores were combined.

4.3 Methods

Lion population estimates and geographic range were initially taken from the IUCN's "Guidelines for the Conservation of Lions in Africa" (GCLA (IUCN SSC Cat Specialist Group, 2018)) as it was approved by African lion Range States and numerous lion experts. Minor edits were then made based on the IUCN SSC Cat Specialist Group's African Lion Database (see online Supplementary material) for full list of populations and references used for this study). In both cases, in the absence of updated survey data, we used expert opinion to provide population estimates and spatial extent of range. Experts were defined as conservation biologists that have extensive knowledge of lions in that region.

Analyses were restricted to free-ranging lion populations (termed a 'geographic population'), which we defined as consisting of all individuals connected via contiguous habitat. If a geographic population crossed national boundaries, it was split into a national subpopulation for analysis at the national level. We included all unfenced lion populations and those populations which were partially fenced but were at least 500 km^2 in extent, and populations which were fully fenced but at least 1,000 km^2 in extent. Although this was a necessarily arbitrary cut-off, these large, fenced areas were classed as free-ranging because they probably allow for ecologically functional lion populations, assuming even the lower end of 1.5 adult lions/100 km^2 cited for southern African semi-deserts (Bauer *et al.,* 2016, 2015). Populations which were within 10 % of that cut-off were considered for inclusion. Only one fell within that scope (South Africa's Hluhluwe-iMfolozi) so that was included in the final analysis. We only included areas where experts said there was confirmed lion presence in the last two lion generations (15 years; since 2006) as our aim was to assess fragility of known populations.

Country boundaries were obtained from the Global Administrative Areas database (GADM 2016) and all spatial analyses were conducted in ArcMap 10.4 (Release 10.4.1; ESRI, Redlands, CA). It is imperative to note that the resultant map does not depict a conclusive current range map for lions, and the estimates do not constitute the total number of wild lions in Africa, but this analysis represents the populations where sufficiently reliable data were available to examine fragility.

Lion populations were assessed at three spatial scales. The first scale was the 'geographic' population scale (i.e., the entire population regardless of whether it spans national boundaries), which accommodates the transboundary nature of many lion populations. We also assessed at a 'national' scale, where geographic populations were split at a national boundary (if a geographic population was split by a country boundary, the population within a single country we called a 'subpopulation'), as countries are the management units at which most policies and decisions are made. Lastly, we assessed fragility at the country level in which we averaged multiple national populations and subpopulations, if appropriate.

4.3.1 Calculation of ecological and socio-political fragility scores

We calculated two fragility scores for lion populations: an ecological and a socio-political score. Both scores comprised a sum of individual variables (see below), which were standardised to produce z-scores before summing. Higher scores represented greater fragility. Some z-scores were inverted from negative to positive in instances when a higher value was associated with lower fragility (e.g., a larger population is less fragile). Individual z-scores were summed to produce a composite measure of fragility (Dickman *et al.,* 2015). Combining factors can provide a more informative picture than examining factors individually, and summing z-scores is an established method for producing composite measures (Andersen *et al.,* 2006; Tanha *et al.,* 2011). Although it could be argued that some factors should be weighted more heavily in our calculations of fragility than others, this was beyond the scope of this study. Researchers interested in developing a weighted index could do so using a similar approach.

4.3.2 Calculating the ecological fragility score of lion populations

The ecological fragility of each lion population was calculated as the sum of standardised values of the ten variables described below (see online supplementary material). The 'exposure to bordering countries' variable was not relevant at the geographic scale and was only calculated at the 'national' and 'country' scales.

(i) Geographic area – populations covering a smaller area were assumed to be more ecologically fragile, as they would be more susceptible to edge effects even if the core population was protected (Woodroffe & Ginsberg, 1998).

(ii) Percentage of wild lions remaining - smaller lion population sizes were assumed to be more vulnerable to extinction and therefore more ecologically fragile.

(iii) Edge-to-area ratio – populations with a higher edge-to-area ratio were assumed to be more ecologically fragile (Woodroffe & Frank, 2005). The edges of some populations bordered features like lakes, where edge effects would presumably be less than those bordering farming or pastoralist areas. The 'hardness' of the edge was not incorporated here, but within the 'intensity of edge effect' calculations.

(iv) Percentage of lion range covered by protected areas – populations with relatively little coverage by protected areas were assumed to be more ecologically fragile. Protected area boundaries were obtained from the World Database on Protected Areas (IUCN and UNEP-WCM, 2018). We minimally modified protected area categorisation due to inconsistent designation across countries, and only used designated and terrestrial protected areas with IUCN categories I-IV (Jacobson *et al.,* 2016).

(v) Population size as a percentage of predicted lion carrying capacity – populations at only a low percentage of predicted carrying capacity were assumed to be more ecologically fragile (Purvis *et al.,* 2000). Fragility here was viewed as the likelihood of the population becoming extirpated, so higher population size relative to carrying capacity was viewed as being more secure, even in cases where populations exceeded the predicted carrying capacity (which would be likely to cause issues in the longer-term). Predicted lion carrying capacity was calculated for this analysis (Loveridge & Canney, 2009).

(vi) Population isolation – populations which were less connected to other lion populations were assumed to be more ecologically fragile, as there is less likely to be genetic mixing with, or recolonisation from, other populations. A connectedness score was calculated as the count of other extant lion populations within 350 km of the focal population, based on a maximum dispersal distance for a male lion of 343 km (Dolrenry *et al.,* 2014), weighted by distance to the focal population. Neighbouring populations within 50 km were given a score of 5, populations between 50 and 99 km away were given a score of 4, populations 100 to 149 km away were given a score of 3, populations 150 to 249 km away were given a 2 and populations 250 to 349 km away were given a 1. These were summed to produce an overall population isolation figure.

(vii) Intensity of edge effect – populations with high human population density on the edges were assumed to be more ecologically fragile, as intense edge effects can have far-reaching impacts even within protected areas (Woodroffe & Frank, 2005; Woodroffe & Ginsberg, 1998). Non-overlapping 30 km buffers were drawn around each extant lion population and these were combined with a human population density map (WorldPop 2020 data) (Linard *et al.,* 2012) to extract an estimate of human population density in the immediate surroundings of lion populations. Buffers were set at 30 km to reflect a reasonable daily movement of a lion, and thus the scale at which regular conflict with human presence is likely. This variable was weighted according to whether there was partial (25 % reduction) or complete (50 % reduction) fencing of the lion population, as fencing largely eliminates the impact of an edge effect (Packer *et al.,* 2013).

(viii) Human population density within the lion population - higher human population density within the same area as the lion population was assumed to increase ecological fragility, due to associated threats such as resource extraction, habitat degradation, prey depletion and human-lion conflict. Human population estimates within the lion range were extracted from the WorldPop data for the year 2020 (Linard *et al.,* 2012). In fully-fenced areas where no humans resided in the lion area, we reduced the WorldPop density to 0 humans/km^2. This applied to Akagera National Park (Rwanda), Liwonde National Park (Malawi), Hluhluwe-Umfolozi (South Africa) and Bubye Valley (Zimbabwe).

(ix) Cattle density within the lion population – greater cattle density within lion range was assumed to increase ecological fragility due to associated threats of human-carnivore conflict, particularly retaliatory or preventative lion killings over depredation (Ikanda & Packer, 2008; Kissui, 2008). As cattle density represents pastoralism the best and is one of the most important cases of human-wildlife conflict (Ikanda & Packer, 2008), we used cattle as a proxy for all livestock. Cattle data were obtained from the Université Libre de Bruxelles/Food and Agriculture (FAO) Gridded Livestock of the World 2010 (GLW 3) dataset (Gilbert *et al.,* 2018). In fully-fenced areas where no humans resided in the lion area, we altered the cattle density to 0 cattle/km^2.This applied to Akagera National Park (Rwanda), Liwonde National Park (Malawi), Hluhluwe-Umfolozi (South Africa) and Bubye Valley (Zimbabwe).

(x) Immediate exposure to influence of bordering nations – a neighbouring country's policies and situation could affect lion populations that adjoin or cross borders (Everatt *et al.,* 2019). The percentage of total area of a lion population influenced by the socio-political score of a neighbouring country (deemed as falling within a 30 km buffer of the border) was weighted by the difference in socio-political scores between the two countries. Hence, if a lion population existed largely in a less socio-politically fragile country (see below) but bordered a country with a higher fragility score, this would increase the fragility of the population.

4.3.3 Calculating the socio-political fragility score of lion populations

The fragility score was calculated by creating a composite measure from the z-scores of the following 12 national-level variables (Due to the size of the tables, Supplementary Tables 1-6 are available online at https://static-content.springer.com/esm/art%3A10.1038%2Fs43247-023-00959-3/MediaObjects/43247_2023_959_MOESM1_ESM.pdf

Supplementary Table 4-1), as defined in source databases (Dickman *et al.,* 2015). Although not an exhaustive list, these 12 variables were identified as key governance, economics, anthropogenic pressure and environmental policy indicators likely to influence the fragility of lion populations, and had comparable data for all 25 of the lion range countries. Each variable was standardised relative to all current lion range countries. The standardised variables contributing to each of the four metrics (governance, economics, anthropogenic pressure and environmental policy) were averaged within each category, and these four metrics summed and then re-scaled to produce an estimate of socio-political fragility (Dickman *et al.,* 2015). Geographic population level estimates of socio-political fragility were calculated as a percentage of a population's range in a given country multiplied by the socio-political score of that country, averaged across all the national population(s) (i.e., subpopulations of the single geographic population).

A) Governance

i) Government effectiveness – Less effective governments are likely to impede successful conservation efforts, so lower effectiveness was assumed to be linked to increased fragility. This was taken as a 10-year average (2011-2020) from the World Bank Worldwide Governance Indicators: http://info.worldbank.org/governance/wgi/.

ii) Political stability – Lower political stability is likely to divert attention and funding away from conservation efforts, limits the will of international agencies to work in the country and inhibits long-term planning. Lower political stability was therefore assumed to be linked to increased fragility. Data as above.

iii) Control of corruption – Corruption is likely to deter investment for conservation and lead to misappropriation of conservation funding, so higher levels of corruption was assumed to be linked to increased fragility. Data as above.

B) Economics

i) Gross Domestic Production (GDP) per capita based on Purchasing Power Parity (PPP) – lower GDP is likely to limit funding for conservation and means that other issues such as food security take priority, so lower GDP was assumed to be linked to increased fragility. GDP based on PPP was used to enable more accurate comparisons between countries. Data averaged across years 2011-2020 from World Bank World Development Indicators: https://databank.worldbank.org/source/world-development-indicators.

ii) Human Development Index (HDI) – With low HDI levels, a country is unlikely to have sufficient resources to invest in conservation, so lower HDI was assumed to be linked to increased fragility. Data as above.

iii) GINI Index – An estimate of the distribution of wealth that measures inequality in income between households, with greater inequality between the richest and poorest assumed to be linked to increased fragility. Data as above.

C) Anthropogenic pressure

i) Annual human population growth rate – higher human growth rates place increasing pressure on land and resources, so higher growth was assumed to be linked to increased fragility. National data averaged across years 2011-2020 from World Bank World Development Indicators: https://databank.worldbank.org/source/world-development-indicators.

ii) Countrywide human population density – higher human density results in higher demand for land and resources, so higher density was assumed to be linked to increased fragility. Data as above.

iii) Global human modification – a measure of the level of human modification on terrestrial land accumulated across 13 stressors (Kennedy *et al.,* 2019). Values were averaged across a lion population. A higher level of modification was assumed to be linked to increased fragility.

D) Policy

i) Conservation Action Plan – Developing an Action Plan represents some level of governmental commitment to conservation, so the absence of a conservation action plan relevant to lions was assumed to be linked to increased fragility. Countries were scored 3 if they had a specific large carnivore action plan developed, 2 for an active National Biodiversity Strategies and Action Plans (NBSAP under the convention on Biological Diversity) that has nothing specific for lions, 1 for a developed but not apparently active NBSAP, or 0 for no carnivore action plan or NBSAP.

ii) Percentage of relevant wildlife treaties signed up to – Another measure of government-level commitment to conservation is the percentage of ten international wildlife treaties deemed relevant to lion conservation that lion range countries have signed up to (Ramsar Convention, World Heritage Convention, CITES, CMS, CBD, African Convention, Bern Convention, SADC Protocol, Lusaka Agreement and TFCA treaties) (Trouwborst *et al.,* 2017). The fewer treaties a state signed up to, the higher the assumed fragility on this metric.

iii) Percentage of land designated as Protected Area – Setting aside protected areas is one example of a country's willingness to commit resources to conservation, so having a smaller percentage set aside at the national level was assumed to be linked to increased fragility. Countrywide data reported from Protected Planet in 2018 for all terrestrial and inland water coverage.

All variables were initially retained because each contributed additional value (e.g., small populations restricted to small, unprotected areas surrounded by high human population density merit more attention than those that are just small populations, even if the processes are related) (Dickman *et al.,* 2015). However, if variables had high Pearson correlation coefficient (i.e., above 0.8), the correlated variables were removed. All governance variables were highly correlated, so only Government Effectiveness was retained after removing control of corruption and political stability (Due to the size of the tables, Supplementary Tables 1-6 are available online at https://static-content.springer.com/esm/art%3A10.1038%2Fs43247-023-00959-3/MediaObjects/43247_2023_959_MOESM1_ESM.pdf

Supplementary Table 4-1To produce an indicator of overall fragility, both ecological and socio-political indices were re-scaled, so the minimum score became 0 (least fragile) and the maximum 1 (most fragile), and then the indices were summed together to produce one composite measure from 0 to 2.

4.4 Results

Our analyses indicated 62 free-ranging geographic lion populations across 25 range countries (see online supplementary material and Supplementary Figure 4-1). This resulted in 84 national lion populations when transboundary populations were split according to national boundaries (Table 4.3, see online supplementary material and Supplementary Figure 4-2).

4.4.1 Ecological characteristics and fragility of geographic lion populations

Of the 62 geographic populations, 41.9 % (n = 26) were estimated to have 50 or fewer lions (Supplementary Figure 4-3). Another ten (16.1 %) of Africa's geographic populations had between 51 and 100 lions and only seven populations (11.3 %) were estimated to have 1,000 or more lions (Supplementary Figure 4-3). The median category for population size was 51-100 lions, while the mode was 0-50.

The 62 geographic populations ranged in size from 156 km^2 (Manyara Ranch) to 249,754 km^2 (Kavango-Zambezi in Angola, Botswana, Namibia, Zambia, and Zimbabwe) with a mean of 30,575 km^2 and a median of 7,442 km^2 (see online supplementary material). Seven populations (10.7 %) spanned over 100,000 km^2 (Etosha-Kunene, Katavi-Ruaha, Kavango-Zambezi, Luangwa-Mana-Tchuma Tchato, Maasai Steppe and Selous-Niassa). Based on WDPA data (UNEP-WCMC 2018), twelve of the populations (19.4 %) were completely encompassed by existing protected areas with IUCN categories I-IV, while an additional 17 populations (27.4 %) had at least 50 % of their area covered by existing protected areas (see online supplementary material). However, nine populations (14.5 %) did not appear to be covered by existing protected areas with categories I-IV to any extent. Collectively, these nine populations represented 64,116 km^2 (4.0 %) of lion range and less than 1,000 lions (n = 790).

Lion populations appeared to be severely depleted compared to their predicted carrying capacity. The populations examined here could potentially hold over four times as many lions (approximately 100,000) based on ecological characteristics (Lindsey *et al.,* 2018; Loveridge & Canney, 2009) (see online supplementary material and Supplementary Figure 4-4). On average, lions were estimated to be at around 33.3 % (range 1.9 % - 328.2 %) of predicted carrying capacity (see online supplementary material). Almost a third of populations (n = 20, 32.3 %) maintained lions at less than 10 % the predicted carrying capacity, while only three populations (5 %) had lions at between 50 and 100 % of carrying capacity (i.e., Akagera, Greater Limpopo, Lake Manyara). In addition, five populations (8.1 %) had lion populations exceeding carrying capacity, ranging from 121.3 % to 328.1 % of the predicted level (i.e., Bubye Valley Conservancy, Greater Mapungubwe, Hluhluwe-Umfolozi, Kidepo Valley and Manyara Ranch).

In terms of connectedness, the most well-connected populations were in East Africa, such as the Southern Maasai Steppe, Katavi-Ruaha and Selous-Niassa. On the other hand, some populations were critically isolated (i.e., the bottom 5 %) with almost no connectedness, such as Niokolo-Koba, Hluhluwe-Umfolozi and Luando Integral Nature Reserve (see online supplementary material). Both human and cattle densities tended to be higher in the Horn of Africa, particularly in Ethiopia, while human and cattle densities were generally lower across lion populations in southern Africa (see online supplementary material).

Ethiopia's Maze National Park lion population was the most ecologically fragile, mainly due to high cattle and human densities within lion range (Figure 4-1, Figure 4-2, Figure 4-3). Other ecologically fragile geographic populations were Lake Manyara, Nechisar and Toro-Semiliki (Table 4.1, Figure 4-2, Figure 4-3). Meanwhile, the lion populations in Selous-Niassa (Tanzania and Mozambique) and Kavango-Zambezi (Angola, Botswana, Namibia, Zambia and Zimbabwe) were the least ecologically fragile (Figure 4-1, Figure 4-2), mainly due to their large sizes and relatively large lion populations, although their fragility scores were increased by relatively low protected area coverage (Figure 4-1).

The 62 geographic populations were split into 84 national populations and subpopulations (if a geographic population was split across 2 or more countries, we called each country-level population a national population or a 'subpopulation') (Table 4.2, Supplementary Figure 4-2 and online supplementary material). The Selous-Mikumi and Okavango-Chobe subpopulations emerged as the least ecologically fragile, with Lake Manyara and Maze the most fragile (Figure 4-2, Table 4.2 and online supplementary material).

Table 4.1. Socio-political, ecological and overall fragility scores of 62 geographic lion populations listed from most to least fragile.

	Population	Rescaled ecological fragility score	Rescaled socio-political fragility	Overall fragility		Population	Rescaled ecological fragility score	Rescaled socio-political fragility	Overall fragility		Population	Rescaled ecological fragility score	Rescaled socio-political fragility	Overall fragility
1	Bush-bush	0.53	1.00	1.53	22	Kasungu	0.46	0.54	1.00	43	Niokolo-Koba	0.45	0.35	0.80
2	Maze	1.00	0.49	1.49	23	Afar-Awash	0.48	0.49	0.97	44	Meru Conservation Area	0.50	0.23	0.73
3	Boma National Park	0.35	0.88	1.23	24	Welmel-Genale	0.45	0.49	0.94	45	Laikipia-Samburu-Marsabit	0.48	0.23	0.71
4	Garamba Complex	0.51	0.72	1.23	25	Bale	0.45	0.49	0.94	46	Lavushi Manda	0.44	0.27	0.71
5	Toro-Semiliki	0.70	0.49	1.19	26	Dinder, Alatash, Bejemis & surroundings	0.45	0.49	0.93	47	Southern Maasai Steppe	0.47	0.23	0.70
6	Nechisar	0.70	0.49	1.19	27	Murchison Falls	0.44	0.49	0.93	48	Greater Mapungubwe	0.37	0.32	0.70
7	Lake Manyara	0.94	0.23	1.17	28	Ogaden	0.44	0.49	0.93	49	Liuwa Plain	0.42	0.27	0.70
8	Bili-Uere Complex	0.44	0.72	1.16	29	Magoe	0.51	0.40	0.91	50	Bubye Valley	0.36	0.33	0.69
9	Yankari	0.52	0.64	1.16	30	Benoue Complex	0.45	0.45	0.90	51	Udzungwa Mountains	0.45	0.23	0.68
10	Integral Nature Reserve and the Luando	0.44	0.70	1.14	31	Akagera	0.38	0.52	0.90	52	Greater Kafue Ecosystem	0.37	0.27	0.64
11	Liwonde and Mangochi	0.60	0.54	1.13	32	Gambella	0.40	0.49	0.89	53	Moyowosi-Kigosi	0.40	0.23	0.63
12	Chebera Churchura, Kaffa,	0.64	0.49	1.13	33	W-Arly-Pendjari	0.43	0.45	0.88	54	Luangwa-Mana-Tchuma Tchato	0.19	0.41	0.60
13	Greater Virunga	0.58	0.54	1.12	34	South Omo Ecosystem	0.37	0.49	0.86	55	Greater Limpopo	0.16	0.40	0.56
14	Zakouma NP and Surrounds	0.42	0.69	1.11	35	Gorongosa-Marromeu	0.46	0.40	0.86	56	Kavango-Zambezi	0.00	0.46	0.46
15	Chinko and surroundings	0.40	0.68	1.08	36	Swaga Swaga	0.61	0.23	0.84	57	Katavi-Ruaha	0.20	0.23	0.43
16	Kainji Lake	0.44	0.64	1.08	37	Kidepo Valley	0.34	0.49	0.84	58	Maasai Steppe	0.07	0.34	0.41
17	Bamingui-Bangoran	0.40	0.68	1.08	38	Borana and South Omo Ecosystem	0.32	0.49	0.81	59	Kgalagadi	0.22	0.19	0.41
18	Waza	0.62	0.43	1.06	39	Manyara Ranch	0.57	0.23	0.80	60	Selous Niassa	0.00	0.38	0.38
19	Babille/Eastern Hararghe	0.54	0.49	1.03	40	Burigi-Chato	0.57	0.23	0.80	61	Etosha-Kunene	0.34	0.03	0.38
20	Maokomo	0.53	0.49	1.02	41	Chizarira-Chirisa	0.47	0.33	0.80	62	Hluhluwe-Umfolozi	0.38	0.00	0.38
21	Vwaza Marsh	0.47	0.54	1.00	42	Saadani	0.57	0.23	0.80					

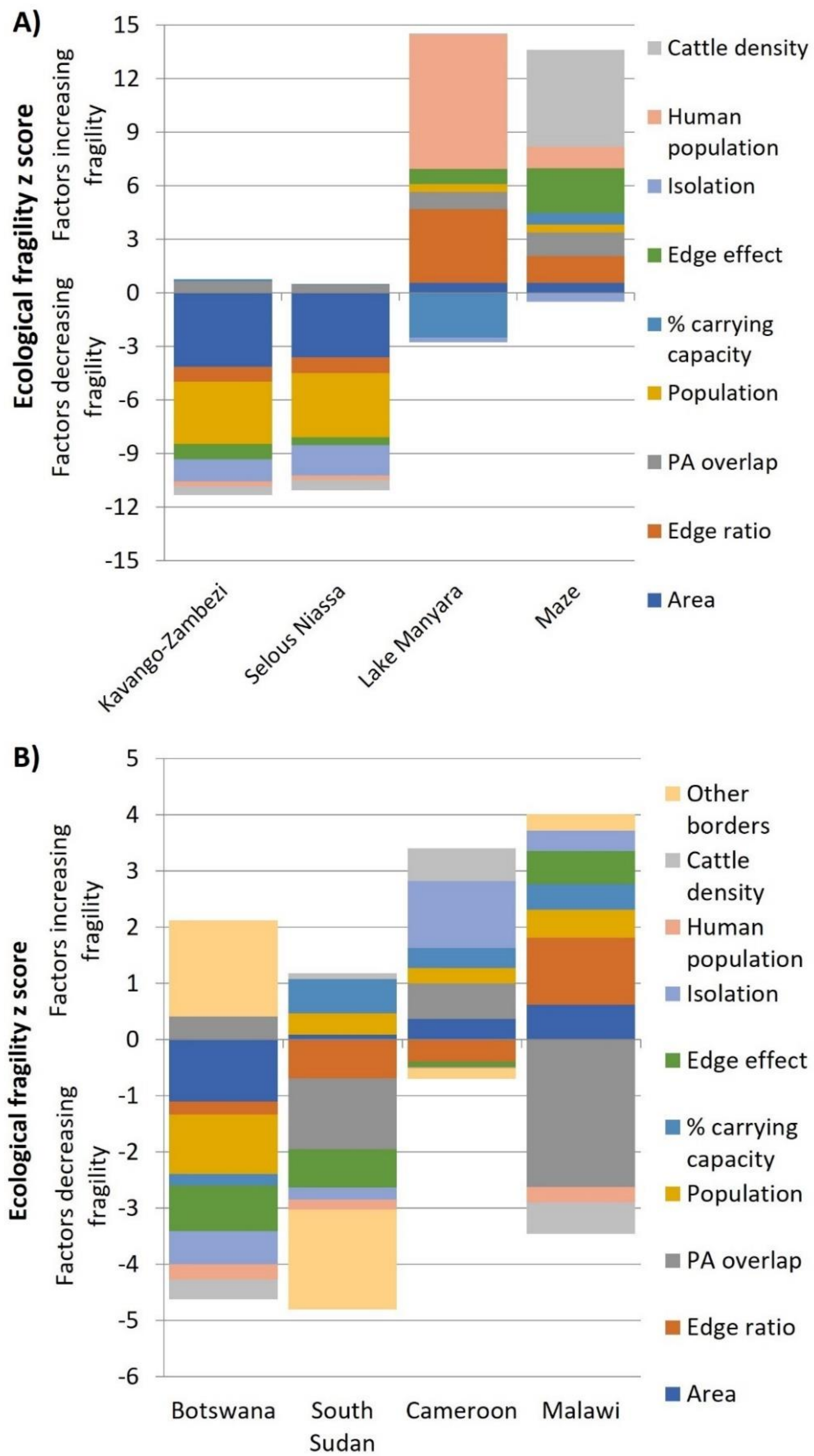

Figure 4-1. Factors contributing towards ecological fragility scores. Factors which rank positively on the y axis increase ecological fragility for those populations, while those which rank negatively reduce ecological fragility. Total z-score is the sum of both positive and negative values. A) Selous-Niassa, Kavango-Zambezi were the least ecologically fragile geographic populations while Lake Manyara and Maze the most. B) Botswana and South Sudan were the least ecologically countries and Cameroon and Malawi the most fragile.

4.4.2 Ecological characteristics and fragility of national lion populations and lion range countries

Fragility score of lion populations and subpopulations were then averaged (if a country had >1 population) and national scores compared (Table 4.2). Based on the data available here, six (24 %) of the 25 lion range countries had a total of fewer than 50 lions and eight countries (32 %) had 1,000 or more (see online supplementary material). Over half of Africa's remaining lion range countries (n = 14, 56 %) each supported less than 1 % of the overall lion population examined in this study (Table 4.3). Current available data (which is often very poor) suggested that Tanzania had by far the largest number of lions, with over 8,000 (34 % of the study total), and just two countries (Tanzania and Botswana) accounted for almost half (48 %) of the total number of lions examined.

Lion range per country varied from just over 1,000 km^2 in Rwanda to over 383,503 km^2 in Tanzania (Table 4.3). Range countries formally protected on average 62.9 % of their area occupied by resident lions, although this varied considerably, from 0 % in Somalia to 100 % or just shy of this in Senegal, South Sudan, Sudan, Uganda and Rwanda (Table 4.3). More than a quarter (n = 7; 28 %) of range countries' lion populations were at <10 % of potential ecological carrying capacity, with South African populations existing at the highest percentage of carrying capacity and Angola the lowest (Table 4.3 and online supplementary material). Edge effects on lion populations were particularly high in Democratic Republic of Congo, Malawi and Uganda, while they were lowest in Botswana, Central African Republic and Namibia (Table 4.3). Senegal's only lion population was the most isolated, with no other populations within 350 km, while Tanzania and Zimbabwe's lion populations were the most well-connected (Table 4.3). Human population density within lion population areas was highest in Tanzania, followed by Ethiopia, while it was very low in both Botswana and Central African Republic (Table 4.3). Cattle density within lion population areas was particularly high in Somalia, followed by Ethiopia, while this was lowest in Angola, the Central African Republic and Niger (Table 4.3).

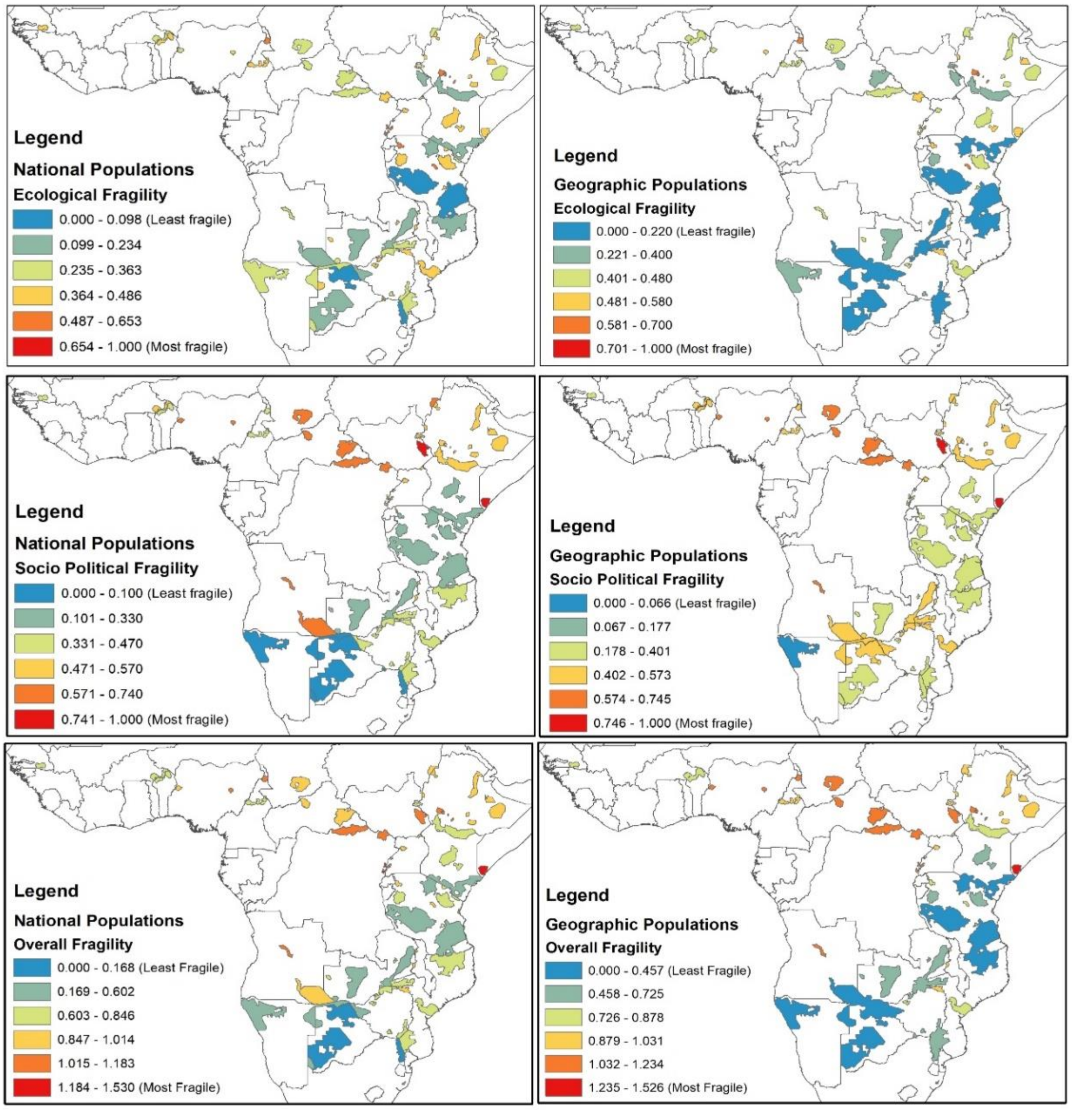

Figure 4-2. The ecological, socio-political and overall fragility scores of 84 national populations (separated by national boundaries) and 62 geographic populations of free-ranging African lions. Ecological fragility of A) national populations and B) geographic populations. Socio-political fragility of C) national populations and D) geographic populations. The overall fragility score for populations is calculated by summing their ecological and socio-political fragility scores. Overall fragility of E) national populations and F) geographic populations.

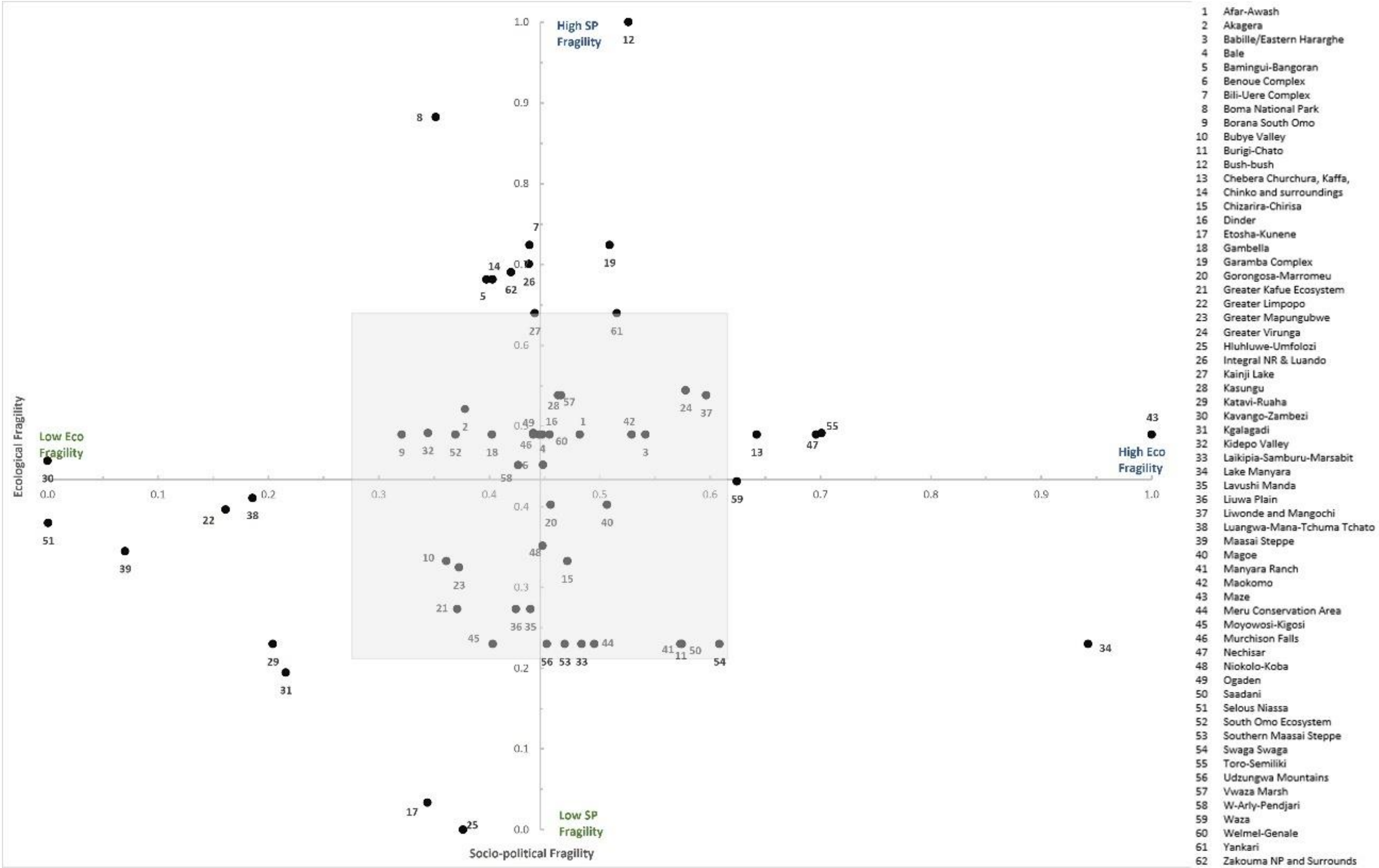

Figure 4-3. Ranking of the 62 geographic lion populations in overall fragility. Populations higher on the y-axis or further to the right on the x-axis are more fragile. The axis lines are drawn at the mean value not at the mid-point of the index. The shaded grid depicts those populations which fall within one standard deviation of the mean.

When considering national lion populations, Cameroon, Malawi and Ethiopia had the most ecologically fragile lion populations (Figure 4-4 and Table 4.3), with populations in the first two countries suffering from large edge effects and small population sizes relative to potential carrying capacity (Figure 4-1 and Table 4.3). National lion populations in South Sudan, Botswana and Angola were the least fragile (Figure 4-1, Figure 4-2 and Table 4.3). In Botswana, high lion population numbers and the population size relative to expected carrying capacity contributed to less fragile scores (Figure 4-1). South Sudan had only a single population, within Boma National Park, which was less fragile primarily because it had low human and cattle densities within and surrounding the lion area and it was well-connected to other populations in Ethiopia (Figure 4-1). Angola's two populations both had low human and cattle densities within and surrounding the lion areas.

4.4.3 Socio-political characteristics and fragility

The 25 range countries assessed here varied markedly in terms of characteristics across the four socio-political categories (see online supplementary material). Note that these scores were calculated at the national level such that all lion population(s) within the country all had the same socio-political score. On our indices, Somalia was the most socio-politically fragile lion range country (Figure 4-4 and Table 4.3, and online supplementary material). It scored above average in fragility for three of the four categories and was particularly vulnerable in terms of the governance and conservation policy categories (Figure 4-5 and online supplementary material). The next most fragile country was South Sudan, where poor scores in both governance and conservation policy categories contributed most to its high fragility (Figure 4-2, Figure 4-5 and online supplementary material). Botswana, South Africa and Namibia were ranked as the least socio-political fragile lion range countries, with relatively good governance and economic scores compared to the other countries examined (Figure 4-2 and online supplementary material).

Socio-political fragility of geographic lion populations was very similar to the results at the national level. Geographic populations largely within Botswana (Kgalagadi and Greater Mapungubwe) were the least fragile. On the other hand, Bush-Bush is entirely within Somalia, the most fragile range country, and therefore is also the most fragile geographic population. Similarly, Boma is the second most fragile population as it is entirely within the second most fragile country, South Sudan.

Table 4.2. Socio-political, ecological and overall fragility scores of 84 national lion populations listed from most to least fragile.

	Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score		Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score		Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score
1	Maze	1.00	0.53	1.53	29	Welmel-Genale	0.41	0.53	0.94	57	Mana Pools, Hurungwe, Sapi, Chewore, Dande and Doma	0.36	0.38	0.74
2	Bush-bush	0.41	1.00	1.41	30	Bale	0.40	0.53	0.93	58	Udzungwa Mountains	0.44	0.29	0.73
3	Virunga	0.54	0.74	1.28	31	Afar-Awash	0.39	0.53	0.92	59	Laikipia-Samburu-Marsabit	0.43	0.29	0.72
4	Lake Manyara	0.99	0.29	1.28	32	Luengue-Luiana and Mavinga	0.19	0.72	0.91	60	Liuwa Plain	0.38	0.33	0.71
5	Nechisar	0.65	0.53	1.18	33	Murchison Falls	0.37	0.53	0.90	61	Bubye Valley	0.31	0.38	0.69
6	Chebera Churchura, Kaffa	0.62	0.53	1.15	34	Swaga Swaga	0.60	0.29	0.89	62	Gonarezhou-Save Valley	0.30	0.38	0.68
7	Toro-Semiliki	0.61	0.53	1.14	35	Manyara Ranch	0.59	0.29	0.88	63	Moyowosi-Kigosi	0.39	0.29	0.68
8	Garamba Complex	0.39	0.74	1.13	36	Ogaden	0.34	0.53	0.87	64	Southern Maasai Steppe	0.38	0.29	0.67
9	Liwonde and Mangochi	0.55	0.57	1.12	37	Magoe	0.42	0.45	0.87	65	Niassa-Quirimbas	0.18	0.45	0.63
10	Boma National Park	0.21	0.89	1.10	38	Saadani	0.58	0.29	0.87	66	Mkomazi	0.33	0.29	0.62
11	Sena Oura	0.39	0.71	1.10	39	Burigi-Chato	0.56	0.29	0.85	67	Sioma Ngwezi	0.27	0.33	0.60
12	Queen Elizabeth	0.55	0.53	1.08	40	Benoue Complex	0.38	0.47	0.85	68	Hwange	0.20	0.38	0.58
13	Yankari	0.41	0.67	1.08	41	South Omo Ecosystem	0.31	0.53	0.84	69	Shashe-Limpopo	0.51	0.07	0.58
14	Waza	0.58	0.47	1.05	42	WAP, Burkina Faso	0.33	0.50	0.83	70	Greater Kafue Ecosystem	0.22	0.33	0.55
15	Bili-Uere Complex	0.30	0.74	1.04	43	WAP, Benin	0.37	0.46	0.83	71	Hluhluwe-Umfolozi	0.45	0.07	0.52
16	Integral Nature Reserve and the Luando	0.32	0.72	1.04	44	WAP, Niger	0.35	0.48	0.83	72	Xaxa	0.49	0.00	0.49
17	Vwaza Marsh	0.44	0.57	1.01	45	Gorongosa-Marromeu	0.38	0.45	0.83	73	Luangwa Valley	0.15	0.33	0.48
18	Babille/Eastern Hararghe	0.48	0.53	1.01	46	Gambella	0.29	0.53	0.82	74	Serengeti-Ngorongoro-Loliondo	0.14	0.29	0.43
19	Kasungu	0.43	0.57	1.00	47	Kidepo Valley	0.29	0.53	0.82	75	Mara-Amboseli-Chyulu-Tsavo-BoniDodori	0.14	0.29	0.43
20	Kainji Lake	0.33	0.67	1.00	48	Niokolo-Koba	0.39	0.40	0.79	76	Khaudum-Caprivi	0.31	0.10	0.41
21	Zakouma NP and Surrounds	0.29	0.71	1.00	49	Greater Limpopo (including Karingani, Banhine)	0.34	0.45	0.79	77	Kalahari Gemsbok	0.32	0.07	0.39
22	Bamingui-Bangoran	0.28	0.70	0.98	50	Chizarira-Chirisa	0.40	0.38	0.78	78	Etosha-Kunene	0.29	0.10	0.39
23	Chinko and surroundings	0.28	0.70	0.98	51	Tchuma Tchato	0.33	0.45	0.78	79	Katavi-Ruaha	0.08	0.29	0.37
24	Maokomo	0.44	0.53	0.97	52	Longido	0.48	0.29	0.77	80	Northern Tuli	0.35	0.00	0.35
25	Akagera	0.41	0.56	0.97	53	Matusadona and Omay	0.39	0.38	0.77	81	Selous-Mikumi	0.00	0.29	0.29
26	Tuli Circle	0.58	0.38	0.96	54	Borana and South Omo Ecosystem	0.23	0.53	0.76	82	Kruger National Park and Adjoining Private Nature Reserves	0.10	0.07	0.17
27	Alatash, Bejemis & surroundings	0.42	0.53	0.95	55	Meru Conservation Area	0.47	0.29	0.76	83	Central Kalahari-Khutse-Gemsbok	0.13	0.00	0.13
28	Dinder	0.31	0.63	0.94	56	Lavushi Manda	0.41	0.33	0.74	84	Okavango-Chobe	0.04	0.00	0.04

Table 4.3. Mean results per country and overall ecological and sociopolitical scores per country (n = 25), which when summed provide an overall fragility score (** denote most fragile countries overall).

Country	No. lion populations	Overall lion range area (km²)	% of overall lion range in country	Mean edge to area ratio	Mean % area overlap with WDPA	Approx % of overall wild lions in country	Mean % of carrying capacity	Mean intensity of edge effect	Mean exposure to other borders	Mean population connectedness (lack of isolation)	Mean human density in lion range	Mean cattle density in lion range	Mean ecological fragility score per country	Rescaled ecological fragility score	Rescaled socio-political score	Country-wide fragility score
Angola	2	95309	7.64	0.05	57.11	0.20	1.64	4.85	0.69	13.50	1.54	0.00	0.26	0.16	0.72	0.88
Benin	1	12347	10.70	0.08	68.96	0.63	16.15	39.71	0.51	12.00	11.82	0.05	0.37	0.60	0.46	1.06
Botswana	4	240521	41.62	0.07	46.43	14.52	47.52	1.88	0.09	22.75	0.83	0.03	0.25	0.13	0.00	0.13
Burkina Faso	1	10407	3.81	0.09	84.12	0.90	19.35	27.68	0.51	12.00	11.02	0.02	0.33	0.45	0.50	0.96
Cameroon	2	19854	4.26	0.06	38.06	1.14	16.43	41.66	0.50	4.50	24.79	0.16	0.48	1.00	0.47	1.47*
Central African Republic	2	54949	8.86	0.04	65.77	0.89	12.95	1.86	0.72	4.50	0.41	0.00	0.28	0.25	0.70	0.95
Chad	2	38420	3.03	0.09	87.49	0.74	5.07	19.94	0.73	6.50	14.22	0.08	0.34	0.47	0.71	1.18
Democratic Republic of the Congo	3	61116	2.63	0.09	52.24	0.35	5.28	102.38	0.75	10.67	33.43	0.01	0.41	0.74	0.74	1.48*
Ethiopia	13	180314	15.96	0.08	36.07	5.06	17.69	69.56	0.64	14.92	40.74	0.20	0.46	0.93	0.53	1.46*
Kenya	3	116819	19.94	0.04	25.02	7.34	23.23	62.70	0.40	20.33	8.55	0.10	0.35	0.50	0.29	0.78
Malawi	3	4268	3.62	0.19	84.83	0.12	11.10	80.45	0.40	13.00	0.81	0.01	0.48	0.99	0.57	1.56**
Mozambique	5	197780	25.12	0.04	10.60	6.18	11.01	20.73	0.44	18.60	8.57	0.01	0.33	0.44	0.45	0.89
Namibia	2	170643	20.71	0.03	19.15	2.93	12.65	2.56	0.13	21.00	1.75	0.05	0.30	0.31	0.10	0.42
Niger	1	2688	0.23	0.13	98.66	0.20	28.29	29.71	0.51	12.00	5.58	0.00	0.35	0.52	0.48	1.00
Nigeria	2	6773	0.75	0.08	97.13	0.08	5.65	53.09	0.70	4.50	23.04	0.02	0.37	0.58	0.67	1.25
Rwanda	1	1001	3.96	0.20	98.70	0.15	86.57	74.02	0.31	15.00	0.00	0.00	0.41	0.72	0.56	1.28
Senegal	1	8234	4.18	0.06	100.00	0.12	2.63	20.05	0.42	0.00	5.04	0.01	0.39	0.68	0.40	1.08
Somalia	1	12346	1.95	0.05	0.00	0.62	44.84	8.92	0.96	8.00	11.08	0.34	0.41	0.72	1.00	1.72**
South Africa	4	33035	2.71	0.12	68.70	9.83	93.85	16.45	0.15	11.75	8.33	0.01	0.34	0.49	0.07	0.56
South Sudan	1	19757	3.15	0.04	100.00	0.31	1.88	9.71	0.85	19.00	9.23	0.10	0.21	0.00	0.89	0.89
Sudan	1	8428	0.45	0.06	99.70	0.65	11.35	12.83	0.64	6.00	14.31	0.05	0.31	0.38	0.63	1.01
Tanzania	13	383503	40.77	0.13	32.03	33.51	39.44	69.27	0.33	25.85	88.35	0.15	0.43	0.81	0.29	1.10
Uganda	4	7808	3.23	0.18	99.31	1.41	49.08	164.54	0.72	11.00	12.56	0.07	0.46	0.91	0.53	1.44
Zambia	5	149720	19.93	0.07	72.07	4.63	7.81	9.06	0.35	21.80	3.92	0.01	0.29	0.28	0.33	0.61
Zimbabwe	7	59438	15.21	0.10	31.29	7.47	44.35	12.39	0.32	23.57	10.49	0.05	0.37	0.57	0.38	0.95

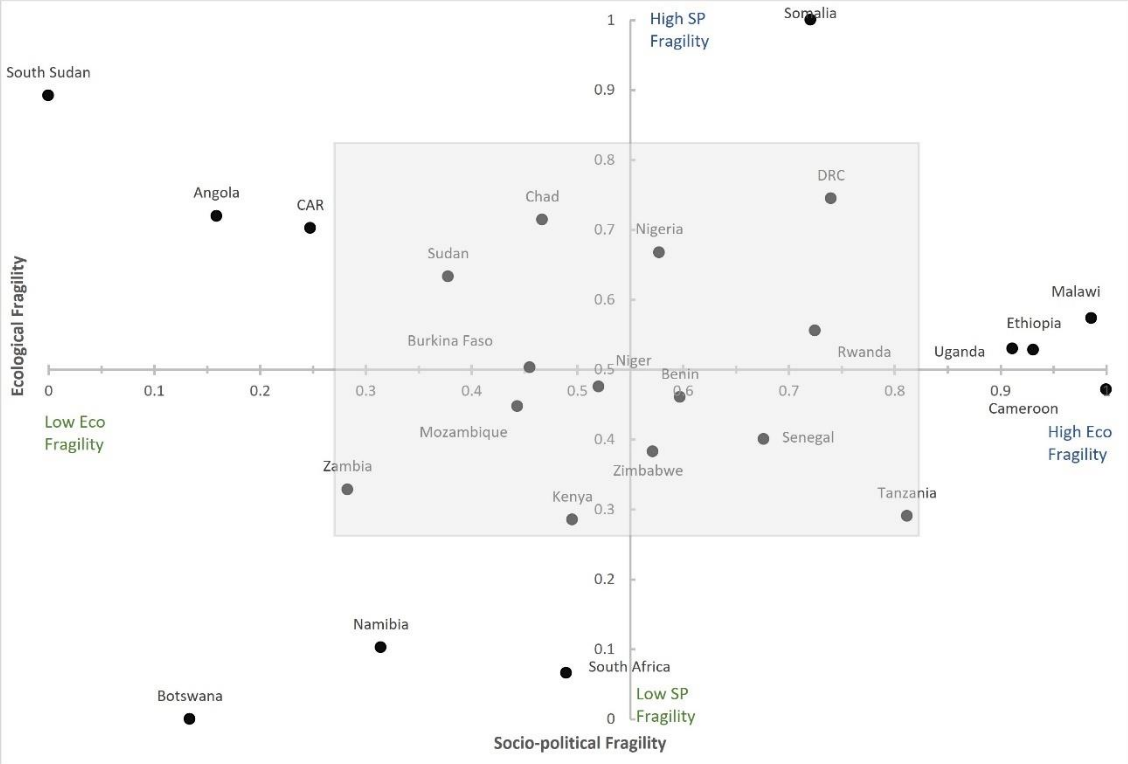

Figure 4-4. Ranking of countries in overall fragility of their lion populations, relative to other lion range countries. Countries higher on the y-axis or further to the right on the x-axis are more fragile. The axis lines are drawn at the mean value not at the mid-point of the index. The shaded grid depicts those populations which fall within one standard deviation of the mean.

4.4.4 Overall fragility of lion populations

Combining the ecological and socio-political scores of each range country provided an overall fragility score. This revealed Somalia as the most fragile lion range country overall, while Botswana was the least fragile (Figure 4-4, and Table 4.3). Almost half of range countries (n = 12; 48 %) scored as highly fragile (above mean) in both metrics: together, those countries represented 39.0 % (735,984 km^2) of lion range.

There was an evident geographic pattern in terms of the location of the most fragile national populations or subpopulations. Those populations with above-average overall fragility were mostly in the northern parts of the lion's remaining range (e.g., Bush-Bush, Afar, Awash and Waza), while the least fragile populations mostly occurred in eastern and southern Africa (e.g., Kruger and Okavango-Chobe; Figure 4-6).

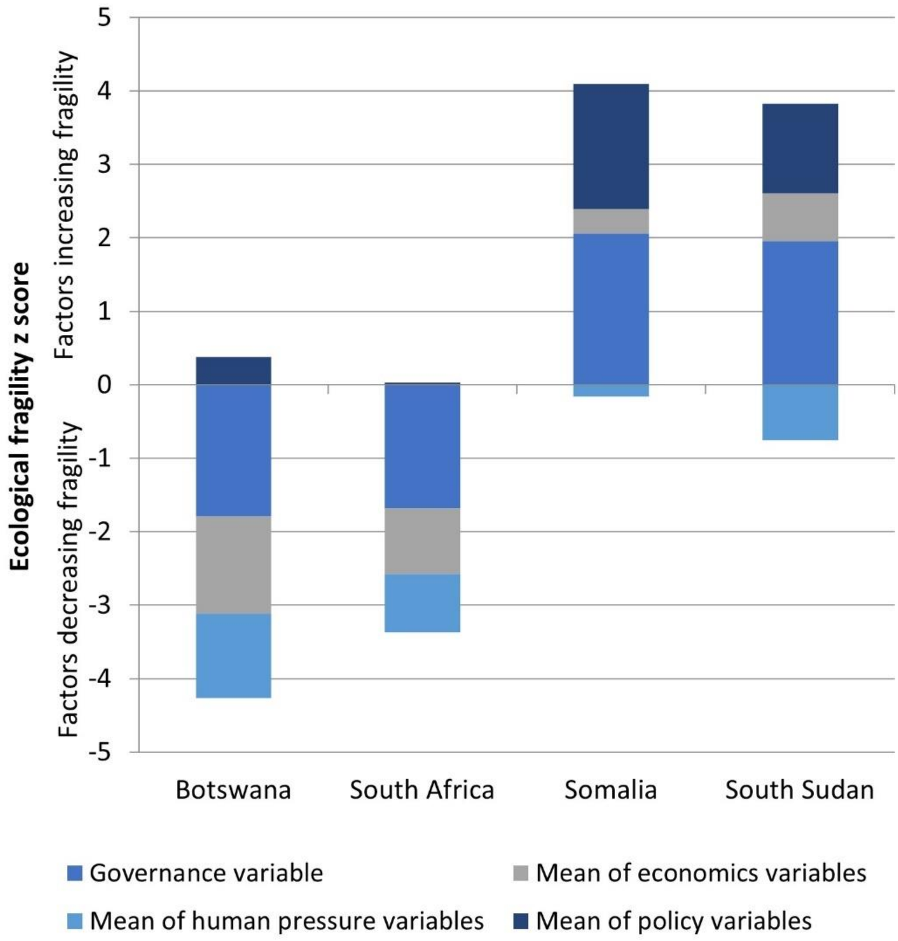

Figure 4-5. Factors contributing towards four countries socio-political fragility scores. Botswana and South Africa were the least socio-politically fragile lion range countries, and South Sudan and Somalia were the most. Factors which rank positively on the y-axis increase socio-political fragility for those countries, while those which rank negatively decrease socio-political fragility. Total z-score is the sum of both positive and negative values.

When examined at a geographic population level, Maze National Park in Ethiopia and Bush-Bush in Somalia emerged as the overall two most fragile populations (Figure 4-3 and Table 4.1). On the other hand, the large lion populations in Kavango-Zambezi and Selous-Niassa were the two least fragile overall (Figure 4-3 and Table 4.1).

Eight geographic populations (Boma National Park, Bush-Bush, Garamba Complex, Lake Manyara, Maze, Nechisar and Toro-Semiliki) had an overall fragility score more than one standard deviation above the mean (Table 4.1), and three of them were in a single country, Ethiopia. Together, these accounted for 1.3 % of Africa's wild lions and 2.4 % of their range (Table 4.1).

Ten geographic populations (Hluhluwe-Umfolozi, Katavi-Ruaha, Etosha-Kunene, Greater Mapungubwe, Luangwa-Mana-Tchuma-Tchato, Greater Limpopo, Maasai Steppe, Kgalagadi, Selous-

Niassa and Kavango-Zambezi) each had combined fragility scores at least one standard deviation below the mean (Table 4.1). Collectively, these relatively less fragile populations represented nearly three quarters (75.8 %) of remaining wild lions, and over half (63 %) of their range (Table 4.1).

There is a long history of papers estimating lion population size and range across Africa, starting in 1975 (1975) and continuing through to present day (Bauer *et al.,* 2015; Chardonnet, 2002; Riggio *et al.,* 2013; Nicholson *et al.,* 2023). This focus on numbers and range is essential, and when conducted in a robust, repeatable way, provides invaluable insights into lion trends and threats. It is relatively straightforward to collect data on ecological aspects of a population, such as its size, extent of formal protection, or the distance to the next closest population. Indeed, these are critically important elements in conservation biology and should be considered in conservation planning for lions (Bauer *et al.,* 2020, 2016; Blackburn *et al.,* 2016; Dolrenry *et al.,* 2014; Lindsey *et al.,* 2013b; Ogutu *et al.,* 2011; Trinkel *et al.,* 2011). However, despite the long focus on understanding lion population dynamics, there has been limited data on specific threats facing each population (Bauer *et al.,* 2020) (but see Everatt *et al.,* 2019). Furthermore, the explicit consideration or evaluation of socio-political factors has been almost completely neglected in wider lion range-wide analyses, despite the critical significance of such factors for conservation.

To better understand and counteract threats, and to develop lion conservation plans that have the highest likelihood of success, socio-political factors must be considered alongside ecological ones (Bauer *et al.,* 2020; Kuiper *et al.,* 2018) . For example, poor governance is often a major limiting factor to effective conservation (Smith *et al.,* 2003), and countries which face major challenges such as conflict, poverty, political instability, low human development or rapidly growing human populations are unlikely to be able to prioritise conservation or conduct it effectively (Bauer *et al.,* 2020; Bonham *et al.,* 2008; Dickman *et al.,* 2015; Irland, 2008; Wright *et al.,* 2007). Therefore, two populations with similar levels of ecological threat could face very different socio-political challenges, and therefore require quite different conservation approaches, engagement of different stakeholders and varying levels of investment. Understanding these differences is necessary to developing effective and meaningful conservation action and a central goal of this research.

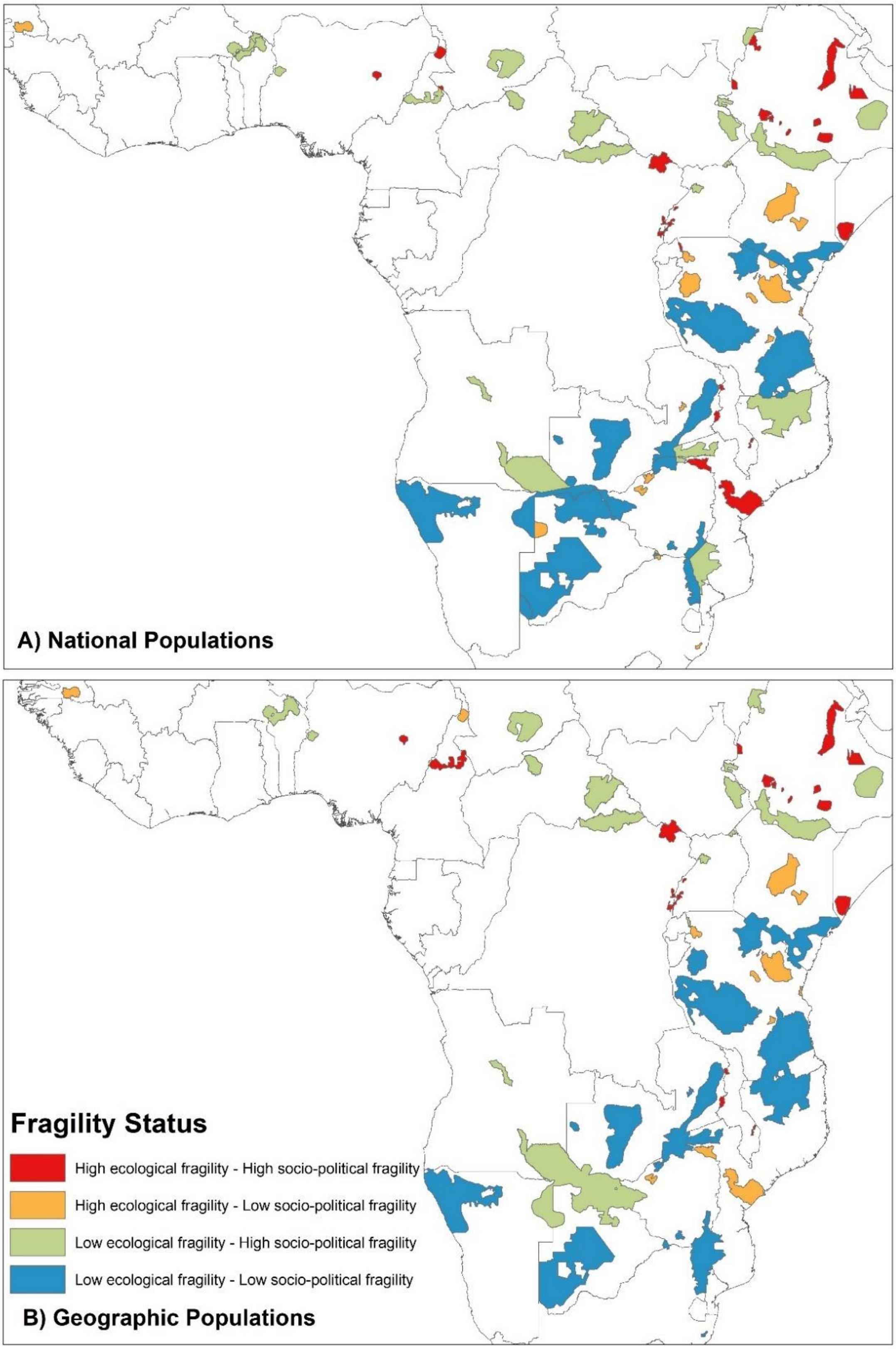

Figure 4-6. The fragility status of all 84 national and 62 geographic lion populations. Populations are colour-coded according to whether they scored high (above-mean) or low (below-mean) on both the ecological and socio-political fragility scale. A) The fragility status of 84 national lion populations. B) The fragility status of 62 geographic lion populations.

For example, populations or range countries with similar scores could have different drivers of fragility. The Etosha-Kunene and Kidepo Valley populations emerged with the same ecological fragility scores of 0.34, suggesting they are both relatively fragile on that index (Figure 4-7). However, the drivers of those scores differed between the two populations: in Kidepo Valley, ecological fragility was driven mainly by a lack of connectedness, relatively small area and high edge-to-area ratio (Figure 4-7). Meanwhile, the primary drivers of fragility for the Etosha-Kunene population were a lack of connectedness with other populations and limited protected area coverage (Figure 4-7). In another example, Cameroon and DRC had very high, and similar, overall fragility scores of 1.47 and 1.48. Yet, the driver of Cameroon's high overall fragility was very high ecological fragility, despite relatively less socio-political fragility. DRC, on the other hand, was relatively fragile ecologically but highly fragile due to socio-political factors such as poor governance and policy indicators. Thus, conservation work may be more needed, and potentially more effective, in the relatively more stable socio-political climate of Cameroon than DRC.

A few geographic populations and countries scored highly on one index of fragility but relatively low on the other. This suggests a need to carefully consider conservation action in these areas due to potentially divergent threats. For example, Lake Manyara was highly fragile ecologically (due in that case largely to its high edge-to-area ratio) but had a relatively low socio-political fragility score. This could suggest a more stable political climate to invest in where focus could be spent on improving local ecological conditions (although in this particular case, Lake Manyara is relatively close to predicted carrying capacity). Similarly, the Maze population has a close-to-average socio-political score but very high ecological fragility score, so here, ecological restoration could result in greater improvement in lion numbers. Other populations, such as Boma and Bush-Bush, score very highly on socio-political fragility but are about average for ecological fragility. This suggests that improving socio-political conditions, rather than ecological ones, should be the primary focus for stemming lion decline or restoring populations.

Making detailed data available on both the ecological and socio-political characteristics of remaining populations should help inform both the actions of conservation practitioners on the ground, and the decisions of those (often outside the field) who allocate scarce resources to conservation, as there is frequently a disconnect between those groups (Game *et al.,* 2013). This work helps inform decision making, or at least provides a framework that can be modified and specialised for future use, as decisions on prioritising where scarce conservation resources are allocated should be transparent (Gerber *et al.,* 2018). The importance of this approach is demonstrated by considering two populations which may look superficially similar in the context normally examined by conservationists. Lions in Swaga Swaga in Tanzania and Yankari in Nigeria are both small populations (<50 individuals each), each covering around 3,000 km^2, and score similarly fragile in terms of their ecological context. However, they occur in very different socio-political contexts – in Yankari, relatively poor government effectiveness, high political instability, high corruption, conflict and high human population densities make it far more socio-politically fragile than the Swaga Swaga population and a very different proposition for investors, as it is likely to need greater resource allocation to effectively manage it. This does not mean that conservation efforts in Yankari are less important (indeed they could be viewed as more ecologically important given that West African lions are Critically Endangered) but that a similar financial investment at the two populations may not result in the same outcomes, and may need to be spent differently. If investors are clear about the level of risk and investment they are happy with, these data could be useful for informing a lion equivalent to the Rhino Impact Investment Project, the first pay-for-results financial instrument for species conservation where investments are scaled to risk and likely outcomes (http://www.rhinoimpact.com/).

This initial analysis is not intended to be a priority-setting exercise, as different conservation groups and funders will have different individual aims. Some stakeholders will prioritise the most imperilled lion populations, others may prefer those with genetic distinctiveness (Bertola *et al.,* 2011) or the last lions in a country or region (Henschel *et al.,* 2014, 2010), while others, equally justifiably, will prioritise safeguarding the few remaining large lion populations (Macdonald, 2016). However, the results presented here will help inform any of those strategies, as they reveal the most notable threats to whichever target populations are chosen and potentially, how to implement effective conservation action.

The lion populations examined fell into one of four quadrants relative to one another, and the categorisation can broadly inform conservation planning. Countries and populations which are classed as above-average for both fragility indices are likely to be viewed by some as top conservation priorities, given the urgency of threats facing them (Henschel *et al.,* 2014). Others, however, may decide that resources should rather be focused on those populations which scored below-average on both fragility indices, as those populations may have the best chance of long-term persistence. Conservationists are likely to be most well-equipped to deal with the threats facing populations which have relatively high ecological fragility but relatively low socio-political fragility. For those, interventions aimed at things like reducing the intensity of edge effects or improving connectivity between populations (Cushman *et al.,* 2016) could substantially improve the overall outlook in terms of fragility. Conversely, improving the status of populations which rank relatively high on socio-political fragility will require a broad suite of involvement from other stakeholders such as policymakers, and rely less on the expertise of conservationists, particularly if they are not particularly ecologically fragile.

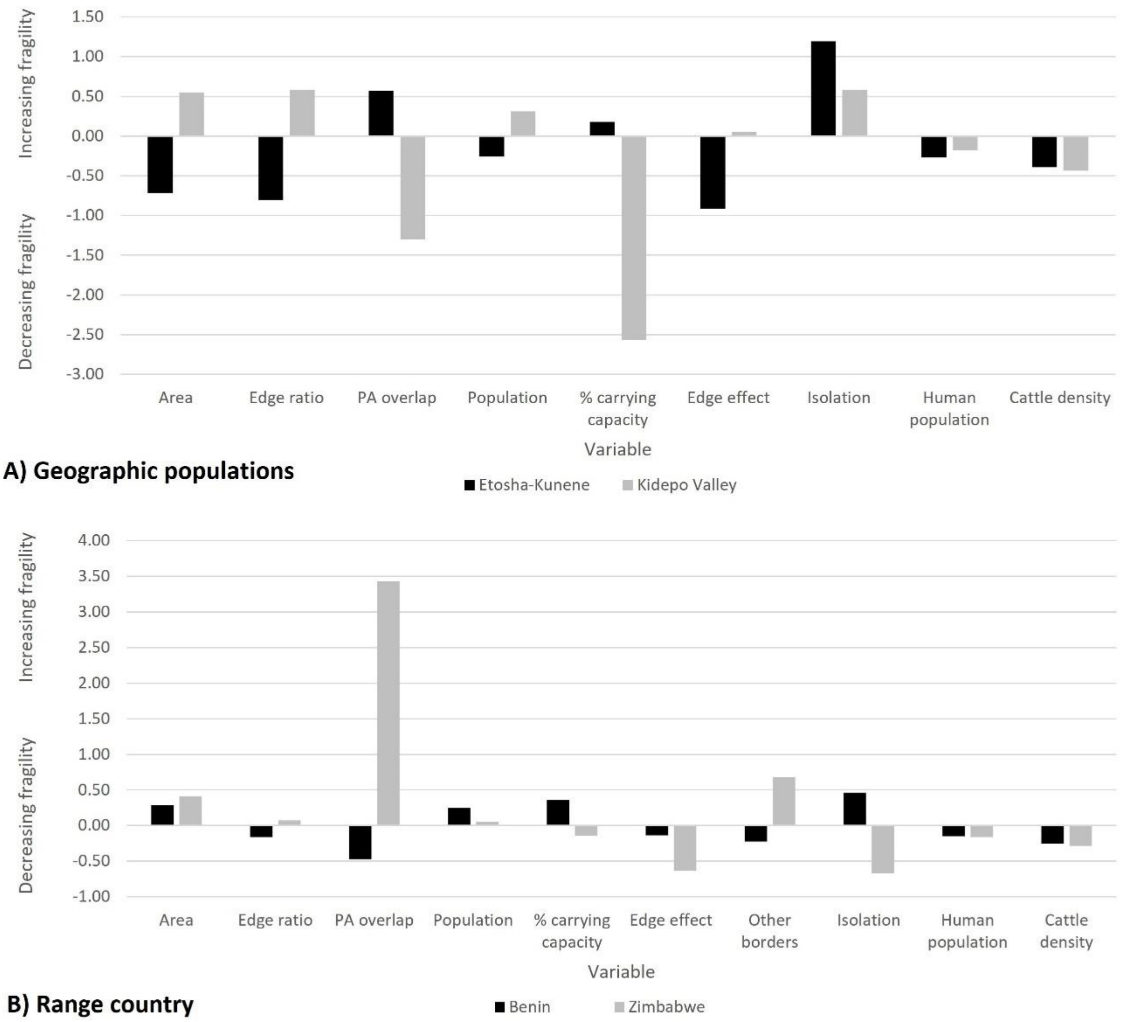

Figure 4-7. Mean z-scores of the constituent variables contributing to the ecological fragility score. Positive z-scores increase ecological fragility while negative ones decrease ecological fragility. Total z-score is the sum of both positive and negative values. A) Two geographic lion populations (Etosha-Kunene and Kidepo Valley) that both had an ecological fragility score of 0.34 but different drivers of fragility. B) Two range countries (Benin and Zimbabwe) are shown that had similar ecological scores (0.372 and 0.366 respectively).

The results of any analysis depend upon which metrics were selected for inclusion, and the methods and scoring systems used (Game *et al.,* 2013). Here, we assumed a linear relationship between our variables and lion fragility, whereas, in reality, relationships (such as between human poverty and wildlife fragility) are likely to be complex, non-linear and site-specific (Brashares *et al.,* 2011; Gray and Moseley, 2005). In addition, we were limited to national-level socio-political statistics, which are unlikely to fully reflect the specific conditions in the rural areas where lions persist. Variables needed to be available across all range countries for inclusion, which limited those which could be selected for analysis.

Furthermore, the data presented here (for all aspects) are a snapshot in time of the situation in each lion range and range country as it is best known at present (and that knowledge may have been gathered some years ago). Some of these variables, such as human-human conflict, could change suddenly and drastically with repercussions for estimates of fragility (see Masiaine *et al.,* 2021 (Masiaine *et al.,* 2021) regarding impacts from the incursion of pastoralists into Loisaba Conservancy in 2017 due to widespread, severe drought). Therefore, this study is intended as a first attempt at collating current knowledge for lion fragility and developing an analytical method, which will hopefully be refined, adjusted and enhanced by others as detailed range-wide knowledge of lion populations and their threats improves.

We are also aware that conservation is rarely aimed at one species – it is important to maintain a functioning ecosystem where species negatively affected by lions, such as smaller carnivores such as wild dogs (*Lycaon pictus*) or cheetahs (*Acinonyx jubatus*) (Swanson *et al.,* 2014), can also thrive. Although this analysis was done for a single species, it can be replicated for other taxa and guilds. A final caveat is that we restricted our analyses to what we defined as 'free-ranging' lion populations, defined as all unfenced populations and partially or fully fenced populations of at least 500 km^2 or 1,000 km^2 respectively. Therefore, this excludes lions in several places, including smaller fenced areas in South Africa (~800 lions), in Nairobi National Park and those reintroduced into fenced areas such as Liwonde National Park in Malawi, making the overall lion population figures look unexpectedly small for those countries.

The results of interdisciplinary analyses such as these can be daunting for conservationists, as many of the most pressing threats, such as poor governance, low human development, and rapidly growing anthropogenic pressures, need to be tackled by other stakeholders, often at national scale and could take a long time to change. This is far from saying that conservation in socio-politically challenging areas is not worthwhile, but rather that for realistic conservation planning, everyone should be aware of the magnitude and specific drivers of threats, so that appropriate actions, timescales and levels of funding can be put in place. Inadequate funding is one of the key constraints in conservation, and this is a particularly pressing issue given the scale of action needed for lions. More than USD 1 billion would be needed annually to maintain lions within current protected areas, with a major shortfall at present (Lindsey *et al.,* 2018). Importantly, this estimate assumes equal costs for all populations, but some of the costs are likely to be substantially higher in those countries with poor socio-political conditions such as poor governance (particularly with high levels of corruption) and intense human pressures. Conversely, conservation dollars may go further in countries with lower purchasing power parity (PPP), so it is a complex scenario and one that requires further in-depth analysis. As a rough estimate based on Packer *et al.,*'s 2013 costs for fenced and unfenced areas, we estimate that the cost of effective lion conservation would likely exceed USD 3 billion per year (Packer *et al.,* 2013). An important detail of the results presented here is that lion range countries presented as more or less fragile in a socio-political sense are done so relative to other lion range countries. These all scored poorly in the Global Multidimensional Poverty Index (Alkire *et al.,* 2019). Almost all African lion range countries are in the top 50 % (highest poverty), with nearly three quarters in the top 25 %. The 10 countries with the most ecologically fragile lion populations are all in the top 50 % of acutely poor countries (Alkire *et al.,* 2019). The global community are expecting some of the poorest countries to carry an expensive burden, which is inequitable and likely unsustainable (Lindsey *et al.,* 2017). Indeed, historically, the lion ranged over wealthier countries within northern Africa, the Middle East and Central Asia, but has been extirpated from those areas. It seems incumbent upon the richest countries to shoulder far more of the cost of future lion conservation.

4.5 Conclusions

Ultimately, these results make clear that given the importance of factors such as governance and economics on the fragility of wildlife populations, effective lion conservation cannot be achieved by conservationists alone. It requires the engagement of many diverse stakeholders, including policymakers, development experts, economists, land-use planners, local communities, local traditional leadership, and all levels of government. Maintaining wild lion populations – whichever ones may be prioritised - will require sustained effort and significant levels of international investment and sustainable funding mechanisms, particularly as many of the key challenges identified here, such as human population and livestock density, are likely to rapidly increase in key lion areas over the coming years. Without such efforts, lion populations will increase in fragility (some possibly beyond recovery), and we will come substantially closer to losing ecologically meaningful populations of this most iconic African predator.

4.5.1 Data availability

Information on the distribution and population sizes of lion are available from the IUCN SSC Cat Specialist Group's African Lion Database. Area specific population sizes are referenced accordingly in the online supplementary material. The study used openly available datasets of Gridded Population of the World Version 4, Gridded Livestock of the World database, and data on protected areas were available from the World Database on Protected Areas (http://www.protectedplanet.net). Data for the ecological and socio-political scores are openly available from sources such as FAO and links are provided in the 'Methods' section and in the online supplementary material. Our data tables with all variables, detailed results and calculations are available to download from https://doi.org/10.6084/m9.figshare.23685675.v1.

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4.7 Supplementary material

Due to the size of the tables, Supplementary Tables 1-6 are available online at https://static-content.springer.com/esm/art%3A10.1038%2Fs43247-023-00959-3/MediaObjects/43247_2023_959_MOESM1_ESM.pdf

Supplementary Table 4-1. Variables contributing to the vulnerability score of African lion populations.

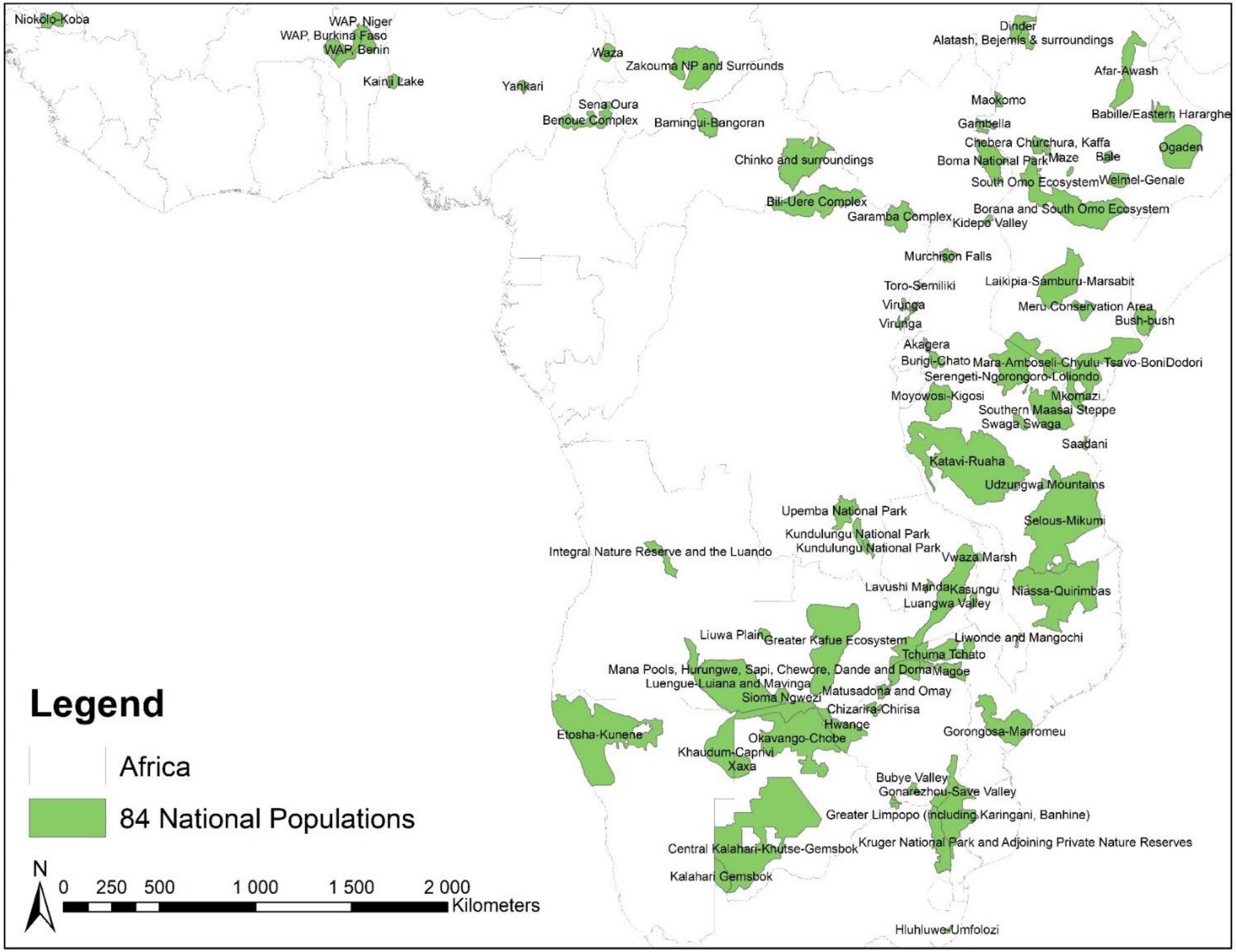
Category	Variable	Direction associated with increased fragility	Justification to include in fragility score	Source
Ecological	Geographic area	Smaller area	Smaller ranges have more area impacted by negative edge effects. Edge effects can negatively impact populations even inside protected areas (Woodroffe & Ginsberg 1998).	This MS; based on lion range
	Percentage of wild lions remaining	Smaller population	Smaller populations have fewer individuals and are at greater risk of extirpation due to stochastic and mechanistic processes (Frankham 2005).	This MS; based on lion population estimates
	Edge-to-area ratio	Higher ratio	Populations with more edge and less interior area are more impacted by negative edge effects such as poaching or encroachment (Saunders *et al.,* 1991; Lindsey *et al.,* 2017).	This Manuscript; calculated in GIS by dividing total perimeter by area
	Percentage of lion range covered by PAs	Lower percentage	Protected areas can provide protection from poaching pressures, habitat encroachment, and human or livestock incursion (Bruner *et al.,* 2001; Bauer *et al.,* 2015a; Bauer *et al.,* 2022).	World Database on Protected Areas (IUCN and UNEP-WCM 2018). Only designated, terrestrial areas with IUCN protection levels 1-4 were used. Protected areas were minimally modified following Jacobson *et al.,* (2016) due to inconsistent designation across countries (e.g., South Africa does not give IUCN protection levels to any of its protected areas, so National Parks were given a designation of 2). Lion range was intersected with protected area in GIS. Lion density was assumed equal across the entire range.
	Population size as % of predicted carrying capacity	Lower percentage	A population closer to predicted carrying capacity is likely better managed and protected now and into the future (Lindsey *et al.,* 2017). Populations persisting at a lower percentage of their carrying capacity are at greater risk of extinction (Purvis *et al.,* 2000).	Predicted carrying capacity from Loveridge and Canney (2009) based on human and ecological factors. Lion densities were summed within lion range and compared with estimated lion population size.

	Population isolation	Smaller score (Less connected/more isolated)	As metapopulation theory predicts, more connected populations are more viable and likely to persist due to migration and colonisation effects (Hanski 1999; Dolrenry *et al.,* 2020).	This MS; calculated in GIS by examining the number and distance of populations from each other. Neighbouring populations within 50km were given a weight of 5, populations between 50 and 99km away were given a weight of 4, populations 100 to 149km away were given a weight of 3, populations 150 to 249km away were weighted by 2 and populations 250 to 349km away were weighted 1. More and closer populations resulted in higher scores.
	Intensity of edge effect	Higher density	Populations with denser human communities on the edges were assumed to be more ecologically fragile, as intense edge effects can have far-reaching impacts even within protected areas (Woodroffe & Ginsberg 1998; Lindsey *et al.,* 2017; Bauer *et al.,* 2022). However, well-maintained fencing can largely eliminate the impact of edge effects on lion populations by e.g., reducing poaching and illegal grazing (Packer *et al.,* 2013).	Human population density is at the 1 km^2 resolution from WorldPop (Linard *et al.,* 2012) for the year 2020. Density was calculated within non-overlapping 30 km buffers drawn around each lion area in GIS. Density was weighted according to whether there was partial (25% reduction) or complete (50% reduction) fencing of the lion population, as fencing largely eliminates the impact of an edge effect (Packer *et al.,* 2013).
	Human population density	Higher density	Denser human populations exert stronger negative pressure on lion populations such as through human-wildlife conflict, poaching, land-use change and habitat loss (Woodroffe & Ginsberg 1998; Packer *et al.,* 2013; Lindsey *et al.,* 2017).	Human population density is at the 1 km^2 resolution from WorldPop (Linard *et al.,* 2012) for the year 2020. Density was averaged in each lion area using GIS. Due to the global extent of the data, local errors are possible. In fully fenced areas where no humans reside in the lion area, we lowered the density to 0 humans/km^2. This applied to Akagera National Park (Rwanda), Liwonde National Park (Malawi), Hluhluwe-Umfolozi (South Africa) and Bubye Valley (Zimbabwe).
	Cattle density	Higher density	More cattle lead to more conflict with lions and other predators and therefore humans are more likely to pre-emptively or in retaliation, harass or kill lions (Kissui 2008; Lindsey *et al.,* 2017, Bauer *et al.,* 2022). As cattle density represents pastoralism the best and is one of the most significant cases of human-wildlife conflict (Ikanda & Packer, 2008).	Cattle density for the year 2010 at ~10 km resolution from Gridded Livestock of the World, v3 (Gilbert *et al.,* 2018). Density was averaged in each lion area using GIS. Due to the global extent of the data, local errors are possible. In fully fenced areas where no humans reside in the lion area, we lowered the density to 0 cattle/km^2. This applied to Akagera National Park (Rwanda), Liwonde National Park (Malawi), Hluhluwe-Umfolozi (South Africa) and Bubye Valley (Zimbabwe).
	Exposure to borders	Lower percentage	A neighbouring country's human population can impact lion populations through transhumant pastoralism or poaching pressure (Everatt *et al.,* 2019).	This MS. This only applied to national populations or subpopulations that were within 30 km of the border with another country. Non-overlapping 30 km buffers were created around each country. The proportion of lion range that fell within a buffer(s) was calculated. The full score was then calculated by multiplying the proportion of the lion area in each country by the country's socio-political score. The lion area's score was then divided by the host country's socio-

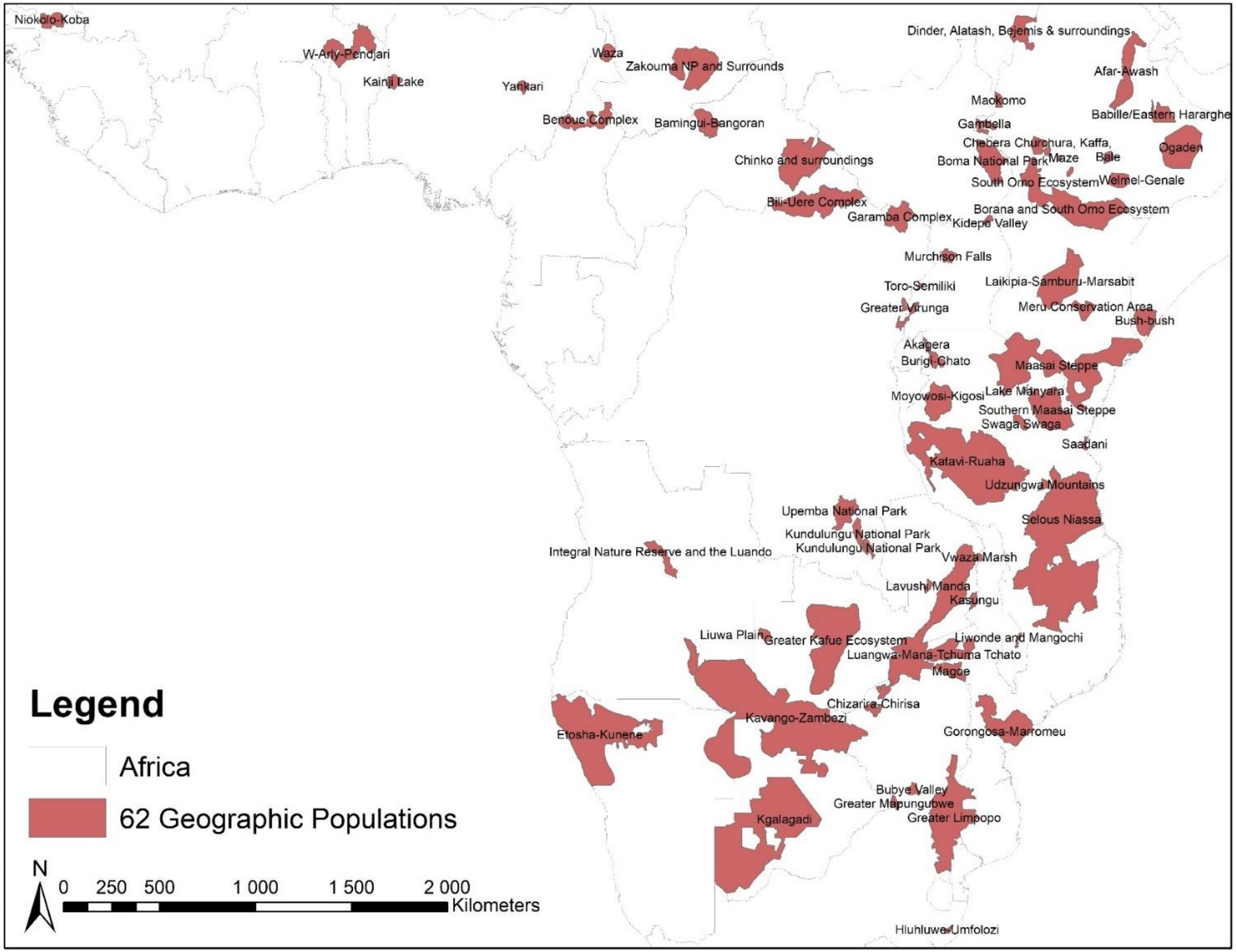
				political score, such that a lion area >30 km from any border would receive a value of 1. The difference from 1 was inverted and converted into a Z-score.
Socio-political: Governance	Political stability	Lower stability	Political instability diverts attention from conservation, limits the will of international agencies or researchers to work in that country, and inhibits long-term planning. Political instability can reduce the effectiveness of protected area management (Wright *et al.,* 2007) and is related to local lion extirpation (Bauer *et al.,* 2022). Collaborative management partnerships can be crucial to safeguarding lions within protected areas (Robson *et al.,* 2022).	World Bank Group: Governance Matters VIII database based on 10-year mean from 2007-2016 http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Government effectiveness	Lower effectiveness	The governmental effectiveness rating refers to a number of related issues as defined by the World Bank, including the quality of civil servants and their degree of independence from political pressures, policy formulation and implementation, and the credibility of governmental commitment to its policies. Increased effectiveness can in turn enhance protected area effectiveness (Wright *et al.,* 2007). Populations of a sympatric large carnivore also showed a strong relationship to strong governance (Kuiper *et al.,* 2018).	World Bank Group: Governance Matters VIII database based on 10-year mean from 2008-2017 http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Control of corruption	Lower control	Corruption can restrict foreign investment needed to sustain protected areas and biodiversity and distort political priorities. Funding that is actually awarded may also be less effective for biodiversity conservation as corrupt officials may divert funds for private use (Schudel 2008). Collaborative management partnerships can be crucial to safeguarding lions within protected areas (Robson *et al.,* 2022).	World Bank Group: Governance Matters VIII database based on 10-year mean from 2007-2016 http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
Socio-political: Economics and	GDP (Gross Domestic Product) per capita PPP (Purchasing power parity)	Lower GDP	Higher levels of gross domestic product (GDP) per capita can be related to improved environmental or biodiversity conservation outcomes within that country, as suggested by the Environmental Kuznets Curve, although the relationship does not always hold (Stern 2004; Mills & Waite 2009; Tan *et al.,* 2022). However,	Data from the World Bank from 2017 or more recent https://data.worldbank.org/indicator/NY.GDP.PCAP.PP.CD?view=chart 2017.

			lions and their prey persisted better in wealthier countries with effective protected areas (Lindsey *et al.,* 2017).	
	Gini Index	Higher GINI index	Inequality is strongly related to biodiversity loss and conservation as less equal societies exert more pressure on natural resources either by individuals or by collective action of institutions and governments (Holland *et al.,* 2009; Billé *et al.,* 2013).	Data from World Bank from 2017 or most recent https://data.worldbank.org/indicator/SI.POV.GINI?view=chart apart from Eritrea
	Human Development Index	Lower HDI	As defined by the World Bank, this Index summarises three dimensions of human development – human lifespans, access to knowledge, and standards of living. Higher levels of human development can improve conservation effectiveness and reduce biodiversity loss (Jha & Bawa 2006). Lions and their prey persisted better in wealthier countries with effective protected areas (Lindsey *et al.,* 2017).	United Nations Development Programme from 2015 or most recent http://hdr.undp.org/en/composite/IHDI
Socio-political: Habitat and human pressure	Human population growth	Higher growth	Denser human populations exert stronger negative pressure on lion populations such as through human-wildlife conflict, poaching, land-use change and habitat loss (Woodroffe & Ginsberg 1998; Packer *et al.,* 2013). Faster growing populations exert greater pressure on ecosystems and influence conservation effectiveness (Balmford *et al.,* 2001).	Countrywide data from World bank based on 10-year mean 2008-2017 https://data.worldbank.org/indicator/SP.POP.GROW?page=6
	Human population density	Higher density	Denser human populations exert stronger negative pressure on the natural environment and increase resource use and are correlated with carnivore declines and extinction (Woodroffe 2000; Packer *et al.,* 2013, Riggio *et al.,* 2013), although the relationship does not always hold (Luck 2007).	Countrywide data from World Population Review 2019, http://worldpopulationreview.com/countries/countries-by-density/
	Global human modification	Increased modification	Expanding agriculture and urbanisation negatively impact biodiversity and land use change is one of the foremost threats to biodiversity worldwide (Dirzo *et al.,* 2014). Lions do not persist in highly modified habitats (Riggio *et al.,* 2013).	Kennedy C.M. *et al.,* 2018; Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S. & Kiesecker, J., 2019, 'Managing the Middle: A Shift in Conservation Priorities based on the Global Human Modification Gradient', Global Change Biology, 25(3), 811–826.

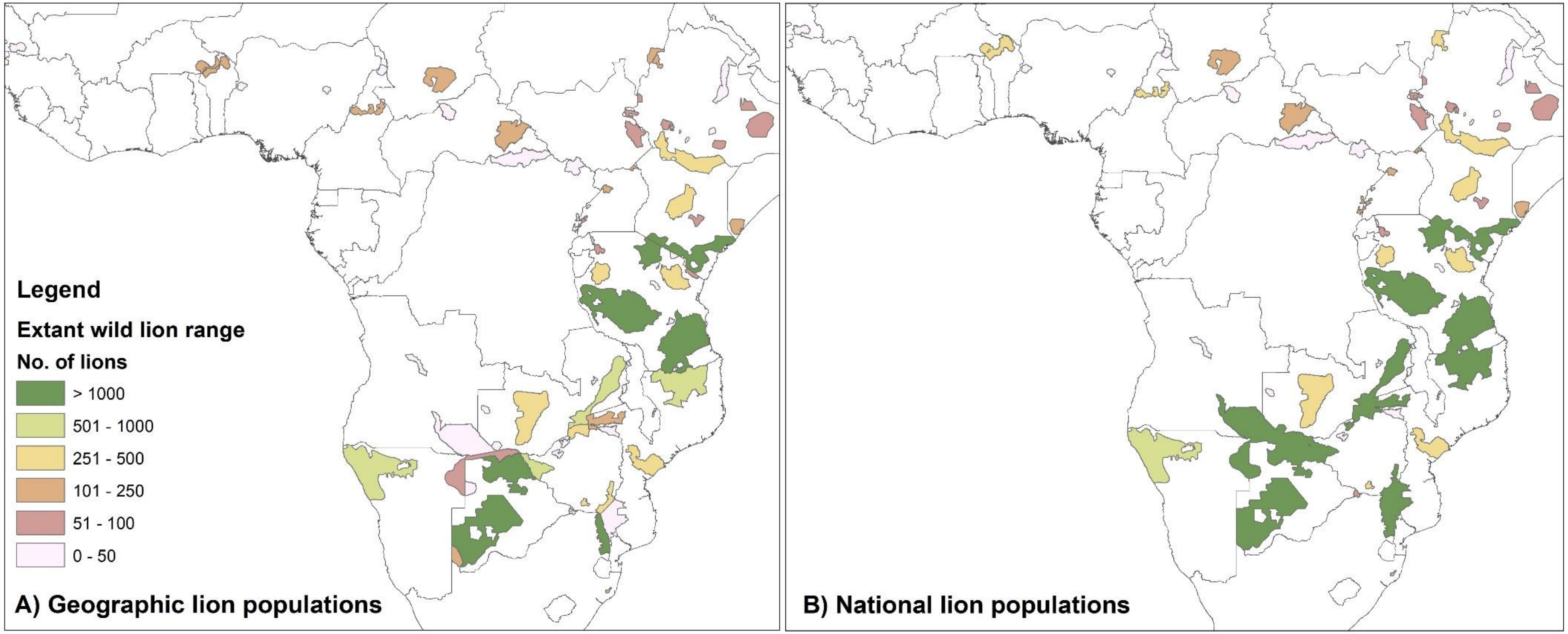
Socio-political: Conservation policy	National level Conservation Action Plan	Lack of Action Plan	Creating, adopting and implementing action plans and strategy documents demonstrate a national commitment to maintaining biological diversity such as lions (Bauer *et al.,* 2015b; Trouwborst *et al.,* 2017; Hodgetts *et al.,* 2018).	Bauer *et al.,* 2015b https://www.cms.int/sites/default/files/document/cms_cop12_inf.33_review-lion-conservation-strategies_e.pdf and CBD National Biodiversity Strategies https://www.cbd.int/nbsap/about/latest/default.shtml
	Percentage of the relevant wildlife treaties signed up to	Absence of or few treaties	Signing wildlife treaties can show government commitment to biodiversity conservation, and if implemented, help stem the decline of biodiversity loss by providing legal protection to lions and other wildlife (Trouwborst *et al.,* 2017; Hodgetts *et al.,* 2018).	Data from Trouwborst *et al.,* 2017 https://natureconservation.pensoft.net/article/13690/
	Percentage of land area designated as Protected Areas (AH)	Low percentage of PA coverage	The amount of land in protection demonstrates a country's willingness to participate in practical conservation efforts. Effective protected areas protect lions and prevent two primary threats to lion conservation: livestock depredation and retaliatory killing and bushmeat poaching (Lindsey *et al.,* 2017; Bauer *et al.,* 2022).	World Database on Protected Areas (WDPA) (2019) https://www.protectedplanet.net/



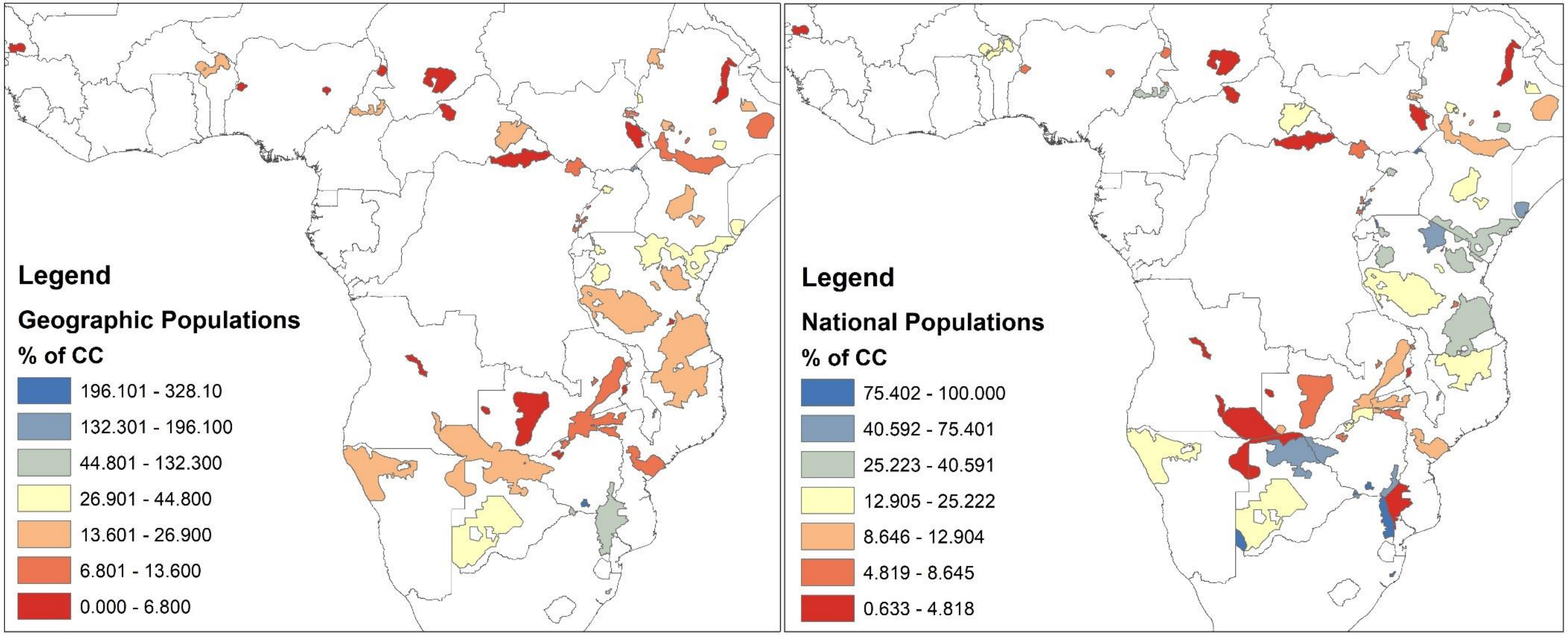
Supplementary Figure 4-1. The location of all 84 national populations with names.



Supplementary Figure 4-2. The location of all 62 national populations with names.



Supplementary Figure 4-3. The location of all 62 geographic and 84 national populations and subpopulations (geographic populations which are separated by national boundaries) of free-ranging African lions included in this study and their respective population categories.



Supplementary Figure 4-4. The percentage of carrying capacity for lions of each of the 62 geographic and 84 national populations or subpopulations (geographic populations which are separated by national boundaries).

CHAPTER 5

Perceived threats and pressures to lions across African regions, and resource availability for their mitigation

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5.1 Abstract

Lion (*Panthera leo*) populations in Africa are declining rapidly across their distribution range because of indirect threats such as habitat loss and encroachment and more direct threats such as targeted killing for parts and poaching. To determine the severity of threats to lion subpopulations across Africa and how this differed across regions, and to identify major threats among them, an online survey of 132 subpopulations was completed by park managers and researchers. Roughly 38 % of lion subpopulations were perceived to have increased over the last five years, 37 % to be stable, 17 % as decreasing, and 8 % had unknown trends. We developed a threat severity index based on the perceived severity of various threats. This index differed significantly among regions, being highest (i.e. most severe) in Central Africa and lowest (i.e. least severe) in southern Africa. Significant differences in the total threat index were related to geographic variables such as region and country and sociological variables such as communities living within the lion habitat, livestock grazing within the area, livestock competition with wildlife as well as mitigation related aspects such as the level of fencing, community engagement and sufficient park resources. Angola, the Democratic Republic of the Congo, Cameroon and Ethiopia had the highest perceived threat severity indices, while Rwanda, South Africa and Namibia had the lowest threat severity. The most severe threats varied significantly across regions and countries. Lack of funding, human encroachment, and loss of prey base emerged as severe local threats, while climate change was identified as the most severe global threat. Perceived resource availability was highest in Rwanda, Chad and Benin and lowest in six countries including Angola, Burkina Faso, Niger, South Sudan, Sudan and Uganda. This study identified the perceived

threats facing lion conservation in Africa, which vary with regional context, highlighting the need for tailored conservation strategies.

5.2 Introduction

The lion (*Panthera leo*) in Africa was once widespread across the continent but has experienced dramatic declines in both population size and range over the last several decades (Loveridge *et al.,* 2022). While most large carnivores have experienced similar declines, the decline in Africa's lion has been particularly severe (Wolf & Ripple, 2017; Loveridge *et al.,* 2022). This has led to the species being listed as Vulnerable on the IUCN Red List of Threatened Species (Nicholson *et al.,* 2023a). These declines have been precipitated by a wide range of both global and local threats and pressures that vary in severity and scale across the continent (Bauer *et al.,* 2020; Lhoest *et al.,* 2022).

A global threat is a situation or event that does not necessarily originate in a localised area and can extend beyond country or region, posing a significant and widespread threat to the entire population, or a large part of it (Hulme *et al.,* 2001). One large scale global threat that will likely affect all species is that of climate change (Hulme *et al.,* 2001; Thuiller, 2004; Araujo *et al.,* 2005; Ziervogel *et al.,* 2014; Carter *et al.,* 2018). In Africa, it is expected that climate change will result in increased temperatures and decreased rainfall (Peterson *et al.,* 2014). Based on climate change models, few new areas would become suitable for lions and much of its range in southern and West Africa will become less suitable, resulting in further unnatural range reduction (Peterson *et al.,* 2014). Another global threat, more applicable at a regional level, is that of civil unrest, local war or violent extremism that can have both direct and indirect impacts on a species and their conservation (Salafsky *et al.,* 2008; Bouley *et al.,* 2018; Bauer *et al.,* 2020; Lhoest *et al.,* 2022; Aglissi *et al.,* 2023). Such forms of conflict can directly impact a species and their conservation through habitat destruction, disruption of conservation efforts, and targeted killing of individuals, while indirectly affecting them through displacement of local communities, illegal wildlife trade, and loss of law enforcement capacity to combat poaching and habitat degradation (Lhoest *et al.,* 2022; Aglissi *et al.,* 2023). Another, albeit much debated, examples of a global threat to lions would be the international ban on lion trophy hunting or the banning of imports of trophy hunted (Lindsey *et al.,* 2013; Makuyana, 2018; Dickman *et al.,* 2019; but see Loveridge *et al.,* 2007; Mweetwa *et al.,* 2018).

Local threats or pressures refer to those that affect a specific area or population and are within the control, to a certain extent, of the area managers to mitigate. These threats can either be through illegal killings (Ikanda & Packer, 2008; Everatt *et al.,* 2019; Loveridge *et al.,* 2020) or related to inadequate local level management (Lindsey *et al.,* 2017, 2018; Loveridge *et al.,* 2023). A well-studied and prevalent local threat would be that of retaliatory killings, which refers to the intentional killing of lions (and other carnivores) in response to perceived or actual loss of livestock or human life (Hazzah, Borgerhoff Mulder & Frank, 2009; Hazzah *et al.,* 2014; Leflore *et al.,* 2020; Felix *et al.,* 2022). The "bushmeat poaching crisis" is a significant and increasing local threat to animal populations in Africa (Luiselli *et al.,* 2019; Loveridge *et al.,* 2020; Mudumba *et al.,* 2021). Lions are frequently caught as by-catch in snares and this has been recognised to negatively impact populations either by limiting population growth or causing local population declines (Loveridge *et al.,* 2020; Mudumba *et al.,* 2021; Montgomery *et al.,* 2023). An emerging threat to lion populations is the targeted poaching of lions for parts and derivatives (Everatt *et al.,* 2019), which are either used in local traditional medicinal practices (Coals *et al.,* 2022) or for the international illegal wildlife trade (Williams *et al.,* 2017a; Everatt *et al.,* 2019). In South Africa, for example, lion parts are used in muthi practices where reported uses of parts included "protection from evil spirits", "power", "healing", "protection" and "sexual health and wellbeing" (Green *et al.,* 2022). As Tiger (*Panthera tigris*) populations began declining, the availability of bones for traditional medicine decreased (Williams *et al.,* 2017a). This resulted in lion being poached in India's Gir National Park and in Africa specifically for parts, which are smuggled into the international wildlife trade in the East to be used as a substitute for dwindling availability of tiger parts (Williams *et al.,* 2017a). Local level threats and pressures that do not involve direct mortalities, but do contribute to a decline in lion populations, include a lack of funding or appropriate management, as well as poorly managed and unregulated trophy hunting (Loveridge *et al.,* 2007; Lindsey *et al.,* 2017, 2018). Wildlife areas require significant financial support and without it, fundamental operations and management implementation is limited (Lindsey *et al.,* 2018, 2021; Bauer *et al.,* 2020; Robson *et al.,* 2022). Limited funds increase an area's risk or likelihood of being overcome by anthropogenic threats that could potentially have been mitigated with the proper resources (Lindsey *et al.,* 2021). Unsustainable trophy hunting levels, through poorly regulated management and high hunting quotas, have been found to cause population declines of lions (Croes *et al.,* 2011; Packer *et al.,* 2011; Groom *et al.,* 2014; Rosenblatt *et al.,* 2014; Creel *et al.,* 2016; Mweetwa *et al.,* 2018).

Individual anthropogenic pressures and threats can negatively impact lion populations but, when combined, can be devastating (Creel *et al.,* 2016; Loveridge *et al.,* 2023). Such an example is Limpopo National Park in Mozambique where high levels of retaliatory killings through human-lion conflict and targeted poaching of lions for parts has resulted in significant population declines in recent years (Everatt *et al.,* 2019). To effectively conserve lions and other carnivores, these threats and pressures and their severity need to be understood (Bauer *et al.,* 2020; Nicholson *et al.,* 2023b). At a site level, this understanding allows effective mitigation measures to be implemented and enforced. At a global level, this understanding plays a critical role in providing high level institutions, policy makers and conventions (such as the IUCN, CITES and CMS) with the information and knowledge required to guide decisions and policies. Conventions rely on scientific research to establish international regulations and guidelines for the conservation and management of wildlife species. Understanding where threats are more severe or where populations are more threatened can guide prioritisation of areas that require more immediate conservation action. To better mitigate threats effectively, as well as developing lion conservation plans that have the highest likelihood of success, it is essential to understand the threat a species faces at both a site/local level or those that may be more of a global nature (and therefore potentially harder to mitigate). In addition, being aware of the severity of those threats and the population level impacts is vital to developing strategies that prioritise more severe threats to prevent further population declines.

Various factors influence the severity of threats and pressures experienced by local wildlife. For instance, areas where livestock can be predated upon are likely to experience increased human-wildlife conflict and increased carnivore killings (Beck *et al.,* 2019; Leflore *et al.,* 2020; Sibanda *et al.,* 2021). The ability to decrease the severity of such a threat can be done, broadly, by implementing effective livestock barriers (e.g., kraaling, exclusion fencing) and community engagement programmes (Sibanda *et al.,* 2021). The level of protection offered to an area through increased resources, anti-poaching patrols and adequate fencing also decreases the severity of potential threats by mitigating them (Packer *et al.,* 2013; Bauer *et al.,* 2015; Lindsey *et al.,* 2018). The level of protection offered by the formal protection status of the park/concession or the authority that is mandated to conserve and protect it could potentially have impacts on the severity of threats to wildlife.

In this study we aimed to determine which threats are perceived to be important for lions across their range, and to assess how these differ at a continental, regional, national and subpopulation level. Data were gathered through a structured questionnaire survey. Threats included direct threats derived from the World Conservation Union–Conservation Measures Partnership (IUCN-CMP) classification of direct threats to biodiversity (Salafsky *et al.,* 2008). Direct threats, enabling stressors (defined as "attributes of a conservation target's ecology that are impaired directly or indirectly by human activities" (Salafsky *et al.,* 2008), and global conditions that directly hinder the effective conservation of lions, were combined in our threat index (see Methods). We also included contributing factors (defined as "ultimate factors, usually social, economic, political, institutional, or cultural, that enable or otherwise add to the occurrence or persistence of proximate direct threats" (Salafsky *et al.,* 2008)) into the threat index (Table 5.1). To broadly measure the severity of threats and pressures, we developed a "threat severity index" using the perceived severity rating of these threats by survey participants. In addition, we aimed to:

- Understand the scale at which specific threats occurred.
- Determine how prevalent targeted poaching for parts was, and what is known about the target markets and target body parts.
- Gather perceptions on past, present and future lion population trends.
- Determine the perceived level of resources available to prevent the illegal killing of lions.
- Identify the key knowledge gaps that exist that would allow the increased understanding of these threats and, therefore, interventions likely to effectively improve the conservation status of lions.

5.3 Methods

5.3.1 Survey Design

To obtain information on the perceived anthropogenic threats and pressures on lions across their African range and on the resources available to reduce anthropogenic mortalities, we conducted a structured questionnaire survey. This was done through online surveys as it allowed a large-scale investigation to be conducted fairly rapidly. It also potentially reduced some of the bias that is often present when questions are asked by an interviewer (Bergen & Labonté, 2020; Stantcheva, 2023). The survey was conducted between August 2021 and July 2022, and responses were solicited from park managers and researchers of as many lion subpopulations in Africa as possible. As this study focused on African lions, the lion population is India was not included.

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 (Nicholson *et al.,* 2023b). 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. In total, 187 experts were invited to complete the survey and responses were received from 145, giving a response rate of 78 %. Ten responses (6.9 %) were removed as the surveys were incomplete. An additional five responses (3.4 %) were removed as the areas they were completed for were confirmed not to have lions. Two surveys (1.4 %) were removed as they were duplications of the same survey. Therefore, completed responses for 132 lion subpopulations were included in this study.

The survey was divided into three parts. Part one gathered information on the area, part two focused on the status of lions and perceived threats to them, and the final section focused on mitigation strategies implemented in the area. A pilot study was not conducted, as our methods were informed by other published studies that conducted similar surveys to obtain information relating to lion conservation and management or threats (e.g., Page *et al.,* 2015; Williams *et al.,* 2017a; Lindsey *et al.,* 2018; Robson *et al.,* 2022). Thus, we built upon previous work by concentrating focus on conducting a more in-depth assessment of the severity of threats to lions and how these differ spatially.

5.3.2 Ethics Clearance

This survey received ethics clearance from the University of KwaZulu-Natal Human and Social Sciences Research Ethics Committee (approval number: HSSREC/00003076/2021).

5.3.3 Threat indices

From a list of threats, respondents were required to indicate whether a particular threat occurred in the area for the past five years and provide a score on its severity (ranging from 0, where the threat to lions does not occur in the area, to 4 where the threat is so severe that it could potentially result in local population extinction). Three indices were created based on the responses to part two of the questionnaire (Table 5.1): (1) a global threat index (GTI), which was made up of four threats; (2) a local threat index (LTI), which was made up of 16 threats; and (3) a total threat index (TTI) that combined all 20 threats. The severity of the global and local threat indices was calculated by summing all severity scores, and the total threat index was determined by summing the local and global threat indices (similar to Page *et al.,* 2015; Lindsey *et al.,* 2017; Robson *et al.,* 2022). The maximum total threat score that could be achieved was 80 (Table 5.1). Higher values, for all indices, indicated more severe threat intensity while lower scores (i.e., closer to 0) indicated less severity, or a more secure lion population. Severity was defined as low (indices below one standard deviation below the mean), medium (between low and high), and high (indices above one standard deviation above the mean).

5.3.4 Resource Availability Index

An index was developed based on the responses to section three of the questionnaire, to determine the resources available to park/area management to reduce the illegal killing of lions. This index was made up of a series of four trichotomous questions where respondents could answer either yes (scoring +1), unsure (scoring 0), or no (scoring -1), based on whether the area management had sufficient funding; staff; correct anti-poaching gear; or enough vehicles. The value for the index, for each of the respondents, was calculated as the sum of the scores of the resource-based questions (Page *et al.,* 2015).

Table 5.1. The threats used to generate the Global Threat Index, Local Threat Index and Total Threat Index for each lion subpopulation surveyed in this study and the corresponding IUCN-CMP (Conservation Measures Partnership) unified threats.

GLOBAL THREAT INDEX (GTI) ***Maximum score = 16***	**IUCN-CMP UNIFIED THREAT**	**LOCAL THREAT INDEX (LTI)** **Maximum score = 64**	**IUCN-CMP UNIFIED THREAT**	**TOTAL THREAT INDEX (TTI)** **Maximum score = 80**
1. Civil unrest/local war that poses direct threats to lions	6 Human intrusions & disturbance 6.2 War, civil unrest & military exercises	***Direct Threats***		
2. Civil unrest/local war and insecurity that reduces the effective management of the area	6 Human intrusions & disturbance 6.2 War, civil unrest & military exercises	1. Lion mortality resulting from motor-vehicle and train collisions	4 Transportation & service corridors 4.1 Roads & railroads	Global Index + Local Index Score
3. Complete ban on lion trophy hunting (local and international), including restrictions on imports of trophy's		2. Bycatch in snares where lions are caught but are not the intended target	5 Biological resource use 5.1 Hunting & collecting terrestrial animals 5.1.2 Unintentional effects (species being assessed is not the target)	
4. Climate change	11 Climate change & severe weather	3. Intended poisoning of scavengers and carnivores (including lions)	5 Biological resource use 5.1 Hunting & collecting terrestrial animals 5.1.3 Persecution/control	
		4. Targeted poaching of lions for their parts	5.1 Hunting & collecting terrestrial animals 5.1.1 Intentional use (species being assessed is the target)	
		5. Cultural killings of lions	5.1 Hunting & collecting terrestrial animals 5.1.1 Intentional use (species being assessed is the target)	
		6. Retaliatory or pre-emptive killing of lions	5.1 Hunting & collecting terrestrial animals 5.1.3 Persecution/control	

		7. Unmanaged trophy hunting (including illegal/unpermitted trophy hunts)	5.1 Hunting & collecting terrestrial animals 5.1.1 Intentional use (species being assessed is the target)	
		8. Disease	8 Invasive & other problematic species, genes & diseases 8.2 Problematic native species/diseases	
		Indirect threats		
		9. Human encroachment for agriculture or settlement	1 Residential & commercial development 1.1 Housing & urban areas 2 Agriculture & aquaculture 2.1 Annual & perennial non-timber crops 2.3 Livestock farming & ranching	
		10. Loss of suitable habitat	1 Residential & commercial development 7 Natural system modifications	
		11. Development of infrastructure adjacent or in the lion range area	1 Residential & commercial development 1.1 Housing & urban areas 1.2 Commercial & industrial areas 1.3 Tourism & recreation areas	
		Contributing factors		
		12. Ineffective population management resulting in issues such as over-population, inbreeding		
		13. Small, isolated lion population that is vulnerable to local extinction		
		14. Loss of natural prey base specifically due to poaching		
		15. Loss of natural prey base due to other factors such as habitat degradation		
		16. Lack of/inconsistent funding for area operations		

5.3.5 Data analyses

As our data for the three indices were not normally distributed (Shapiro-Wilk normality tests: Global W = 0.85, p-value < 0.0001; Local W = 0.977, p-value < 0.05 and total threat index W = 0.968, p-value < 0.05), Kruskal-Wallis H tests were used to determine differences in the index values within each variable, and statistical significance was set at 0.05. To identify significant differences among groups while minimising the risk of making incorrect conclusions because of multiple testing, we used the Dunn's test with the Holm correction (Vickerstaff *et al.,* 2019). Data analyses and statistical computations were performed using RStudio (Kronthaler & Zöllner, 2021). R (version 4.2.1) was used for programming and data manipulation.

We assessed whether geographical variables (country and region), protection and governance variables (authority, formal protection), sociological variables (communities living within the area, livestock competition with wildlife, and people's attitudes towards wildlife) and mitigation variables (fencing, area resources, livestock barriers, routine patrols conducted, and community engagement) had any effect on the threat indices. In this study, we aimed to identify which factors had significant effects on the threat indices, and thus pose threats and pressures to lion subpopulations (Table 5.2). By assessing the influence of these variables, we sought to gain a deeper understanding of the complex factors contributing to anthropogenic threats and pressures on lion subpopulations across Africa.

5.4 Results

5.4.1 Summary

More than half of surveyed subpopulations were from southern Africa (56 %; n = 74). Within the region, South Africa and Mozambique had the most responses (18 % and 9.9 % respectively). West Africa had the fewest responses (5.3 %; n = 7), but this was to be expected as there are few remaining subpopulations (Henschel *et al.,* 2014). Eighteen responses were from Central Africa (13.64 %), mostly from the Central African Republic (4.6 %; n = 6) and Cameroon (3.8 %; n = 5). Twenty-five percent of survey responses were from East Africa (n = 33). In total, we surveyed managers and researchers associated with 132 lion subpopulations totalling 1,183,435.26 km^2, or 75 % of remaining lion range.

Table 5.2. The variables tested to determine whether there was a significant relationship with the local, global and total threat indices. Each threat index was made up of the severity score perceived by respondents for each threat, these severity scores were summed to calculate an overall threat index value to measure severity for each index. The response options are provided, as well as the motivation for use of the variable, the predicted impact on the indices, and references associated with it.

VARIABLE	POSSIBLE RESPONSES	VARIABLE MOTIVATION	PREDICTION	REFERENCES
Authority	Private, government, public-private partnership, community, community-government partnership	Resource availability varies across authority, which influences the level of management and its effectiveness.	Lower severity scores in subpopulations where there is management from private or government.	Page, 2014; Lindsey *et al.,* 2017; Bauer *et al.,* 2020
Formal protection	Yes, no	Formally protected areas can provide better protection from anthropogenic pressures	Lower severity scores in subpopulations in formally protected areas	Bruner *et al.,* 2001
Communities presently living within the area	No, yes, unsure	Denser human populations exert negative pressure on lion populations through conflict, poaching, and land use change and are correlated with declines and extinction.	Higher severity in subpopulations with people living in the area	Woodroffe, 2000; Packer *et al.,* 2013; Riggio *et al.,* 2013; Lindsey *et al.,* 2017
Livestock grazing in the area	No but it is allowed, no and it is not allowed, unsure, yes and it is allowed, yes but it is not allowed	More livestock leads to increased conflict, potentially resulting in lion mortalities. Where grazing occurs illegally could indicate less management and higher opportunities for illegal activities (potentially poaching).	Higher severity where illegal grazing occurs.	Ikanda & Packer, 2008; Kissui, 2008; Lindsey *et al.,* 2017; Bauer *et al.,* 2020
Livestock competition with wildlife	Yes, no, unsure, other	Resource competition from livestock threatens wild herbivores because of decreased food availability, which would ultimately negatively impact lion populations due to a declining natural prey base.	Higher threat severity in subpopulations where there is resource competition between livestock and wildlife.	Fynn *et al.,* 2016; Bauer *et al.,* 2020
Peoples attitude towards wildlife	Very positive, somewhat positive, neutral, somewhat negative, very negative, unsure	Negative attitudes result in decreased tolerance, which can increase hostility and lead to increased anthropogenic killings.	Higher severity scores in subpopulations where people's attitudes are more negative.	Bruskotter & Wilson, 2014; Page-Nicholson *et al.,* 2017

Fencing	Fully fenced, partially fenced, not fenced at all	Fencing can reduce negative interactions between wildlife and people	Lower severity scores in subpopulations enclosed with fencing.	Packer *et al.,* 2013; Bauer *et al.,* 2015
Sufficient park resources	Strongly agree, agree, somewhat agree, neither agree nor disagree, somewhat disagree, disagree, strongly disagree, unsure	More park resources (e.g., equipment, funding, staff) contribute to better protection of wildlife and management of threats.	Lower severity where resource availability is higher. Where resource availability is lower, threat scores will be higher.	(Lindsey *et al.,* 2017, 2018; Bauer *et al.,* 2020)
Livestock barriers	Yes, no, don't know	Mitigation activities such as livestock barriers reduce human-lion conflict and therefore retaliatory killings.	Lower severity scores in subpopulations where livestock barriers are implemented.	Sibanda *et al.,* 2021
Routine patrols conducted	Yes, no, don't know	Reductions in poaching instances where patrols are done.	Lower severity scores where patrols are conducted	Xu *et al.,* 2020; Dancer *et al.,* 2022
Community engagement	Yes, no, don't know	Human-lion conflict is lower and lion killings fewer when there is effective community-based interventions and engagement.	Lower severity scores where community engagement is implemented.	Sibanda *et al.,* 2021

5.4.2 Perceived lion subpopulation trends

Most lion subpopulations in the last five years were perceived have increased (37.9 %; n = 50) or to have remained stable (37.1 %; n = 49; Supplementary Figure 5-2). However, 17 % of surveyed subpopulations were perceived to be decreasing (n = 22), while trends were unknown for 8.3 % of subpopulations (n = 11). Generally, most surveyed lion subpopulations were expected to increase (39.4 %; n = 52) or remain stable (37.12 %, n = 49) over the next five years. Decreasing subpopulation trends were anticipated for 12.88 % (n = 17) of Africa's surveyed subpopulations.

Central African subpopulations were mostly considered to have decreased in the last five years (38.9 %; n = 7), but future trends appeared more optimistic as 61 % (n = 11) of surveyed subpopulations were expected to increase in numbers. East African subpopulations were largely considered to have remained stable for the last five years (42.2 %; n = 14) and the same trend was expected over the next five years (36.7 %; n = 12). Most surveyed subpopulations in southern Africa have had an increasing trend (47.3 %; n = 35) but were anticipated to become more stable (43.2 %; n = 32). Over the past five years, West African lion numbers have exhibited diverse trends, with two subpopulations perceived to have experienced declines, two increased in numbers, two remained stable, and one subpopulation where trends were unknown.

Of concern is that nine (6.8 %) subpopulations were expected to become extinct in the next decade, including five transient populations: Sibiloi (Kenya), Kasanka (Zambia), Coutada 13 (Mozambique), Vwaza (Malawi) and Kasungu (Malawi) National Parks, and four resident populations: Bale Mountains (Ethiopia), Waza (Cameroon), Benoué (Cameroon) and W (Burkina Faso) National Parks.

5.4.3 Local Threat Index (LTI)

Table 5.3. Kruskal-Wallis Test results assessing the differences between responses for variables and the Local Threat Index. For the country variable, only the two lowest and two highest countries are shown. Significant differences calculated by the Kruskal-Wallis test are shown in bold.

	VARIABLE	CATEGORIES (IN ORDER FROM LOWEST TO HIGHEST THREAT INDEX)	KRUSKAL-WALLIS TEST
Local Threat Index	Region	Southern Africa (x̄ 16.73 ± 9.07, n = 74)	**$\chi^2_{(3)} = 17.95$, P < 0.0001**
		West Africa (x̄ 17.86 ± 5.43, n = 7)	
		East Africa (x̄ 21.03 ± 10.15, n = 33)	
		Central Africa (x̄ 28 ± 9.47, n = 18)	
	Country	Benin (x̄ 11.5, ± 3.5, n =2)	**$\chi^2_{(25)} = 55.58$, P < 0.0001**
		South Africa (x̄ 11.79 ± 5.9, n = 24)	
		Cameroon (x̄ 36.2 ± 2.28, n = 5)	
		Angola (x̄ 42 ± 0, n = 1)	
	Authority	Private (x̄ 13.56 ± 10.17, n = 18)	$\chi^2_{(4)} = 8.69$, P > 0.05
		Government (x̄ 19.98 ± 10.29, n = 86)	
		Public-Private Partnership (x̄ 20.8 ± 7.94, n = 20)	
		Community-Government Partnership (x̄ 22.2 ± 3.311, n = 5)	
		Community (x̄ 24 ± 9.54, n = 3)	
	Formal protection	No (x̄ 17.81 ± 9.40, n = 16)	$\chi^2_{(1)} = 0.12$, P > 0.05
		Yes (x̄ 19.62 ± 10.04, n = 116)	
	Communities presently living within the area	No (x̄ 15.94 ± 8.32, n = 71)	**$\chi^2_{(2)} = 17.51$, P < 0.0001**
		Unsure (x̄ 21 ± 0, n = 1)	
		Yes (x̄ 24.47 ± 10.31, n = 60)	
	Livestock grazing within the area	No but it is allowed (x̄ 4 ± 1.414, n =2)	**$\chi^2_{(4)} = 29.09$, P < 0.0001**
		No and it is not allowed (x̄ 14.25 ± 7.44, n =48)	
		Unsure (x̄ 15 ± 0, n =1)	
		Yes, and it is allowed (x̄ 21.25, ± 9.61, n = 32)	
		Yes, but it is not allowed (x̄ 23.96 ± 9.79, n =49)	
		No (x̄ 16.19 ± 9.61, n =58)	**$\chi^2_{(3)} = 11.83$, P < 0.01**
		Unsure (x̄ 18 ± 7.21, n = 5)	

	Livestock competition with wildlife	Other (x̄ 21.62 ± 10.67, n = 13)	
		Yes (x̄ 22.35 ± 9.59, n = 55)	
	People's attitude towards wildlife	Very positive (x̄ 14.9 ± 9.68, n = 10)	$\chi^2_{(5)}$ = 5.88, P > 0.05
		Somewhat positive (x̄ 18.65 ± 8.71, n = 44)	
		Neutral (x̄ 18.81, ± 9.84, n = 26)	
		Somewhat negative (x̄ 19.97 ± 9.82, n = 38)	
		Very negative (x̄ 24 ± 5.1, n = 6)	
		Unknown (x̄ 24.88 ± 17.41, n = 8)	
	Sufficient area resources	Unsure (x̄ 9.33 ± 7.02, n = 3)	**$\chi^2_{(7)}$ = 33.859, P < 0.0001**
		Strongly agree (x̄ 11.56 ± 6.92, n = 16)	
		Neither agree nor disagree (x̄ 15.38 ± 5.78, n = 8)	
		Somewhat agree (x̄ 16.56 ± 8.22, n = 16)	
		Agree (x̄ 18.15 ± 9.98, n = 20)	
		Somewhat disagree (x̄ 19.29 ± 8.30, n =17)	
		Disagree (x̄ 21.45 ± 8.15, n = 29)	
		Strongly disagree (x̄ 28.13 ± 10.86, n = 23)	
	Fencing	Fully fenced (x̄ 13.24 ± 7.68, n = 29)	**$\chi^2_{(2)}$= 18.09, P < 0.0001**
		Partially fenced (x̄ 17.74 ± 8.28, n = 23)	
		No fenced at all (x̄ 22.11 ± 10.96, n = 80)	
	Livestock barriers	No (x̄ 19.14 ± 8.87, n = 102)	$\chi^2_{(1)}$ = 0.54, P < 0.05
		Yes (x̄ 20.3 ± 10.27, n = 30)	
	Routine patrols conducted	Yes (x̄ 18.92 ± 9.81, n = 118)	$\chi^2_{(2)}$ = 1.769, P > 0.05
		No (x̄ 23.17 ± 10.41, n = 12)	
		Don't know (x̄ 25 ± 15.56, n = 2)	
	Community engagement	No (x̄ 15.79 ± 9.68, n = 43)	**$\chi^2_{(1)}$ = 8.102, P < 0.005**
		Yes (x̄ 21.15 ± 9.65, n = 89)	

The average LTI for all surveyed subpopulations (Table 5.1 and Figure 5-2) was 19.40 (1 SD ± 9.95, range 1 – 46). There were significant regional differences in LTI (Table 5.3: $\chi^2_{(3)}$ = 17.95, P < 0.001), with Central African LTI significantly higher than other regions (P < 0.05), and East Africa LTI significantly higher than southern Africa (P < 0.05). There were significant differences among countries ($\chi^2_{(25)}$ = 55.56, P < 0.001), but not among subpopulations ($\chi^2_{(129)}$ = 130.379, p > 0.05). At a country level, Angola had the highest LTI (x̄ 42.00 ± 0, n = 1), followed by Cameroon (x̄ 36.20 ± 2.28, n = 5) and the Democratic Republic of the Congo (x̄ 34.0 ± 2.65, n = 3). Benin had the lowest LTI (x̄ 11.5 ± 3.5, n = 2), followed by South Africa (x̄ 11.79 ± 5.9, n = 24). Ethiopia's Chebera Churchura NP and Omo NP both had the highest threat indices of all subpopulations (each scoring 46), followed by Mozambique's Coutada 13 (44) and Angola's Luengue – Luiana NP (42). Subpopulations with the lowest LTI were Ongava Game Reserve (1, Namibia), Rifa Zambezi Valley (2, Zimbabwe), Welgevonden Game Reserve (3, South Africa), Thanda Private Game Reserve (3, South Africa), and the Greater Lebombo Transfrontier Conservation Area (3, Mozambique).

Subpopulations that had communities living within the area had significantly higher LTI than those without (Table 5.3; $\chi^2_{(2)} = 17.51$, $P < 0.001$). Local threat indices ($\chi^2_{(2)} = 18.09$, $P < 0.001$) were significantly lower for subpopulations that were fully fenced than those that had no fencing at all ($P < 0.001$), areas that had partial fencing had significantly lower LTIs than non-fenced areas ($P < 0.05$) but had higher LTI than fully fenced areas ($P < 0.05$). At a local level, subpopulations that were enclosed by some level of fencing, had significantly lower local threat indices. Most populations surveyed (n = 80, 60.61 %) had no fencing at all, while 39.4 % of populations surveyed had some fencing (21.97 % fully fenced and 17.42 with partial fencing). None of the surveyed populations in Central or West Africa were fully fenced, and only one population in East Africa (Kenya) was fully fenced. Of the fully fenced populations, 96 % (n = 28) occurred in southern Africa (21 in South Africa).

A subpopulation's LTI varied significantly with the perceived level of resources available to managers ($\chi^2_{(7)} = 33.859$, $P < 0.000$), and were significantly higher for subpopulations where resources were inadequate when compared with other resource availability levels (Table 5.2, $P < 0.05$). Surprisingly, subpopulations where engagement with the community was carried out had a higher LTI ($\chi^2_{(1)} = 8.102$, $P < 0.05$) than where community engagement was not carried out. However, this might be because community engagement was carried out where communities experienced conflict and/or were perceived to be a threat to lions.

The local threat index did not vary significantly with authority (type of governance), formal protection, people's attitudes, and whether livestock barriers were erected (methods to prevent livestock grazing) or routine patrols were conducted (Table 5.3 and Supplementary Table 5-1).

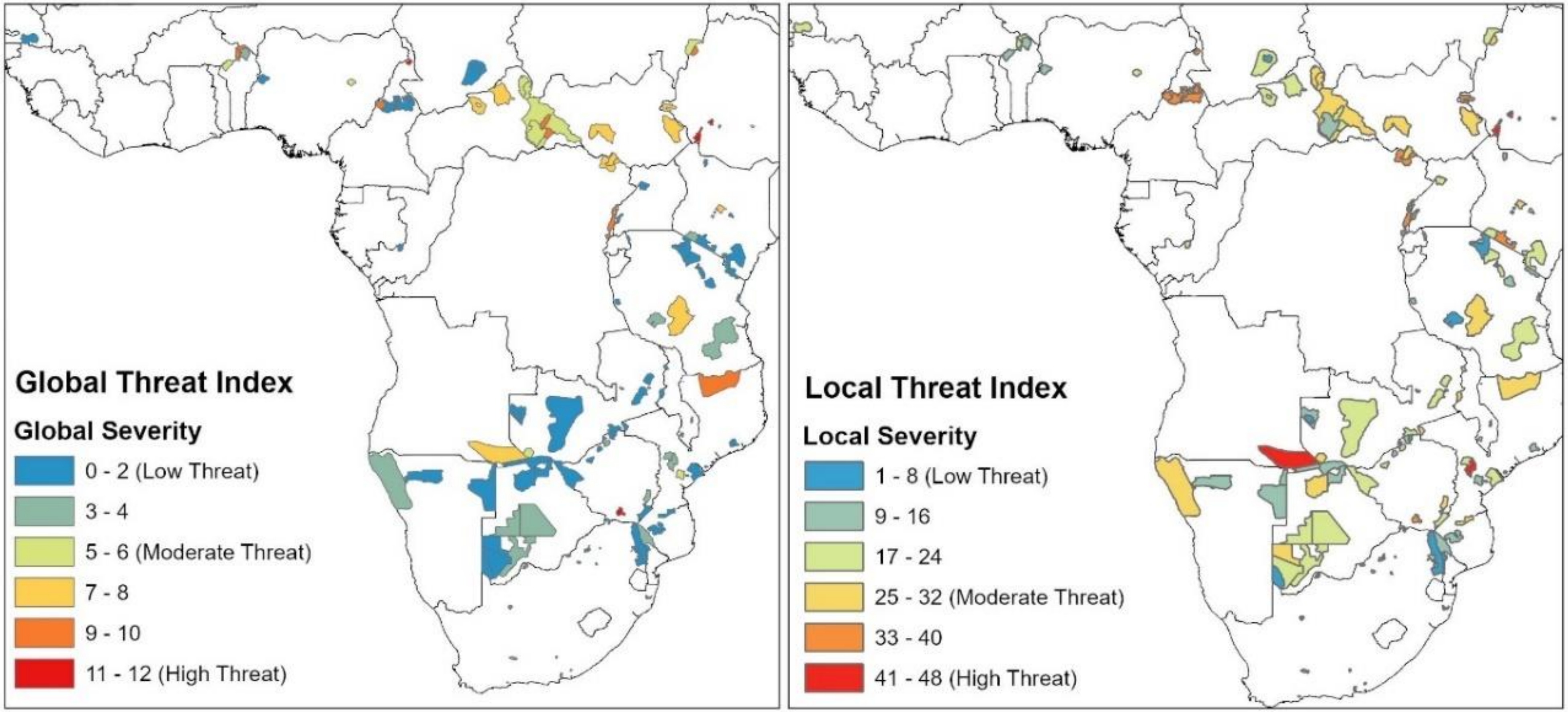

Figure 5-1. Global and local threat indices for 132 lion subpopulations in Africa surveyed in this study.

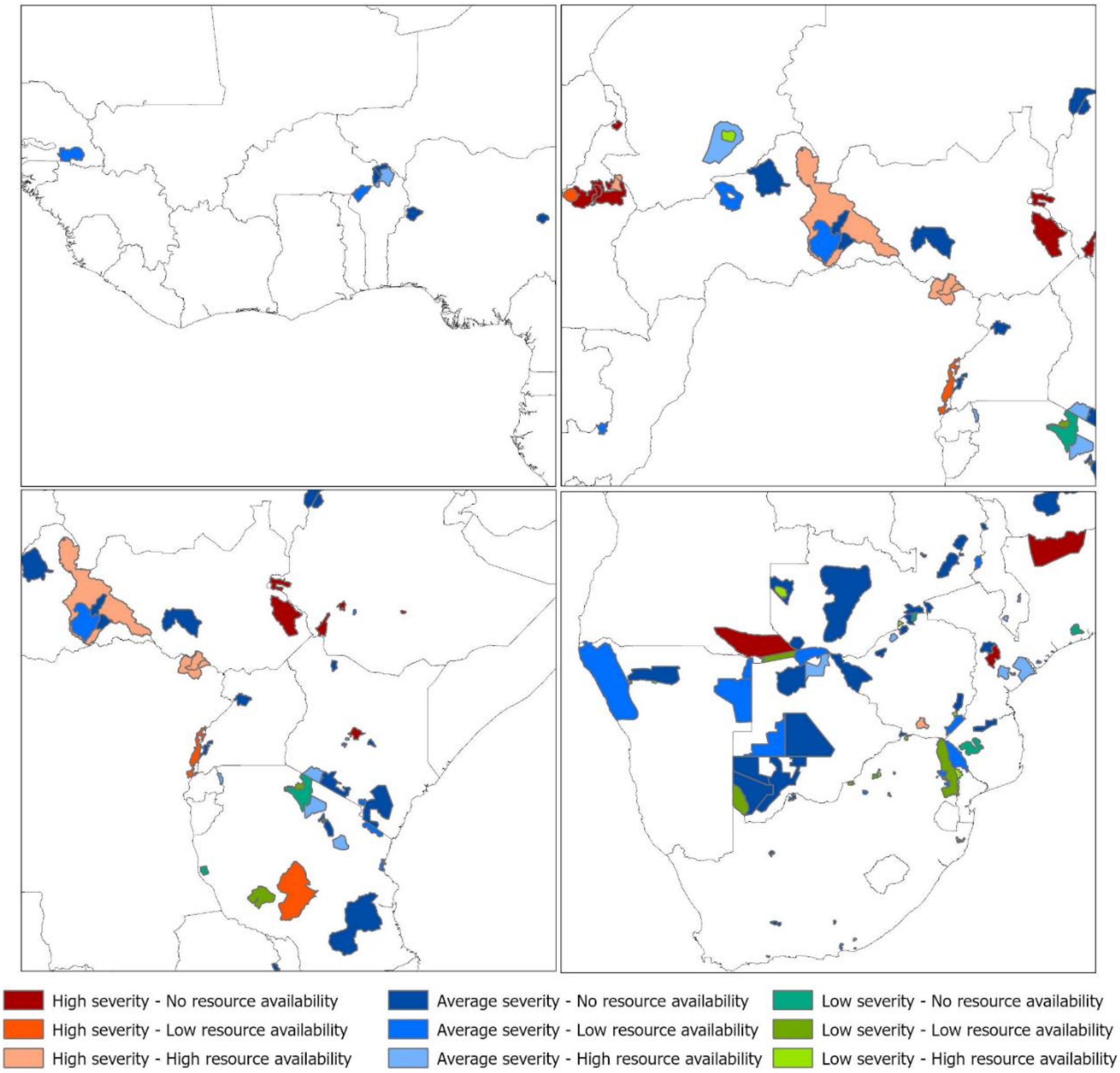

Figure 5-2. Overall perceived threat severity for subpopulations surveyed in this assessment and the perceived resource availability to area managers to prevent the illegal killing of lions. Severity was defined as low (indices below one standard deviation below the mean), medium (between low and high) and high (indices above one standard deviation above the mean).

When local threat severity was examined, most populations experienced medium severity (Supplementary Table 5-2; n = 86, 65.2 %). Across Africa, 16.7 % (n = 22) of lion subpopulations surveyed faced high local threat severity, with most of Central Africa's populations in this category (n = 11, 61.1 %). Most lion subpopulations in East (n = 23, 69.7 %), southern (n = 51, 68.9 %) and West Africa (n = 6, 85.7 %) were in moderate local severity category. Ten countries (Cameroon, Central African Republic, Chad, Democratic Republic of the Congo, Ethiopia, Kenya, Tanzania, Angola, Mozambique and Zimbabwe) had subpopulations that were considered to experience high local threat severity (Supplementary Table 5-2). All lion subpopulations in Cameroon, Democratic Republic of the Congo and Angola experienced high local threat severity.

5.4.4 *Global Threat Index*

Table 5.4. Kruskal-Wallis Test results assessing the differences between responses for variables and the Global Threat Index. For the country variable, only the two lowest and two highest countries are shown. Significant differences calculated by the Kruskal-Wallis test are shown in bold.

	VARIABLE	CATEGORIES (IN ORDER FROM LOWEST THREAT SCORE TO HIGHEST)	KRUSKAL-WALLIS TEST
Global Threat Index	Region	Southern Africa (x̄ 2.07 ± 2.13, n = 74)	**$\chi^2_{(3)} = 20.675$, P < 0.0005**
		East Africa (x̄ 3.88 ± 3.61, n = 33)	
		West Africa (x̄ 5.14 ± 3.03, n = 7)	
		Central Africa (x̄ 5.83 ± 3.54, n = 18)	
	Country	Gabon (x̄ 0, ± 0, n = 1)	**$\chi^2_{(25)} = 53.201$, P < 0.0001**
		Malawi (x̄ 1 ± 0.82, n = 4) & Rwanda (x̄ 1 ± 0, n = 1)	
		Democratic Republic of the Congo (x̄ 8.3 ± 0.58, n = 3)	
		Niger & Burkina Faso (each: x̄ 9 ± 0, n = 1)	
	Populations		$\chi^2_{(129)} = 130.233$, P > 0.05
	Authority	Community (x̄ 0.67 ± 0.58, n = 3)	$\chi^2_{(4)} = 5.17$, P > 0.05
		Community-Government Partnership (x̄ 2.6 ± 1.14, n = 5)	
		Government (x̄ 3.14 ± 3.27, n = 86)	
		Private (x̄ 3.33 ± 0.05, n = 18)	
		Public-Private Partnership (x̄ 3.85 ± 3.03, n = 20)	
	Formal protection	No (x̄ 2.25 ± 2.24, n = 16)	$\chi^2_{(1)} = 0.761$, P > 0.05
		Yes (x̄ 3.33 ± 3.21, n = 116)	
	Communities presently living within the area	No (x̄ 2.66 ± 2.75, n = 71)	$\chi^2_{(2)} = 5.388$, P > 0.05
		Yes (x̄ 3.73 ± 3.39, n = 60)	
		Unsure (x̄ 9 ± 0, n = 1)	
	Livestock grazing within the area	No but it is allowed (x̄ 1 ± 0, n = 2)	**$\chi^2_{(4)} = 17.745$, P < 0.005**
		No and it is not allowed (x̄ 1.94 ± 2.18, n = 48)	
		Unsure (x̄ 2 ± 0, n = 1)	
		Yes, and it is allowed (x̄ 3.13, ± 2.96, n = 32)	
		Yes, but it is not allowed (x̄ 4.59 ± 3.54, n = 49)	
	Livestock competition with wildlife	No (x̄ 2.33 ± 2.70, n =58)	**$\chi^2_{(3)} = 11.4189$, P < 0.05**
		Other (x̄ 3.23 ± 2.45, n = 13)	
		Unsure (x̄ 3.4 ± 3.36, n = 5)	
		Yes (x̄ 4.14 ± 3.45, n = 55)	
	People's attitude towards wildlife	Very negative (x̄ 2 ± 2.61, n = 6)	$\chi^2_{(5)} = 6.886$, P > 0.05
		Somewhat negative (x̄ 2.45 ± 2.48, n = 38)	
		Very positive (x̄ 2.8 ± 3.58, n = 10)	
		Neutral (x̄ 2.96, ± 2.68, n = 26)	
		Somewhat positive (x̄ 3.79 ± 3.18, n = 44)	
		Unknown (x̄ 5.63 ± 5.21, n = 8)	
	Fencing	Partially fenced (x̄ 2.17 ± 2.12, n = 23)	$\chi^2_{(2)} = 4.69$, P > 0.05
		Fully fenced (x̄ 2.38 ± 2.58, n = 29)	

		No fenced at all (x̄ 3.79 ± 3.41, n = 80)	
	Sufficient area resources	Unsure (x̄ 0.67 ± 1.15, n = 3)	**$\chi^2_{(2)}$ = 19.64, P < 0.05**
		Neither agree nor disagree (x̄ 1.25 ± 1.16, n = 8)	
		Strongly agree (x̄ 1.63 ± 1.89, n = 16)	
		Somewhat disagree (x̄ 2.71 ± 2.64, n =17)	
		Somewhat agree (x̄ 12.94 ± 2.89, n = 16)	
		Disagree (x̄ 3.48 ± 3.11, n = 29)	
		Agree (x̄ 3.6 ± 3.22, n = 20)	
		Strongly disagree (x̄ 5.13 ± 3.84, n = 23)	
	Livestock barriers	No (x̄ 3.07 ± 3.06, n = 102)	$\chi^2_{(2)}$ = 0.736, P > 0.05
		Yes (x̄ 3.63 ± 3.62, n = 30)	
	Routine patrols conducted	Yes (x̄ 3.08 ± 3.05, n = 118)	$\chi^2_{(2)}$ = 2.251, P > 0.05
		Don't know (x̄ 4 ± 5.66, n = 2)	
		No (x̄ 4.25 ± 3.55, n = 12)	
	Community engagement	No (x̄ 2.58 ± 2.74, n = 43)	$\chi^2_{(2)}$ = 2.24, P > 0.05
		Yes (x̄ 3.49 ± 3.26, n = 89)	

The average GTI for all surveyed subpopulations (Table 5.1 and Figure 5-2) was 3.19 (1SD ± 3.12) and varied significantly across regions ($\chi^2_{(3)}$ = 20.68, P < 0.001) (Table 5.4). Central Africa and West Africa had the highest GTI (5.83 ± 3.54 and 5.14 ± 3.02 respectively), with the GTI for East Africa (3.88 ± 3.61) significantly lower than for Central Africa, and GTI for southern Africa significantly lower (2.07 ± 2.13) than all other regions (P < 0.05). GTI differed significantly among countries ($\chi^2_{(25)}$ = 53.201, P < 0.001) and were highest in Burkina Faso and Niger (GTI of 9), followed by the Democratic Republic of the Congo (8.33). GTI were lowest in Gabon (0, n = 1), Malawi (1 ± 2.13, n = 4) and Rwanda (0, n = 1).

Twenty-one subpopulations received a GTI of 0 including five in South Africa, five in Mozambique, three in Tanzania and Zimbabwe, two in Kenya, and one each in Namibia, Kenya and Malawi. Four subpopulations had the highest global indices: Ethiopia's Chebera Churchura NP and Omo NP (index of 12 each), followed by Waza NP and Zimbabwe's Bubye Valley Conservancy (index of 11 each).

GTI varied significantly depending on whether competition with wildlife occurred, and whether livestock were grazing in the area (Table 5.4 and Supplementary Table 5-1). Significant differences in GTI were only observed when comparing the levels of whether respondents felt that they were sufficiently equipped enough to reduce the illegal killing of lions (Table 5.3). Respondents who strongly disagreed that sufficient resources were available had significantly higher global indices than other responses (P < 0.001).

GTI did not vary significant with different levels of authority, formal protection, or people's attitudes towards wildlife (Table 5.4 and Supplementary Table 5-1). In terms of mitigation, whether livestock barriers, community engagement or routine patrols were conducted did not significantly affect GTI (Table 5.4).

When global threat severity was examined, most subpopulations were perceived to experienced medium severity (Supplementary Table 5-1; n = 56, 42.42 %). Half of Central Africa's subpopulations (Supplementary Table 5-2; n = 9, 50 %), and 29 % (n = 2) of West African lion subpopulations were perceived to experience high global threat severity (n = 5). Most subpopulations in West Africa (71 % (n = 5), and 33.3 % (n = 11) in East Africa were perceived to experience medium global severity. Thirty-three percent of East African (n = 11)) and 45.9 % of southern African (n = 34, 45.9 %) subpopulations were perceived to experience average global threat severity. All lion subpopulations in Burkina Faso, Niger, Angola, South Sudan and the Democratic Republic of the Congo experienced high global threat severity (Supplementary Table 5-2).

5.4.5 Summary of the Total Threat Index (TTI)

Table 5.5. Kruskal-Wallis Test Results assessing the differences between geographic variables and the Total Threat Index. For the country category, only the two lowest and two highest countries are shown. Significant differences calculated by the Kruskal-Wallis test are shown in bold.

INDEX	VARIABLE	CATEGORIES (IN ORDER FROM LOWEST THREAT SCORE TO HIGHEST)	KRUSKAL-WALLIS TEST
Total Threat Index	Region	Southern Africa (x̄ 18.8 ± 10.36, n = 74)	**$\chi^2_{(3)} = 22.02$, $P < 0.0001$**
		West Africa (x̄ 23 ± 6.83, n = 7)	
		East Africa (x̄ 24.91 ± 12.85, n = 33)	
		Central Africa (x̄ 33.83 ± 11.22, n = 18)	
	Country	South Africa (x̄ 13.79, ± 6.88, n = 24)	**$\chi^2_{(25)} = 58.47$, $P < 0.0001$**
		Rwanda (x̄ 14 ± 0, n = 1)	
		Democratic Republic of Congo (x̄ 42.3 ± 3.06, n = 3)	
		Angola (x̄ 50 ± 0, n = 1)	
	Populations		$\chi^2_{(129)} = 129.69$, $P > 0.05$
	Authority	Private (x̄ 16.89 ± 12.19, n = 18)	$\chi^2_{(4)} = 5.92$, $P > 0.05$
		Government (x̄ 23.12 ± 12.6, n = 86)	
		Public-Private Partnership (x̄ 24.65 ± 10.36, n = 20)	
		Community (x̄ 24.67 ± 9.02, n = 3)	
		Community-Government Partnership (x̄ 24.8 ± 4.21, n = 5)	
	Formal protection	No (x̄ 20.06 ± 9.71, n = 16)	$\chi^2_{(1)} = 0.225$, $P > 0.05$
		Yes (x̄ 22.95 ± 12.34, n = 116)	
		No (x̄ 18.61 ± 9.98, n = 71)	**$\chi^2_{(2)} = 16.299$, $P < 0.001$**
		Yes (x̄ 27.2 ± 12.77, n = 60)	

	Communities presently living within the area	Unsure (x̄ 30 ± 0, n = 1)	
	Livestock grazing within the area	No but it is allowed (x̄ 5 ± 1.414, n =2)	**$\chi^2_{(4)}$ = 31.306, P < 0.0001**
		No and it is not allowed (x̄ 16.19 ± 8.66, n =48)	
		Unsure (x̄ 17 ± 0, n =1)	
		Yes, and it is allowed (x̄ 24.38, ± 11.56, n = 32)	
		Yes, but it is not allowed (x̄ 28.55 ± 12.01, n =49)	
	Livestock competition with wildlife	No (x̄ 18.52 ± 11.31, n =58)	**$\chi^2_{(3)}$ = 13.496, P < 0.001**
		Unsure (x̄ 21.4 ± 9.91, n = 5)	
		Other (x̄ 24.85 ± 11.63, n = 13)	
		Yes (x̄ 26.49 ± 12.08, n = 55)	
	People's attitude towards wildlife	Very positive (x̄ 17.7 ± 12.39, n = 10)	$\chi^2_{(5)}$ = 4.35, P > 0.05
		Neutral (x̄ 21.77, ± 10.96, n = 26)	
		Somewhat negative (x̄ 22.42 ± 11.63, n = 38)	
		Somewhat positive (x̄ 22.45 ± 10.81, n = 44)	
		Very negative (x̄ 26 ± 6.87, n = 6)	
		Unknown (x̄ 30.5 ± 22.58, n = 8)	
	Fencing	Fully fenced (x̄ 15.62 ± 9.23, n = 29)	**$\chi^2_{(2)}$ = 17.47, P < 0.0001**
		Partially fenced (x̄ 19.91 ± 9.4, n = 23)	
		No fenced at all (x̄ 25.9 ± 12.46, n = 80)	
	Sufficient Park resources	Unsure (x̄ 10 ± 8, n = 3)	**$\chi^2_{(7)}$ = 35.46, P < 0.0001**
		Strongly agree (x̄ 13.19 ± 7.93, n = 16)	
		Neither agree nor disagree (x̄ 15.38 ± 5.78, n = 8)	
		Somewhat agree (x̄ 19.5 ± 9.86, n = 16)	
		Agree (x̄ 21.75 ± 12.04, n = 20)	
		Somewhat disagree (x̄ 33.26 ± 12.98, n =17)	
		Disagree (x̄ 24.93 ± 10.6, n = 29)	
		Strongly disagree (x̄ 33.26 ± 12.98, n = 23)	
	Livestock barriers	No (x̄ 22.21 ± 12.33, n = 102)	$\chi^2_{(1)}$ = 0.84, P > 0.05
		Yes (x̄ 23.93 ± 11.18, n = 30)	
	Routine patrols conducted	Yes (x̄ 22 ± 11.89, n = 118)	$\chi^2_{(2)}$ = 2.16, P > 0.05
		No (x̄ 27.42 ± 12.18, n = 12)	
		Don't know (x̄ 29 ± 21.21, n = 2)	
	Community engagement	No (x̄ 18.37 ± 11.05, n = 43)	**$\chi^2_{(1)}$ = 6.58, P < 0.05**
		Yes (x̄ 24.64 ± 12.05, n = 89)	

The average TTI for all subpopulations was 22.6 (± 1SD 12.06; range: 1-58, Figure 5-3 and Figure 5-4). TTI results differed significantly across regions ($\chi^2_{(3)}$ = 22.02, P < 0.0001), with the TTI in Central Africa (33.83 ± 1SD 11.22) significantly higher than East Africa ($\chi^2_{(3)}$ = 22.02, P < 0.005, TTI = 24.91 ± 12.85), West Africa ($\chi^2_{(3)}$ = 22.02, P < 0.05, TTI = 23 ± 6.83) and southern Africa ($\chi^2_{(3)}$ = 22.02, P < 0.001, TTI = 18.79 ± 10.36); the latter also being significantly lower than East Africa. Angola had the highest overall threat index (50.0 ± 0, n = 1), followed by Democratic Republic of the Congo (42.33 ± 3.05, n = 3) and Cameroon (41.40 ± 6.02, n = 5). Two subpopulations in southern Africa

(South Africa (13.79 ± 6.88, n = 24) and Namibia (14.50 ± 9.83, n = 6)) and one in Eastern Africa (Rwanda 14.00 ± 0, n = 1) had the lowest TTI. TTI varied among subpopulations but not significantly ($\chi^2_{(129)}$ = 129.69, P > 0.05). Ethiopia's Chebera Churchura NP and Omo NP both had the highest TTI of all subpopulations (each scoring 58), with Angola's Luengue – Luiana NP and Cameroon's Waza NP next highest (50 and 48 respectively). Five subpopulations had the lowest TTI, all in southern Africa and fenced: Ongava Game Reserve (1, Namibia), Rifa Zambezi Valley (2, Zimbabwe), Welgevonden Game Reserve (3, South Africa), Thanda Private Game Reserve (4, South Africa) and the Greater Lebombo Transfrontier Conservation Area (4, Mozambique).

Similar trends were observed in the TTI as in the LTI and GTI (Supplementary Table 5-1). Region, country, level of fencing, communities living in the area, livestock grazing within the area, livestock competition with wildlife and the level of park resources all significantly effected TTI. A full description is available in the supplementary material.

5.4.6 Resource availability and overall threat severity

Almost half of the surveyed lion populations (n = 65, 49.24 %) are reportedly not equipped with sufficient resources to adequately reduce the illegal killings of lions. Only a quarter of surveyed areas were perceived to have high resource availability. Almost half of the surveyed populations in southern Africa (n = 35, 47.3 %) had low resource availability. The Resource Availability Index (RAI) was lowest, indicating the least resources, in East Africa (-2 ± 2.94), followed by West Africa (-1.71 ± 3.09; Figure 5-4). Southern Africa and Central Africa, while still not sufficiently equipped, scored -0.83 ± 3.4 and -0.17 ± 3.60 respectively (Figure 5-4) with Central Africa perceived to have less resources than southern Africa.

Most lion populations surveyed in this study (n = 47, 35.61 %; Table 5.3) experience average threat severity and low resource availability (Figure 5-4 and Supplementary Table 5-2). Cameroon, the Democratic Republic of the Congo, Ethiopia and Angola all had high overall threat severity scores (Figure 5-4) while Benin, Rwanda, Namibia and South Africa had low overall threat severity scores (Figure 5-4).

Populations in Central Africa mostly faced high threat severity but with high resource availability (n = 5, 27.78 %). East African lion populations were mostly faced with medium severity and low resource availability (n = 12, 39.19 %); the same was experienced in southern Africa (n = 29, 39.19 %). Interestingly, West Africa experienced medium threat severity and high resource availability (n = 4, 57.14 %).

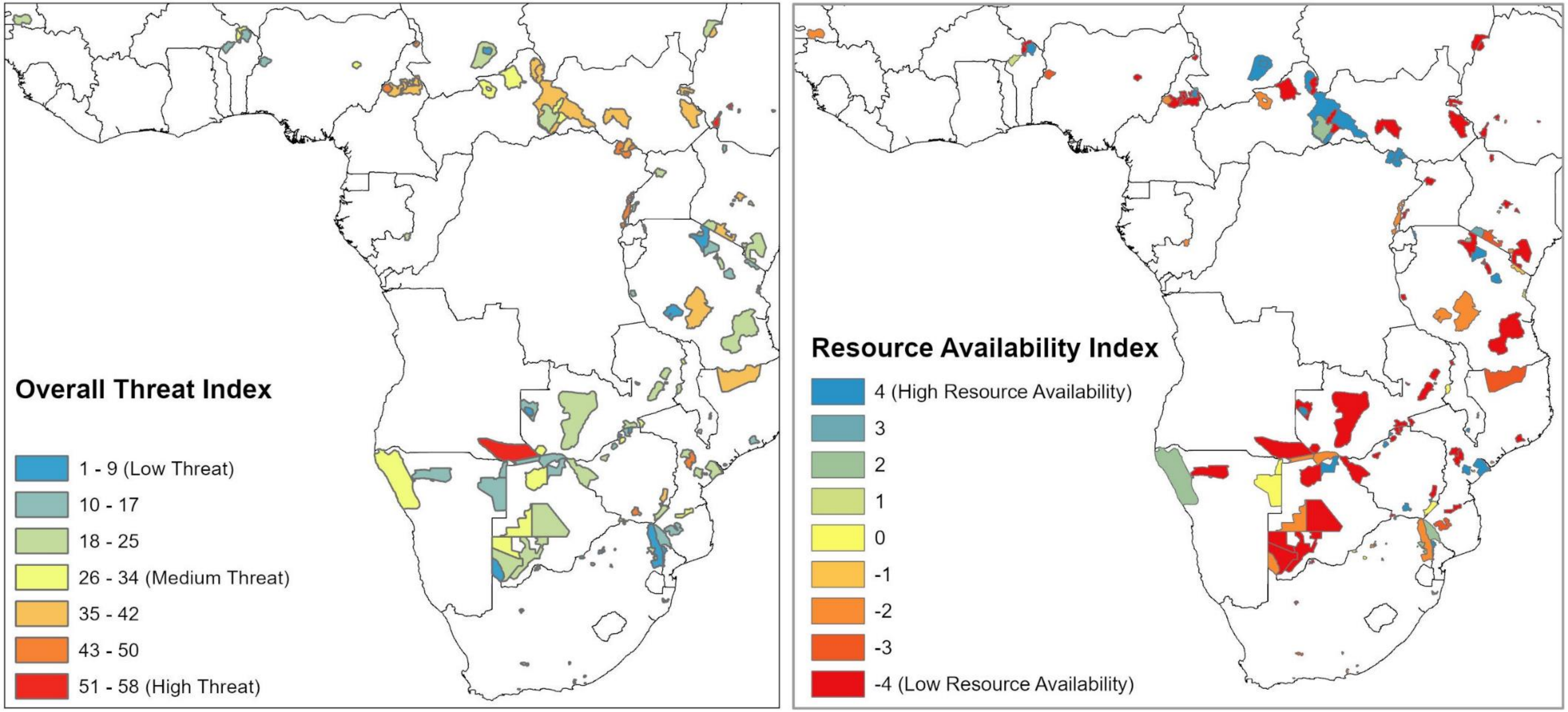

Figure 5-3. Total threat index, indicating the perceived level of threat severity (higher numbers indicate perceived higher/more severe threats) and the perceived Resource Availability Index of 132 lion subpopulations.

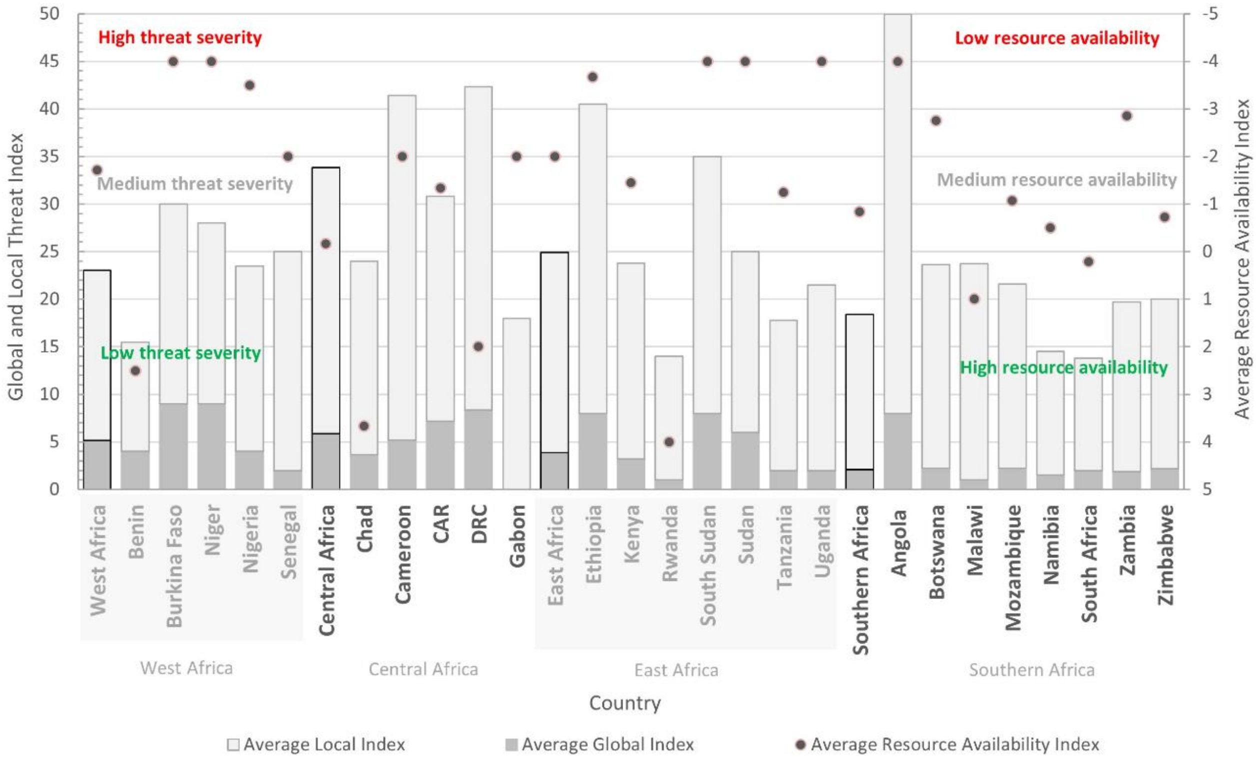

Figure 5-4. The average local and global threat index scores, when summed, give a total threat index for regions and countries. Increasing threat indices indicate increasing perceived threat severity. Average Resource Availability Index is also shown for each region and country. The High threat severity category includes values one standard deviation above the mean and higher, the low threat severity category includes values one standard deviation below the mean and below, and medium threat severity category includes values between high and low severity.

5.4.7 Perceived poaching metrics

Lions were not considered safe from poachers in almost half of surveyed subpopulations (47.7 %, n = 63, Figure 5-5) and were considered safe in only 39 % (n = 52) of subpopulations. Regionally, lions were mostly considered unsafe from poachers (West Africa 42.8 % of subpopulation, Central Africa 61 %, East Africa 42.4 % and southern Africa 47.3 %). Of the 66 % of survey subpopulations that experienced poaching of lions, 20.7 % (n=18) had an increasing poaching trend of lions, 23 % (n = 20) felt that poaching trends were the same, 42.5 % (n = 37) were unsure of trends, and only 13.8 % (n = 12) had decreased trends. However, detailed records of lion mortalities were reportedly only kept by 57.6 % of lion subpopulations surveyed (n= 76), 28.8 % (n = 38) did not keep records, and 13.6 % (n = 18) of respondents for those subpopulations were unsure.

5.4.8 Perceived threats of poaching to lions across their range

Lions were poached for parts in 30 % (n = 40) of surveyed subpopulations (Table 5.5, Figure 5-6). The most frequent parts that were sought were skin, claws teeth, fat, and bones (all four > 50 % in the subpopulations reporting poaching for parts). Most respondents were unsure of the market for these parts (n = 15, 37.5 %) and only two respondents felt they were solely for the international market. Generally, it was perceived that parts were collected for both local and international markets (n = 12, 30 %). However, 27.5 % (n = 11) of those respondents who thought lions were poached for parts, thought that the parts were for the local markets within country. Based on the responses, uses for parts ranged from strengthening the body, curing diseases, increasing power and improving the immune system (Table 5.5).

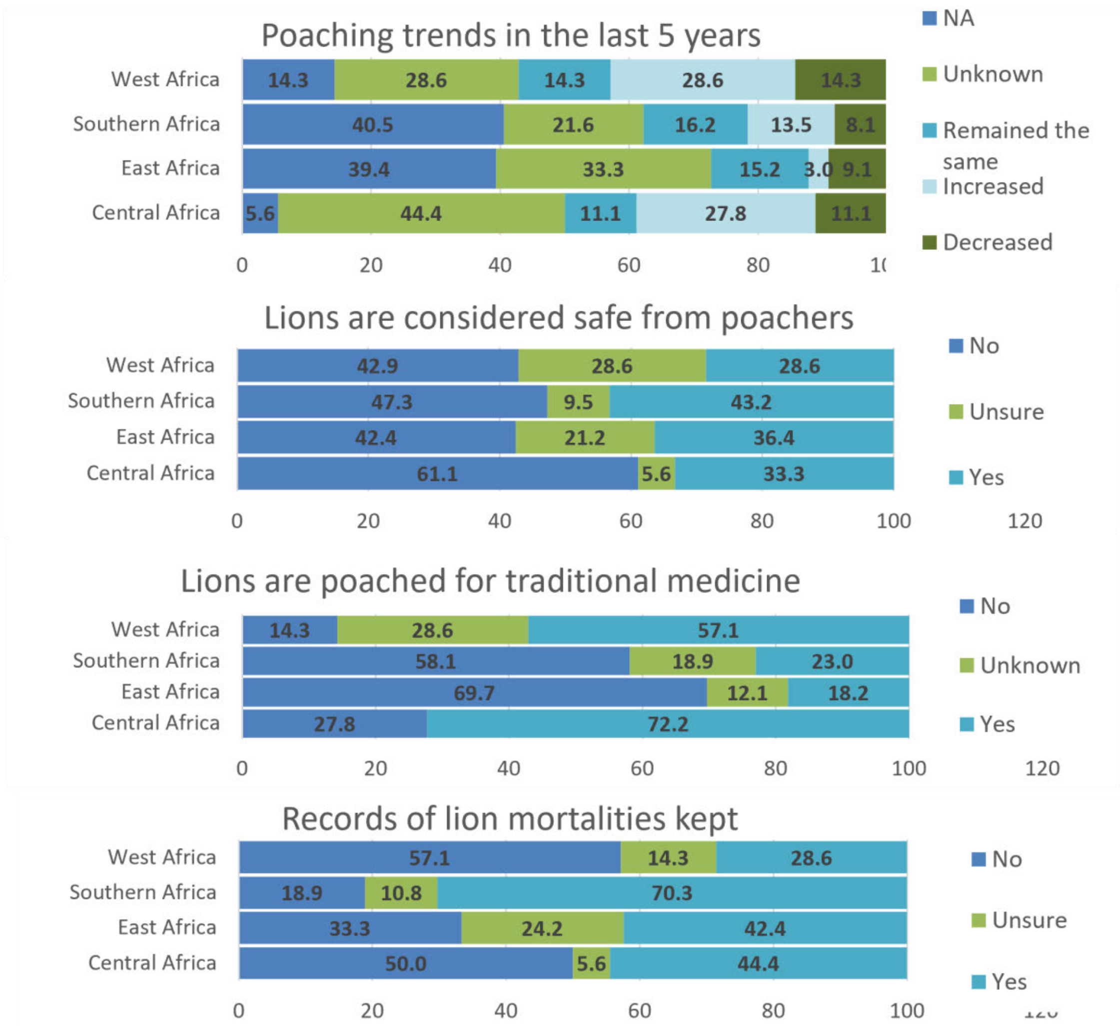

Figure 5-5. Responses to questions relating to poaching of lions per region in Africa (reported as percentages, n = 132).

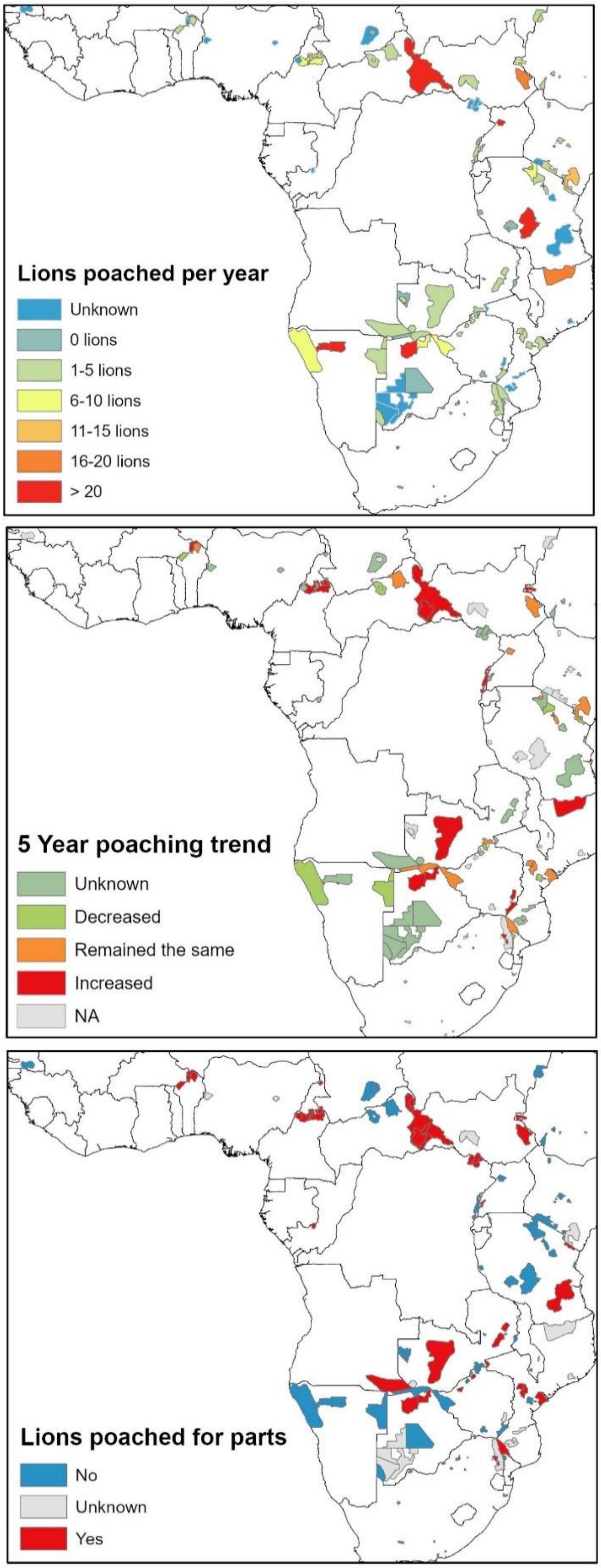

Figure 5-6. The number of lions killed per annum, the five-year poaching trend and whether lions are poached for parts as perceived by the 132 surveyed subpopulations.

Table 5.6. Populations where lions are targeted for parts across Africa, the intended markets and uses.

Region	Country	Population	Are lions poached for parts in the area?	Claws	Teeth	Whole face	Skin	Tail	Fat	Bones	Meat	Other	Unsure which parts	If lions are poached for local traditional medicine (or belief-based use) what are they used for?
Central Africa	Cameroon	Benoue NP	Yes, but unsure of market				✓	✓	✓	✓				local medicine, to strengthen the body, health and invulnerability.
	Central African Republic	Vovodo Safari Area	Yes, but unsure of market										✓	
	Central African Republic	Eastern CAR wilderness	Yes, but unsure of market	✓	✓		✓	✓	✓	✓				
	Gabon	Plateaux Bateke NP	Yes, for both markets		✓		✓							
	Chad	Sena Oura NP	Yes, for both markets	✓	✓		✓	✓	✓	✓				The fat is used as a balsam, it is believed that it will make you invulnerable. The skin and tail are used by chiefs and other traditional important people as a status symbol. Fat and testicles - Viagra/stamina.
	Democratic Republic of Congo	Garamba Hunting Domains: domaine de chasse Azande, domaine de chasse Gangala na Bodio, domaine de chasse Mondo Missa	Yes, for both markets	✓	✓		✓		✓	✓				Teeth, fat, skin used for spiritual use (fat matures infants, teeth protects people etc.)
	Cameroon	Faro NP and associated concessions	Yes, for both markets	✓	✓		✓							Gris-gris, traditional fetishes and curatives.
	Cameroon	Bouba Ndjida NP	Yes, for both markets		✓		✓	✓	✓	✓				improve health, durability, invulnerability and endurance and strength.
	Cameroon	Hunting concessions in the Benoue Complex	Yes, for both markets	✓	✓		✓	✓	✓	✓				increase of force(sexual and health), better immune system(less diseases), invulnerable, etc.
	Central African Republic	Aire de Conservation de Chinko (Chinko Conservation Area)	Yes, for local markets within the country	✓	✓		✓							Medicine and status. A long list of different treatments for different diseases and magic believes. Lion parts are send over international transhumance and traders to large markets in Khartoum and Nigeria.
	Democratic Republic of Congo	Garamba NP	Yes, for local markets within the country	✓	✓		✓	✓	✓	✓		Urine		Lion fat to treat disease and burns. Teeth to treat poisoning. Apply to babies to allow them to walk earlier. Used as a lotion Rituals and "witchcraft" for

														protection. Tail used as a sign of power. Bones are burnt and used as an anti-venom.
	Cameroon	Waza NP	Yes, for local markets within the country	✓	✓	✓	✓	✓	✓	✓		Urine		
	Central African Republic	Andre Felix NP and Yata Ngaya reserve	Yes, for local markets within the country	✓	✓		✓	✓	✓	✓				
East Africa	Ethiopia	Gambella NP	Yes, but unsure of market				✓							
	Tanzania	Nyerere NP, Selous Game Reserve	Yes, for both markets	✓			✓		✓					Skins for witch doctor use. Claws for trade.
	Tanzania	Mkomazi NP	Yes, for local markets within the country	✓	✓				✓					They said lion fat cure many diseases and also they use some body parts for superstition.
	South Sudan	Boma NP	Yes, for local markets within the country	✓			✓	✓			✓			Eating lion is believed to make you stronger. Mainly amongst the youth.
	Uganda	Queen Elizabeth NP (QENP)	Yes, for local markets within the country	✓			✓	✓	✓					
	Tanzania	Kijereshi Game Reserve	Yes, for local markets within the country	✓	✓		✓		✓					They use fats to healer some people.
Southern Africa	Mozambique	Coutada 11	Yes, but unsure of market	✓	✓	✓								
	South Africa	Dinokeng Game Reserve	Yes, but unsure of market	✓	✓	✓	✓	✓	✓	✓				
	Angola	Luengue - luiana NP	Yes, but unsure of market	✓	✓	✓	✓	✓	✓	✓				
	South Africa	Welgevonden Game Reserve	Yes, but unsure of market	✓	✓									
	Zimbabwe	Chizarira NP	Yes, but unsure of market	✓	✓		✓		✓					
	Zimbabwe	Charara Safari Area	Yes, but unsure of market	✓	✓		✓		✓					
	Zambia	Kafue NP, Greater Kafue Ecosystem Game Management Reserves	Yes, but unsure of market				✓		✓	✓		Eyes & organs		Lion fat, lion eyes, lion organs are all used for increasing power of an individual and witchcraft.
	South Africa	Kruger APNRs	Yes, but unsure of market	✓	✓	✓								
	Zambia	South Luangwa NP, North Luangwa NP, Luambe NP	Yes, but unsure of market				✓		✓					

	South Africa	Mapungubwe NP	Yes, but unsure of market	✓	✓									
	Mozambique	Chawalo Safari Area	Yes, but unsure of market										✓	
	Mozambique	Limpopo NP	Yes, for both markets	✓	✓		✓		✓	✓				
	Botswana	Okavango Delta , Moremi Game Reserve and surrounding WMAs	Yes, for both markets	✓	✓		✓		✓	✓				Lion fat is sought after, not sure for what purpose, but I suspect for strength and protection. Claws and teeth also as symbol of strength, in some cases skins used by Chiefs.
	Mozambique	Coutada 9	Yes, for local markets within the country	✓	✓	✓	✓			✓	✓			They are used in traditional medicine.
	Mozambique	Coutada 13	Yes, for local markets within the country	✓	✓	✓	✓			✓	✓			
	Botswana	Chobe NP & surrounding areas.	Yes, for the international market	✓	✓	✓	✓	✓	✓	✓	✓			
	South Africa	Kariega Game Reserve, Indalo Protected Environment	Yes, for the international market							✓	✓		✓	
West Africa	Benin	Pendjari NP	Yes, for both markets	✓	✓	✓	✓	✓		✓				Power; increase possibilities of power; Obtain higher positions of responsibility; Being feared in society; fortune.
	Burkina Faso	W National Park	Yes, for both markets	✓	✓	✓	✓	✓	✓	✓				for a mix of medicinal and religious uses.
	Niger	W National Park	Yes, for both markets	✓	✓	✓	✓	✓	✓	✓				there is a wide range of uses, some of which are medicinal, like for lion fat, or traditional/religious, lion for skins.
	Benin	W National Park	Yes, for local markets within the country	✓			✓		✓	✓				strengthen human health (growth, immune system).
			Total	31	29	11	32	16	25	21				
			Percentage of total	77.5	72.5	27.5	80	40	62.5	52.5				

Table 5.7. The average severity score of each of the local and global threats and pressures for African and each region. Colour palette demonstrates most severe (red) to less severe (blue) within regions.

		CENTRAL AFRICA	EAST AFRICA	SOUTHERN AFRICA	WEST AFRICA	AFRICA
LOCAL	Human encroachment	2.67	1.91	1.38	0.71	1.65
	Development of infrastructure close to or within the area	1.11	1.58	1.33	0.86	1.34
	Targeted poaching of lions for their parts	2.44	0.94	1.18	2.29	1.35
	Loss of natural prey base driven by poaching	2.67	1.64	1.26	2.71	1.62
	Loss of natural prey base driven by other factors such as habitat degradation	2.22	1.76	1.11	1.29	1.43
	Bycatch in snares	1.72	1.18	1.30	0.43	1.28
	Intended poisoning of carnivores	2.39	1.39	1.12	1.43	1.38
	Lion cultural killings	0.67	1.00	0.30	1.14	0.57
	Retaliatory or pre-emptive killing of lions	2.67	1.91	1.22	1.43	1.60
	Lion mortality from vehicle and train collisions	0.39	0.30	0.34	0.29	0.33
	Unmanaged trophy hunting	0.33	0.58	0.38	0.00	0.40
	Loss of suitable habitat	2.06	1.88	1.27	1.00	1.52
	Lack of/inconsistent funding for area operations	2.50	2.03	1.51	1.71	1.79
	Disease	1.28	1.03	0.91	0.29	0.95
	Small, isolated lion population	2.17	1.21	1.09	1.86	1.31
	Poor and ineffective population management	0.72	0.73	1.04	0.43	0.89
	Average	***1.75***	***1.32***	***1.05***	***1.12***	***1.21***
GLOBAL	Civil unrest/local war that poses threats directly to lions	1.67	0.79	0.27	1.57	0.66
	Civil unrest/local war that reduces the effective management	2.17	1.06	0.32	2.14	0.86
	Ban on lion trophy hunting	0.39	0.39	0.54	0.00	0.45
	Climate change	1.61	1.64	0.93	1.43	1.23
	Average	***1.46***	***0.97***	***0.52***	***1.29***	***0.80***

Based on the severity scores, the most severe local threats across Africa were perceived to be a lack of or inconsistent funding for operations (average severity score of 1.79, Table 5.7, Figure 5-7 and Supplementary Figure 5-1. Graphical representation of the average severity score of each of the local and global threats and pressures for African and each region), human encroachment for agriculture or settlement (1.65), and a loss of natural prey base resulting from poaching (1.62) (Table 5.7). The most severe threats in Central Africa were perceived to be human encroachment (2.67), loss of prey base from poaching (2.67) and retaliatory killings or pre-emptive killing of lions to protect livestock (2.67). In East Africa, the three most severe threats were a lack of or inconsistent funding (2.03), retaliatory or pre-emptive killings (1.91) and human encroachment (1.91). In southern Africa, the three most severe threats were lack of or inconsistent funding (1.51), human encroachment (1.38) and development of infrastructure adjacent or within the area (1.33). In West Africa, severity of threats was perceived to be highest for the loss of natural prey base because of poaching (2.71), targeted poaching of lions for their parts (2.29), and small, isolated lion populations (1.86). Central Africa had the highest average severity score (1.75), followed by East Africa (1.32), West Africa (1.12) and southern Africa (1.05).

The most severe global threat for Africa was perceived to be climate change (1.23; Table 5.7 and Figure 5-7 and this was the most severe threat within East Africa (1.64) and southern Africa (0.93). Within Central Africa, the most severe global threat was civil unrest or local war that poses direct threats to lions (2.17), while in West Africa civil unrest and local war, which reduces the effectiveness of protected area management, was perceived to be the most severe threat (2.14). For global threats, Central Africa had the highest average severity (1.46), followed by West Africa (1.29), East Africa (0.97) and southern Africa (0.52).

5.5 Discussion

Here, we used questionnaire surveys of park managers and researchers to assess the perceived severity of threats to lion subpopulations across the African continent. Lion subpopulations in Central Africa had the highest perceived threat severity scores. At the local scale, human encroachment, lack (or depletion) of natural prey, retaliatory killing by farmers, and lack of funding were seen as the primary threats to lions. On a global scale, climate change was seen as the primary threat in East and southern Africa, while civil unrest or local war was considered the greatest risk in Central and West Africa.

All evidence suggests that declines in African lion populations are expected to continue, and the recent Red List Assessment estimated that lion populations in Africa have a 41 % probability of declining by 33 % within three lion generations (Nicholson *et al.,* 2023a). Regionally, the probability of a 33 % decline within three generations was estimated to be 74 % in West Africa, 36 % in East Africa, 33 % in Central Africa, and 20 % in southern Africa (Nicholson *et al.,* 2023a). Our study found similar trends, with East and southern Africa perceived to have more optimistic past and future population trends compared to Central and West Africa. As human populations grow and the interface between wildlife and people becomes more pronounced, it is inevitable that anthropogenic threats and pressures on the natural environment will continue (Nazarevich, 2015; Rull, 2022). Understanding the anthropogenic threats and pressures on individual subpopulations is critical in developing and implementing effective conservation action (Bauer *et al.,* 2020). Where subpopulations face combinations of threats, more targeted and intense conservation action will be required. This is especially so in areas where resources are inadequate. This is especially the case for Cameroon, the Democratic Republic of the Congo, Ethiopia and Angola as they were perceived to experience high threat severity and have insufficient resources and populations are isolated (Nicholson *et al.,* 2023, this study). Subpopulations within these countries should therefore be prioritised for conservation funding and action. We identified nine subpopulations expected to become extinct in the next decade, and as the lion is listed as Vulnerable, this is of concern and these areas should also be prioritised.

Considering that the lion in West Africa is regionally listed as Critically Endangered (Henschel *et al.,* 2014), it would have been expected that threat severity is significantly higher, and that resource availability were low. However, we found the opposite, which could be because of optimistic perceptions of future lion subpopulations. In addition, considerable attention has been given to West African lion subpopulations over the past two decades (IUCN, 2006a; Bauer & Nowell, 2010; Henschel *et al.,* 2010, 2014), which could be resulting in more positive conservation action and outcomes, thereby reducing threats. However, our results indicate that subpopulations in West Africa still have inadequate resource availability and medium to high severity, indicating that this region should continue to be prioritised for conservation action.

As to be expected, areas where communities were living within the same area as lions lived and livestock grazing in the area occurred, particularly where it was illegal, had higher severity scores than those without, indicating that the presence of livestock can play a potentially significant role in increased threats. This indicates that our results are consistent with these previous finding (see (Patterson *et al.,* 2004; Schuette *et al.,* 2013; Tumenta *et al.,* 2013; Boulhosa & Azevedo, 2014; Carvalho *et al.,* 2015). As a result of this, increased threats such as human-lion conflict (Blackburn *et al.,* 2016; Lindsey *et al.,* 2017; Leflore *et al.,* 2020; Gueye *et al.,* 2022), disease transmission (Miguel *et al.,* 2017) and habitat degradation (Bauer *et al.,* 2020; Frank, 2023) may occur. Fencing effectively reduces human-lion conflict, thereby reducing lion mortalities through retaliatory or pre-emptive killings (Packer *et al.,* 2013; di Minin *et al.,* 2021). Indeed, we did find that areas that were fenced had a significantly lower local threat severity scores.

Several direct threats were identified in this study, including the prevalence of illegal grazing, which may result in increased human-lion conflict with more lions killed (Lindsey *et al.,* 2017; Bauer *et al.,* 2020). Illegal grazing is evidently a more notable problem in West Africa where it occurred in all seven surveyed subpopulations. Poaching for parts has typically been understood to occur in select southern African subpopulations, for example, Limpopo National Park in Mozambique where 35 % of human-caused mortalities were because of the targeted poaching for parts (Everatt *et al.,* 2019). However, it is concerning to note how much more widespread this threat is, with lions being poached for parts in the W-Arly-Penjari Complex (Niger, Benin, Burkina Faso), the Benoué Complex (Cameroon), the Eastern Central African Republic Wilderness (including Chinko Reserve), Kafue National Park (Zambia), Boma National Park (South Sudan) and Gambella National Park (Ethiopia). While this threat could potentially contribute to local population declines, as it has done in Limpopo National Park (Everatt *et al.,* 2019; Mole & Newton, 2020), there is limited information available on this threat and the scale to which it is happening. We recommend that more attention is given to understanding this threat to determine its local level population impacts and scale, particularly in West and Central Africa.

Impacts of civil war and unrest, most severe in Central and West Africa, creates a unique environment of insecurity and lawlessness, which amplifies existing threats and can also contribute to the reduction of protected area management efficiency (Lhoest *et al.,* 2022; Aglissi *et al.,* 2023). This has resulted in local extinctions of lions in Comoé National Park (Côte d'Ivoire), where, following the civil war in 2002, the park was abandoned, resulting in all the intensification of existing threats, causing the demise of many species within Comoé (Aglissi *et al.,* 2023). This is an incredibly challenging threat to mitigate, and requires large-scale intervention from international stakeholders, not just from within country (Lhoest *et al.,* 2022).

Where management has sufficient resources to protect and conserve lions, the perceived threats to them was lower and where resources are limited, lions possibly experience more negative human pressures and as a direct consequence, have decreasing numbers (Lindsey *et al.,* 2017). Where area management is considered to be poor, or funding is insufficient, it exacerbates existing threats and pressures (Lindsey *et al.,* 2017; Bauer *et al.,* 2020). Resources for conservation and protected area management are unevenly distributed across conservation areas (Lindsey *et al.,* 2017). The lack of, or inconsistent, funding for area operations was perceived to be the most severe threat at a continent level, and for both southern and East Africa at a regional level. The challenge of insufficient, or a lack of consistent, funding is widespread (Lindsey *et al.,* 2018; Bauer *et al.,* 2020; Nicholson *et al.,* 2023b). Protected areas with lions collectively require between USD 1.2 to USD 2.4 billion annually, but Lindsey *et al.,* (2018) calculated that these areas only receive USD 381 million per annum. Between 88 % and 94 % of protected areas with lions are insufficiently funded (Lindsey *et al.,* 2018). Nicholson *et al.,* (2023b) estimated that to adequately safeguard all areas with lions, approximately USD 3 billion would be required annually. Generating greater investment for areas with lions would not only increase the conservation success for lions, but would have far reaching benefits including social, economic and ecological benefits (Lindsey *et al.,* 2018; Nicholson *et al.,* 2023b). Areas that are well funded and have sufficient resources (e.g., vehicles, anti-poaching equipment, staff) are able to reduce the impact of threats, thereby protecting wildlife populations (Bauer *et al.,* 2020). One caveat to note in our study regarding the level of resources available is that we reported on perceptions. Most surveyed subpopulations were perceived to be under-resourced, but it must be noted that the measures respondents used to define sufficient resources was based purely on their own opinion. For example, our study highlighted many areas in Tanzania which were reported to have low resource availability, but up to date assessments, such as Lindsey *et al.,* (2018) are required to gain objective understanding of resourcing.

Data that are gathered through questionnaire type surveys may present several challenges. Firstly, responses gathered in this manner are often based on personal experiences, perceptions and opinions rather than quantitative data (Stantcheva, 2023). Respondents may be influenced by personal biases, social desirability, or lack of expertise, leading to inaccuracies in their responses (Bergen & Labonté, 2020; Stantcheva, 2023). However, caution was taken in the interpretation of the data and we have indicated in our aims and throughout the paper that this study presents perceptions of the reality from experts we surveyed. Importantly, responses were calibrated by having the same metric of severity across respondents, who are likely to have access to the most up-to-date information on the sampled sites. To date, most studies that assess threats are subpopulation specific (Hazzah *et al.,* 2009; Rosenblatt *et al.,* 2014; Ogutu *et al.,* 2016; Everatt *et al.,* 2019; Aebischer *et al.,* 2020) and we present the first continental overview of threats facing Africa's lions; we see the comparison across subpopulations not as a weakness but as a strength.

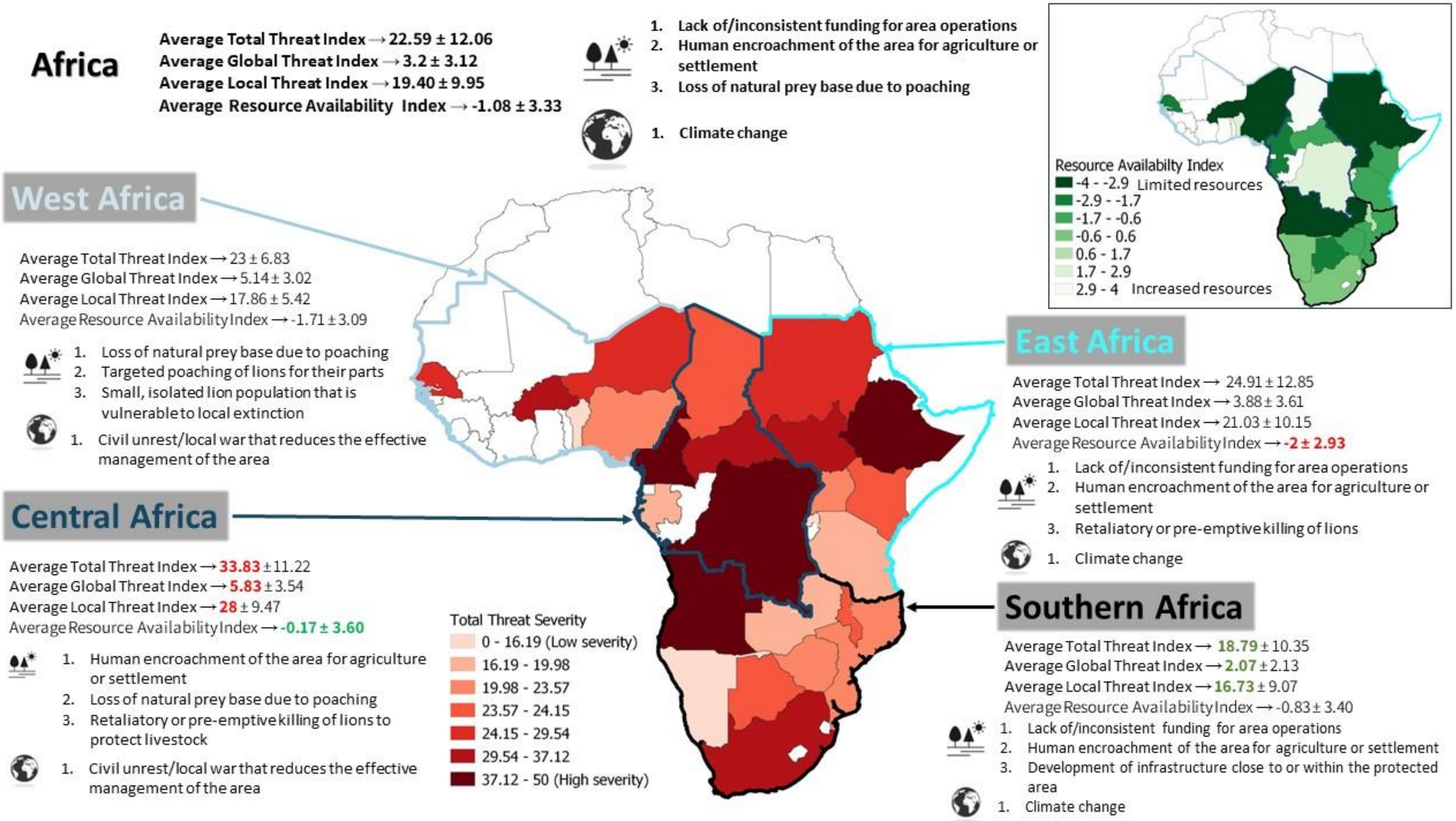

Figure 5-7. Summary of the total, global and local indices for Africa as a whole, and each region individually. Central Africa had the highest perceived severity of global and local threats and therefore had the highest threat index. Southern Africa had the lowest perceived threat scores of all four regions. The average Total Threat Index per country is illustrated in the centre map with darker shades of red illustrating higher threat indices. The Resource Availability Index (RSI) per region is also given for Africa and per region, and the average per country is shown in the top right inset map. The three most severe landscape level local threats (shown by the landscape icon) are shown per region and for Africa as well as the highest perceived global threat (in this case – continental, illustrated by the global icon).

5.6 Conclusions

We provide preliminary insight into the threats experienced across lion subpopulations in Africa, and how these differ across regions. We highlight the complex dynamics affecting lion subpopulations in Africa, emphasising the importance of considering regional and local contexts in conservation efforts. We have provided insights into the perceived severity of these threats for a large subset of Africa's lion subpopulations, and we recommend that this work be developed further using more robust measures of severity and impact. The assessment of these threats should be integrated into regional conservation strategies, and we recommend that these be updated, as they were last done in 2006 (IUCN, 2006b, 2006a; Nowell *et al.,* 2006). In addition, very few mitigation and conservation strategies include aspects of climate change, and we recommend that measures such as habitat restoration and climate change adaptation initiatives be considered and included to enhance the resilience of lion subpopulations. In conclusion, this research provides a nuanced understanding of the current state of lion subpopulations in Africa, shedding light on their geographical distribution, perceived trends, and the multifaceted threats they face. The regional disparities in responses underscore the importance of considering diverse ecosystems and conservation challenges across the continent. Our findings emphasise the need for tailored conservation strategies, recognising the unique challenges faced by different regions.

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5.8 Supplementary material

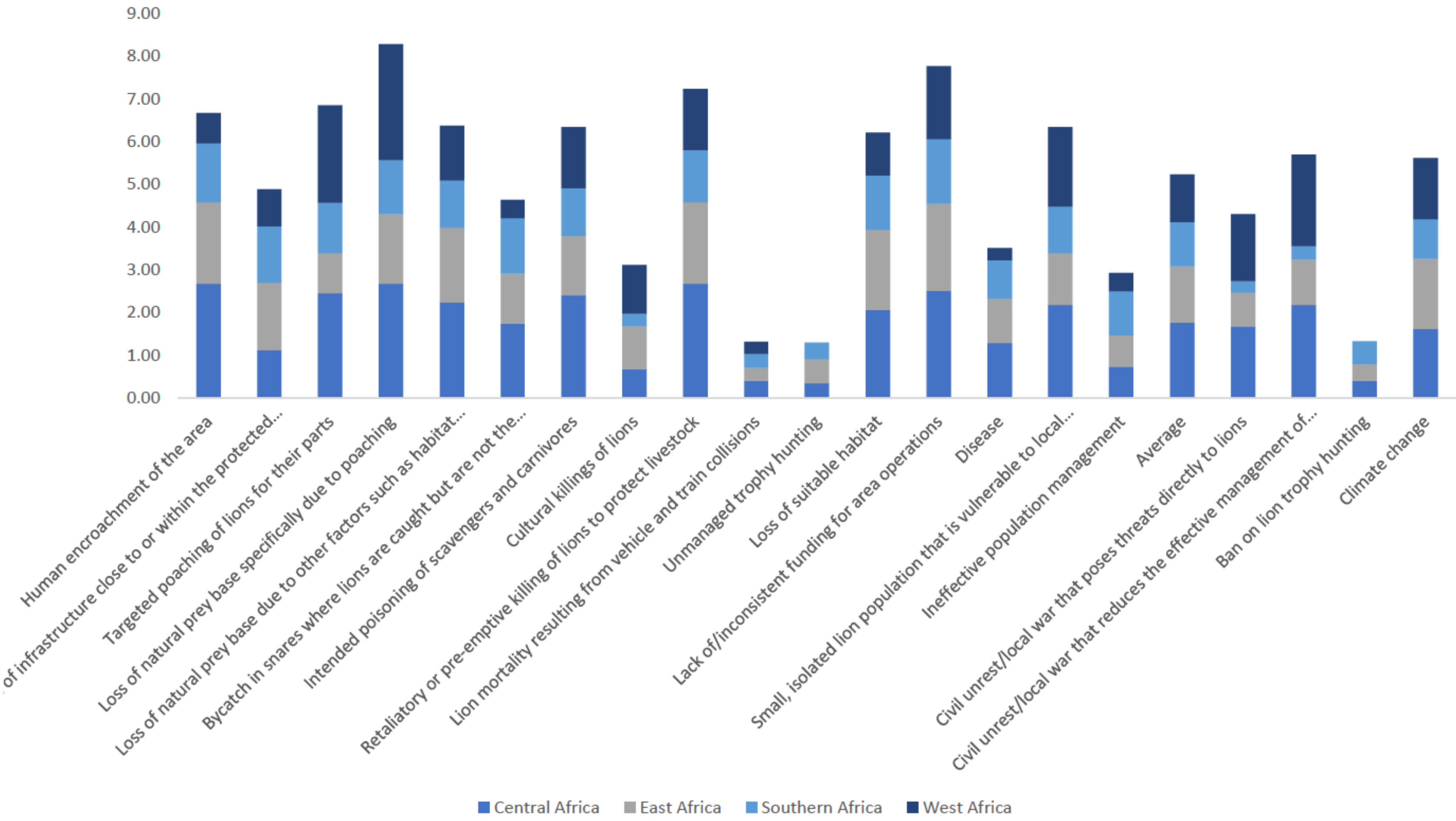
Supplementary Table 5-1. Summary of the variables that were found to significantly influence the threat indices.

VARIABLE	LOCAL	GLOBAL	OVERALL
Region	Yes	Yes	Yes
Country	Yes	Yes	Yes
Populations	No	No	No
Authority	No	No	No
Formal protection	No	No	No
Fencing	Yes	No	Yes
Communities presently living within the area	Yes	No	Yes
Livestock grazing within the area	Yes	Yes	Yes
Livestock competition with wildlife	Yes	Yes	Yes
People's attitude towards wildlife	No	No	No
Routine patrols conducted	No	No	No
Community engagement	Yes	No	Yes
Livestock barriers	No	No	No
Sufficient park resources	Yes	Yes	Yes

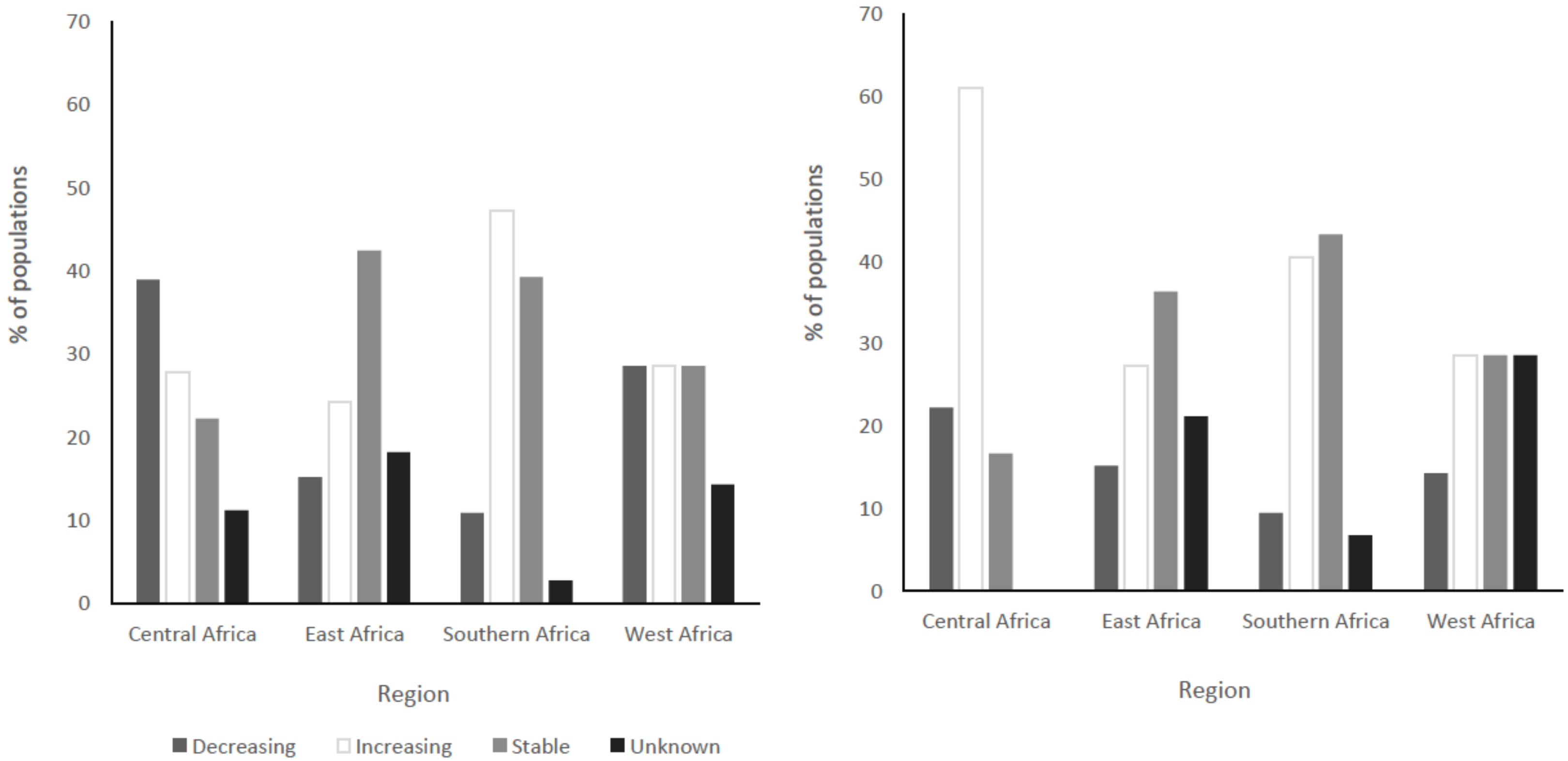
Supplementary Table 5-2. Summary of the number of subpopulations within each severity category for the local and global threat indices.

LOCAL SEVERITY						GLOBAL SEVERITY				
	Low local severity	**Medium local severity**	**High local severity**	**Total**			**No global severity**	**Low global severity**	**Medium global severity**	**High global severity**
Central Africa	**1 (5.55%)**	**6 (33.33%)**	**11 (61.11%)**	**18**		**Central Africa**	**1 (5.56%)**	**2 (11.11%)**	**6 (33.3%)**	**9 (50%)**
Cameroon			5 (100%)	5		Cameroon		1 (20%)	2 (40%)	2 (40%)
Central African Republic		4 (66.67%)	2 (33.33%)	6		Central African Republic			3 (50%)	3 (50%)
Chad	1 (33.33%)	1 (33.33%)	1 (33.33%)	3		Chad		1 (33.33%)	1 (33.3%)	1 (33.3%)
Democratic Republic of Congo			3 (100%)	3		Democratic Republic of Congo				3 (100%)
Gabon		1 (100%)		1		Gabon	1 (100%)			
East Africa	**4 (12.12%)**	**23 (69.69%)**	**6 (18.18%)**	**33**		**East Africa**	**5 (15.15%)**	**8 (24.24%)**	**11 (33.3%)**	**9 (27.3%)**
Ethiopia		2 (33.33%)	4 (66.67%)	6		Ethiopia			2 (33.3%)	4 (66.6%)
Kenya	1 (11.11%)	7 (77.78%)	1 (11.11%)	9		Kenya	2 (22.22%)	2 (22.22%)	3 (33.3%)	2 (22.22%)
Rwanda		1 (100%)		1		Rwanda		1 (100%)		
South Sudan		2 (100%)		2		South Sudan				2 (100%)
Sudan		1 (100%)		1		Sudan			1 (100%)	
Tanzania	3 (25%)	8 (66.67%)	1 (8.33%)	12		Tanzania	3 (25%)	5 (41.67%)	3 (25%)	1 (8.33%)
Uganda		2 (100%)		2		Uganda			2 (100%)	
Southern Africa	**18 (24.32%)**	**51 (68.92%)**	**5 (6.75%)**	**74**		**Southern Africa**	**15 (20.27%)**	**21 (28.38%)**	**34 (45.9%)**	**4 (5.41%)**
Angola			1 (100%)	1		Angola				1 (100%)
Botswana		8 (100%)		8		Botswana		1 (12.5%)	7 (87.5%)	
Malawi		4 (100%)		4		Malawi	1 (25%)	2 (50%)	1 (25%)	
Mozambique	1 (7.80%)	10 (76.92%)	2 (15.38%)	13		Mozambique	5 (38.46%)	2 (15.38%)	5 (38.5%)	1 (7.69%)
Namibia	2 (33.33%)	4 (66.67%)		6		Namibia	1 (16.67%)	3 (50%)	2 (33.3%)	
South Africa	11 (45.83%)	13 (54.17%)		24		South Africa	5 (20.83%)	5 (20.83%)	13 (54.2%)	1 (4.17%)
Zambia	1 (14.29%)	6 (85.71%)		7		Zambia		4 (57.14%)	3 (42.9%)	
Zimbabwe	3 (27.27%)	6 (54.54%)	2 (18.18%)	11		Zimbabwe	3 (27.27%)	4 (36.36%)	3 (27.3%)	1 (9.09%)
West Africa	**1 (14.2%)**	**6 (85.71%)**		**7**		**West Africa**			**5 (71.4%)**	**2 (28.57%)**
Benin	1 (50%)	1 (50%)		2		Benin			2 (100%)	

Burkina Faso		1 (100%)		1		Burkina Faso				1 (100%)
Niger		1 (100%)		1		Niger				1 (100%)
Nigeria		2 (100%)		2		Nigeria			2 (100%)	
Senegal		1 (100%)		1		Senegal			1 (100%)	
Grand Total	**24 (18.18%)**	**86 (65.15%)**	**22 (16.67%)**	**132**		**Grand Total**	**21 (100%)**	**31 (100%)**	**56 (100%)**	**24 (100%)**



Supplementary Figure 5-1. Graphical representation of the average severity score of each of the local and global threats and pressures for African and each region.



Supplementary Figure 5-2. Population trends of lions in in the last five years (left) and the next five years (right) according to survey responders.

CHAPTER 6

Synthesis, conclusions and recommendations

6.1 Background

The lion is one of the world's most iconic carnivore species, but like many carnivores (Fernández-Sepúlveda & Martín, 2022), its populations are dwindling, and globally, it is threatened with extinction (Nicholson *et al.,* 2023a). The purpose of this PhD study was to critically assess the conservation status of lion populations in Africa. This critical assessment included a review of current survey methodologies for lions (Chapter 2), assessed their conservation status according to the IUCN Red List of Threatened Species (Chapter 3), determined the fragility (defined as a species' vulnerability to extinction, Nilsson & Grelsson, 1995) of subpopulations (Chapter 4), and evaluated perceived threats to the species across its African range (Chapter 5). In this final chapter, I synthesise my key findings and explore their broader implications in an era of unprecedented biodiversity loss and intense anthropogenic pressures (Craigie *et al.,* 2010; Pimm *et al.,* 2014; Nazarevich, 2015; Durant *et al.,* 2017; Cowie *et al.,* 2022; Rull, 2022). While these studies were focused on lion, they also apply to conservation and monitoring of other large carnivores. Furthermore, since lions are an umbrella species (Macdonald *et al.,* 2015; Trouwborst *et al.,* 2017), conservation action targeted at them will have benefits to other species and their ecosystems.

In this chapter I provide: (1) a summary of key findings, (2), possible linkages between socio-political and ecological fragility (i.e. their vulnerability to extinction) and perceived anthropogenic threat severity, (3) the importance of these findings, (4) opportunities for further research and, (5) provide recommendations for both policy, decision-makers and practitioners.

6.2 Summary of key findings

Chapter two: The state of current survey methodology for lions

Understanding and monitoring the trends and changes in the population status of a species is a fundamental part of their conservation (Braczkowski *et al.,* 2020a). By conducting a systematic literature review, I assessed the various methods used for surveying lions in the past two decades. These methods included direct observations using individual identification with (Rosenblatt *et al.,* 2014; Beukes *et al.,* 2017) and without (Kissui & Packer, 2004; Bouley *et al.,* 2018) capture-recapture, genetics-based surveys (Tende *et al.,* 2010), spoor counts (also called spoor transects or track counts) (Bauer *et al.,* 2014; Henschel *et al.,* 2010; Stander, 1998), call-up surveys (Ogutu & Dublin, 2002; Mohammed *et al.,* 2019), and camera trap studies with capture-recapture analysis (Kane *et al.,* 2015;

Elliot & Gopalaswamy, 2017; Strampelli *et al.,* 2022; Western *et al.,* 2022). Each method has its own strengths and weaknesses, and it was evident that not all are suited for density or population size estimation, for example, index-based surveys (see: Belant *et al.,* 2019; Dröge *et al.,* 2020). In this chapter, I emphasised the urgent need to create harmonised methods and guidelines to survey lions and other large African carnivores. I provided a recommendation on how this could be done to guide researchers and managers in identifying the most suitable method to survey carnivores based on their research question and their resources available.

Chapter three: Conservation status of lions

This chapter focused on the IUCN Red List assessment (RLA) of lions, which was published recently (Nicholson *et al.,* 2023a). There is a long history of studies aiming to estimate lion populations in Africa, starting in 1975 (Myers, 1975) and continuing through to the present day (Bauer *et al.,* 2015, 2018; Chardonnet, 2002; Nicholson *et al.,* 2023; Riggio *et al.,* 2013). The 2015 RLA for lions was based on a trend analysis using data from a sample of monitored populations (Bauer *et al.,* 2016). However, because of challenges related to the quality and comparability of lion population estimates at a continental scale for many populations, the current RLA could not be based on actual population decline (Nicholson *et al.,* 2023a). Therefore, the assessment team used range decline as a proxy for which to infer population decline (Nicholson *et al.,* 2023a). This method has been used by various other studies (e.g., Ripple *et al.,* 2014; Wolf & Ripple, 2017). Along with my co-assessors, I concluded that lions have experienced a 36 % decline in range in the past 21 years (three lion generations), and therefore a similar decline in population is suspected. In the RLA, we estimated that extant lion range in 2023 was ~1,571,296 km^2, which is only 6 % of its historical range (Nicholson *et al.,* 2023a). This is an estimated 36 % range decline since 2002 (three lion generations), where lion range was estimated to be 2,460,986 km^2 (Nicholson *et al.,* 2023a). Based on this significant decline in range, which is synonymous with a decline in population size, a 36 % decline in population was suspected. Therefore, lions met the requirements for a Vulnerable listing (Red List criteria A2abcd).

Chapter four: Fragility of Africa's lion populations

This chapter (Nicholson *et al.,* 2023b), was aimed at assessing the fragility of known lion populations. Along with my co-authors, I used a novel approach combining socio-political (e.g., political stability, human development index, human population growth rate) and ecological variables (e.g., population isolation, population size as a percentage of predicted carrying capacity, geographic area) to determine the fragility of lion populations in Africa (Nicholson *et al.,* 2023b). I found that factors behind their declines could be either ecological or socio-political and, when used together, provide a more holistic approach to identifying threatened populations and their drivers. Based on these results, targeted mitigation for populations would vary and needs to be carefully considered, as solutions for one population may not be suited for another (Bauer *et al.,* 2020; Di Minin *et al.,* 2021). When socio-political and ecological fragility were combined, lion populations in Maze National Park and Bush-Bush (Somalia) were the most fragile while Kalahari-Gemsbok (South Africa) and Etosha-Kunene (Botswana) the least. At a country level, this chapter revealed that lion populations in Cameroon and Malawi had the highest ecological fragility, whereas those in Somalia, followed by those in South Sudan, were the most socio-politically fragile. When ecological and socio-fragility were combined, Somalia was the most fragile and Botswana the least. The results of this study indicated the importance of considering factors relating to governance, economics and policy when determining the fragility of wildlife populations (Dickman *et al.,* 2015; Kuiper *et al.,* 2018; Nicholson *et al.,* 2023b). For example, while one population may not appear to be fragile when only considering ecological variables, its fragility may be far greater when socio-political variables are considered.

Chapter five: Anthropogenic threats to lions, resource allocation and regional comparisons

In this chapter, I broadly aimed to determine which threats are perceived to be most severe for lions across their range, and assessed how these differ at a continental, regional, national and subpopulation level. Data were gathered through a structured questionnaire survey of 132 lion populations. To quantify and compare the severity of threats and pressures, three "severity indices" were developed (global, local and total, the latter resulting from summing the global and local indices) using the perceived severity rating of these threats by survey participants. Based on our results, we were able to determine that threat severity and anthropogenic threats differed across regions. The Total Threat Index (TTI) differed significantly among regions, being highest (i.e., most severe) in Central Africa and lowest (i.e., least severe) in Southern Africa. Significant differences in the TTI were related to geographic variables (region and country), sociological variables (communities living within the lion habitat, livestock grazing within the area, livestock competition with wildlife) and mitigation related variables (the level of fencing, community engagement and sufficient park resources). Angola, the Democratic Republic of the Congo, Cameroon and Ethiopia had the highest perceived threat severity, while Rwanda, South Africa and Namibia had the lowest threat severity. Local threats in East Africa were mainly identified as a lack of funding, human encroachment, and retaliatory or pre-emptive killings. Central Africa's most severe local threats included human encroachment, loss of prey base from poaching, and retaliatory killings. In West Africa, the most severe local threats to lions were the loss of natural prey base due to poaching, targeted poaching of lions for parts, and small, isolated populations, with civil unrest and local war being perceived to be the most severe global threat to lions in the region. In Southern Africa, climate change was identified as the most severe global threat while the most severe local threats included a lack of funding, human encroachment, and development of infrastructure adjacent or within lion habitats. Across regions, the most severe local threats included inadequate funding, human encroachment, and loss of natural prey. Climate change was identified as the most severe global threat to lion populations.

I also assessed the perceived resource availability to reduce the illegal killing of lions. Perceived resource availability was highest in Rwanda, Chad and Benin and lowest in six countries including Angola, Burkina Faso, Niger, South Sudan, Sudan and Uganda. My study indicated that resource allocation was perceived to be insufficient across populations. This supports the findings of other studies such as Lindsey *et al.,* (2018), where most protected areas with lions were found to be insufficiently funded.

6.3 Exploring potential links between fragility and threat severity

To understand the larger threat landscape of lions in Africa, I created a bubble graph to visually depict the socio-political and ecological fragility of lion populations (see Chapter four and Nicholson *et al.,* 2023b) in relation to the severity of anthropogenic threats (the Total Threat Index – see Chapter five). This was done to identify relationships between fragility and threat severity and to gain further insight into threats to lions in Africa. I was only able to do this for 39 lion populations in Africa where individual lion populations were regarded as the same in both studies. For example, Selous was defined as one population in the same way for both threat and fragility studies but in Chapter 4, Gorongosa, Coutada 10 and 11 were considered as one population and assessed as such, but in Chapter 5, these populations were separated (resulting in three individual threat index values). While this is a reduced sample, it is still representative of populations across all four African regions.

For this comparison, I created four categories of overall fragility as depicted on Figure 6.1: A) socio-politically fragile and ecologically acceptable, B) socio-politically and ecologically fragile, C) socio-politically acceptable and ecologically fragile, and D) socio-politically and ecologically acceptable. For the purpose of this assessment, populations were defined as fragile when they scored one standard deviation above the mean and acceptable when they scored one standard deviation below. In this case, acceptable does not indicate a lack of fragility but rather, when compared with other populations, it is less fragile. It must be noted that while not all populations are included in this assessment, it does not mean they are not fragile or don't experience anthropogenic threats. What is presented here is a preliminary assessment into the potential trends and relationship between socio-politically and ecological fragility and threat severity. There is value in exploring this relationship with a larger sample of populations.

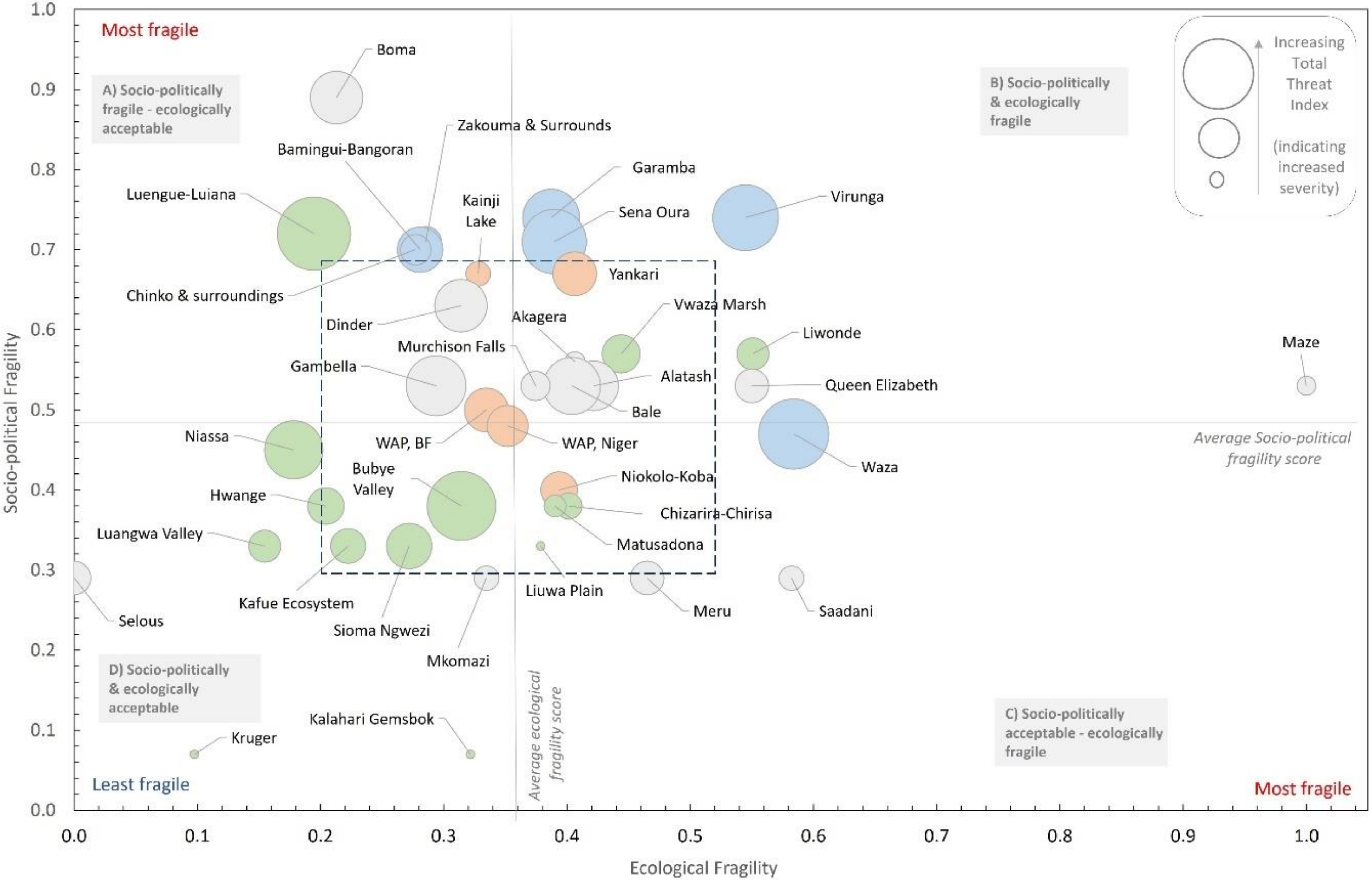
An ideal state for populations is where they are considered both socio-politically and ecologically acceptable and when anthropogenic pressures are less severe or limited. Here, populations are predicted to have a lower likelihood of experiencing population declines, and are at a low risk of localised extinction. Eleven populations (28.2 %) were socio-politically and ecologically acceptable but only four of those are considered to have low threat severity (Figure 6.1). This was found to be the case with Kruger National Park and Kalahari-Gemsbok (both in South Africa), and, to some extent, Mkomazi (Tanzania) and Luangwa Valley (Zambia).

Populations in Southern Africa have similar ecological and socio-political fragility as well as threat severity (Figure 6.1), with most populations (57.1 %, n = 14 were considered socio-politically and ecologically acceptable). This regional observation and difference in status has been observed in several other studies (see: Bauer *et al.,* 2015). Central African populations are of particular concern. All seven populations score one standard deviation above the mean for either socio-political or ecological fragility with three populations (43 %) being both socio-politically and ecologically fragile (Figure 6.1). Each population has high threat severity, especially Waza (Cameroon), Sena Oura (Chad) and Virunga and Garamba (Democratic Republic of the Congo). These populations are likely at much greater risk of significant population declines than most others. East African populations predominantly scored around the mean for their fragility scores, with Saadani (Tanzania), Maze (Ethiopia), Queen Elizabeth (Uganda) and Boma (South Sudan) being the most fragile. Boma (Soth Sudan), Dinder (Sudan), Gambella (Ethiopia), Bale (Ethiopia) and Alatash (Ethiopia) all face high threat severities. Populations in West Africa all fall around the mean for fragility and have medium threat severity, meaning there are some anthropogenic threats for each population.

By assessing the fragility of populations combined with the level of severity of anthropogenic threats they are perceived to experience, I can identify multiple populations of particular concern. Populations that are expected to have increased risk of extinction, or significant population declines, are those that are highly socio-politically or ecologically fragile and also have high threat severity. . When already fragile, these additional pressures could push populations to a higher overall fragility. For example, a population that is already fragile and experiences high severity of anthropogenic threats (such as poaching and conflict), would experience population size reduction and ultimately increase its' ecological fragility – increasing the population's overall fragility and, therefore, threat of extinction. These populations include: Luengue-Luiana (high socio-political fragility and the highest threat severity), Virunga (high socio-political and ecological fragility and high threat severity), Waza (high ecological fragility and high threat severity), Sena Oura and Garamba (both high socio-political fragility and threat severity), and Boma (the highest socio-political fragility and high threat severity).

This emphasises the need to understand all possible drivers of pressures and threats on a population to design and implement conservation action that addresses the root causes of population declines (Everatt *et al.,* 2014; Bauer *et al.,* 2020). These may be socio-political or ecological influences or direct anthropogenic threats. For example, Maze (Ethiopia), has high ecological fragility, but a relatively low threat index. If funding is focused on addressing anthropogenic threats only, one might not see as positive results on the population itself as one would hope. However, if conservation action addresses the ecological drivers of fragility (since Maze is ecologically fragile), combined with mitigating anthropogenic threats, there may likely be a more impactful conservation outcome.

Understanding why some species are fragile within their range and others are not, is fundamental conservation science that is impactful and beneficial to species conservation (Cardillo *et al.,* 2004). Carnivores are especially vulnerable to extinctions and their fragility, or extinction risk, can be driven by a series of factors: biological traits (such as life history traits (Forero-Medina *et al.,* 2009; Obbard *et al.,* 2010)), and exposure to anthropogenic threats (Cardillo *et al.,* 2004; Bauer *et al.,* 2020). Driving those threats, and influencing the effectiveness of the conservation action, is the socio-political landscape (Dickman *et al.,* 2015; Kuiper *et al.,* 2018; Nicholson *et al.,* 2023b). According to a study by Cardillo *et al.,* (2004), the understanding of relative and interacting effects of both biological traits (which in their study included range size and population density, which I considered as ecological factors within this study) and anthropogenic threats on a species' fragility is limited. Gaining a better understanding of these factors will aid in more effective conservation. (Obbard *et al.,* 2010; Nicholson *et al.,* 2023b). Additionally, considering socio-political factors is essential as these elements influence the implementation and success of conservation measures, shaping the overall effectiveness of conservation initiatives (Dickman *et al.,* 2015). (Dickman *et al.,* 2015; Bauer *et al.,* 2020).



Most fragile
Boma
A) Socio-politically fragile - ecologically acceptable
Zakouma & Surrounds
Bamingui-Bangoran
Garamba
Luengue-Luiana
Kainji Lake
Sena Oura
Virunga
B) Socio-politically & ecologically fragile
Increasing Total Threat Index
(indicating increased severity)
Yankari
Chinko & surroundings
Vwaza Marsh
Dinder
Akagera
Liwonde
Maze
Murchison Falls
Gambella
Alatash
Queen Elizabeth
Bale
Niassa
WAP, BF
WAP, Niger
Average Socio-political fragility score
Waza
Bubye Valley
Niokolo-Koba
Hwange
Chizarira-Chirisa
Matusadona
Luangwa Valley
Liuwa Plain
Kafue Ecosystem
Meru
Saadani
Selous
Sioma Ngwezi
Mkomazi
D) Socio-politically & ecologically acceptable
Average ecological fragility score
Kalahari Gemsbok
C) Socio-politically acceptable - ecologically fragile
Kruger
Least fragile
Most fragile
Socio-political Fragility
Ecological Fragility
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure 6-1. A preliminary assessment of the fragility and threat severity of a sample of the surveyed populations. The socio-political and ecological fragility (Chapter 4, Nicholson *et al.,* 2023b) scores of 39 lion populations in Africa symbolised using the total threat index (TTI, Chapter 5). The TTI is depicted as bubbles for each population; where bigger bubbles denote higher threat severity (and therefore higher TTI values) and smaller bubbles denotes less threat severity. The fragility scores (score between 0 to 1) indicate how fragile a population is to extinction based on socio-political variables (e.g., human population growth, government effectiveness, political stability) and ecological ones (e.g., population isolation, cattle density, geographic area). The TTI was devised as a means by which to measure the severity of a combination of local (e.g., poaching, habitat loss) and global (e.g., warfare, climate change) threats to lions. The colour of the bubbles depicts the regions, orange for West Africa, blue for Central Africa, grey for East Africa and green for Southern Africa. The dotted grid delineates those populations that fall within one standard deviation above and below the mean for both ecological and socio-political fragility.

6.4 Importance of the results of this study and their role in understanding current and guiding future lion conservation and management

Challenges with existing data and the gold standard for future data

The challenge with existing data is that it has often not been collected in a way that allows reliable interpretation of the population size and trend. This is the case with many lion populations in Africa. This is especially true in Central and West Africa where the few completed population surveys have been done with methods unreliable for determining abundance (Belant *et al.,* 2019; Dröge *et al.,* 2020). As not all surveys use appropriate methodologies, assessing trends becomes more challenging (Elliot & Gopalaswamy, 2017). A further challenge is that survey results are often only published several years after survey work has been completed (see Chapter 2). This poses a challenge as decisions are generally made with available (published) information and this information is likely outdated by the time it is published. This results in conservation action or management decisions being made with information that may no longer be relevant. For example, cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*) were surveyed in Kruger National Park in 2009 but survey results were only published in 2014 (Marnewick *et al.,* 2014). Another example is of leopards (*Panthera pardus*) surveyed in 2012 in the Serengeti but the results were only published in 2020 (Maximillion *et al.,* 2020) or spotted hyena (*Crocuta crocuta*) in Nechisar National Park (Ethiopia) that were surveyed in 2009 but published in 2014 (Yirga *et al.,* 2014). Another challenge when assessing trends is that survey methods often change from one survey period to another. For example, lions in Queen Elizabeth National Park (Uganda) were surveyed using call up surveys in 2009, estimating 140 lions (Omoya *et al.,* 2014) and were surveyed again in 2018 using a random-search encounter and individual identification approach, which estimated 71 lions (Braczkowski *et al.,* 2020b). While these population estimates suggest a decline, it is important to note that each method has varying measures of reliability and accuracy (Elliot & Gopalaswamy, 2017; Braczkowski *et al.,* 2020b).

Population numbers are a fundamental cornerstone in understanding a population and are used to guide their conservation status (Bauer *et al.,* 2016; Braczkowski *et al.,* 2020; Nicholson *et al.,* 2023), quota setting for hunting and non-detriment findings (Edwards *et al.,* 2014), and priority setting for funding and conservation action (Bottrill *et al.,* 2008), among other things. For these to be done effectively and ensure positive and impactful conservation, population size estimates need to be reliable and robust (Braczkowski *et al.,* 2020b). The current challenges in existing lion surveys and the resulting population estimates emphasise the urgent need to develop harmonised methods for surveying lions that will contribute to more reliable and robust species level assessments, such as the RLA, and the IUCN Green Status of species (which is a standardised framework for measuring threatened species recovery (Akçakaya *et al.,* 2018)). Reliable population estimates that allow comparison across time and space are fundamental to species conservation. This focus on numbers and range is essential, and, when conducted in a robust, repeatable way, provides valuable insights into lion trends and threats. New and innovative methodologies for surveying large carnivores (Elliot & Gopalaswamy, 2017; Braczkowski *et al.,* 2020b; Strampelli *et al.,* 2022; Western *et al.,* 2022) bring optimism that determining reliable trends in lion populations will become possible in future, allowing for more robust and reliable RLAs. I recommend that harmonised methods and guidelines be developed to ensure these methods are implemented in a reliable manner (Chapter 2) and results made publicly available for them to be incorporated into conservation planning and species assessments.

Urgent need and prioritisation of funding conservation in Africa

In Chapter 5, I demonstrated that the conservation and management of most of Africa's lion populations are perceived to be insufficiently funded or equipped to prevent the illegal killing of lions and other wildlife. To effectively conserve lion populations in Africa, it is estimated that more than USD 3 billion per year is required (Chapter 4; Nicholson *et al.,* 2023b).

When examining the Global Multidimensional Poverty Index (Alkire *et al.,* 2019), almost all lion range countries in Africa were ranked among those with highest poverty (the top 50 %), with nearly three-quarters in the top 25 % (Nicholson *et al.,* 2023b). Effective conservation interventions can be costly investments, and poor countries will not be able to cover these without the support of the international community (Alkire *et al.,* 2019; Nicholson *et al.,* 2023b). It is often expensive and economically unsustainable to expect such countries to meet the minimum funding needs to effectively conserve lion (and other wildlife) populations in Africa on their own (Nicholson *et al.,* 2023b). This burden cannot be held by Africa alone, and funding assistance and contributions to conserve lions is urgently needed. As the lion is an apex predator, successful lion populations are an indicator of functional ecosystems (Aebischer *et al.,* 2020; Everatt *et al.,* 2015). Consequently, this financial aid would also benefit the restoration of other species and entire landscapes, with resulting ecosystem services and other planetary health benefits for human beings (Everatt *et al.,* 2015; Lindsey *et al.,* 2018). This aligns with the Global Biodiversity Framework's which calls for 30 % of the world's terrestrial, inland water, and coastal and marine areas to be in effective protection and management by 2030 (CBD, 2023). It is also encompassed in the Sustainable Development Goal 15, which is "Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss" (The Global Goals. 2023). While USD 3 billion certainly seems a large amount, it truly pales in comparison when examining other, potentially less important, expenditures, such as forecast digital ad spending worldwide (USD 601.84 billion in 2023, up 9.5% from USD 549.51 billion in 2022) (Lebow, 2023). Another example is the substantial revenue generated by the global sports industry through various channels, including broadcasting, merchandise, and ticket sales. In 2023, the global sports market was estimated to be worth around USD 512.14 billion in 2023 (The Business Report Company, 2023), which is more than 170 times the estimated lion conservation costs. Funding for conservation is limited and insufficient to meet the world's conservation needs (Murdoch *et al.,* 2007). This requires that those resources are used effectively and where they are most impactful or have the highest return-on-investment (ROI) (Murdoch *et al.,* 2007; Evans *et al.,* 2011; Tear *et al.,* 2014; Kuiper *et al.,* 2018). Various types of prioritisation approaches can be used to increase the effective ROI for conservation interventions (Evans *et al.,* 2011; Di Minin *et al.,* 2021). When conservation funds are prioritised effectively, the benefits can be far-reaching. Prioritising of conservation funds to maximise ROIs can be through focusing on habitats or important ecoregions (Tear *et al.,* 2014), targeting specific threats or species (Di Minin *et al.,* 2021), endangered species (Valenzuela-Galván *et al.,* 2008), or through focused conservation actions (Tear *et al.,* 2014). One such example where a targeted conservation intervention had high ROI through social and environmental benefits was demonstrated by Di Minin *et al.,* (2021). They demonstrated that fencing was a cost-effective strategy to reduce human-wildlife conflict in countries where this threat was relatively severe. As a result, strategic fencing would not only prevent lion and elephant (*Loxodonta africana*) population declines, but could also provide benefits to people through community support and providing protection from wildlife (Di Minin *et al.,* 2021).

Influencing policy and conservation

IUCN RLAs are an important tool used by international conventions, researchers, decision-makers and policymakers regarding the conservation of lions (Chapter 3; Rodrigues *et al.,* 2006; Maes *et al.,* 2015; Kratschmer *et al.,* 2021; van Huynh, 2023). The previous RLA for lions was last published in 2016 (Bauer *et al.,* 2016) and required updating. Using the best available information for the species, I undertook to update the global assessment for the species and, based on this, the lion was listed as Vulnerable under criteria A2abcd (Nicholson *et al.,* 2023a). While this is not a change in their status, it still indicates that the conservation of the species has not improved since 1996 when the lion was first listed as Vulnerable (Nowell & Bauer, 2004).

The last lion regional conservation strategies were developed in 2006 (IUCN, 2006a, 2006b), and some threats and objectives outlined in these strategies are likely no longer relevant today. These strategies need to be updated considering the latest available information on lion populations, including their status (Nicholson *et al.,* 2023a), their socio-political and ecological fragility (Nicholson *et al.,* 2023b), the threats to them – both at a site and regional level (Bauer *et al.,* 2020), and updated policies and legal instruments such as the Joint Convention on International Trade in Endangered Species of Wild Fauna and Flora and Conventional on Migratory Species' African Carnivores Initiative (Hellinx, 2020). The implementation efficacy of these strategies through National Action Plans should be assessed and lessons learnt should be considered and integrated into the updated strategies.

Across their range, the status of lions differs (Bauer *et al.,* 2015, 2018; Nicholson *et al.,* 2023a). Lions in West Africa are listed as Regionally Critically Endangered (Henschel *et al.,* 2014, 2015). (Miller *et al.,* 2016)(Miller *et al.,* 2016)India's population of lions is listed as Regionally Endangered because of its small population size and area of occupancy (Breitenmoser *et al.,* 2008). National assessments have been completed for South Africa (Miller*et al.,* 2016), Namibia (Hanssen *et al.,* 2022), Kenya (KWS, 2022) and Uganda (WCS 2016). No other national assessments exist for the species. As lion populations in most of their range are vulnerable to some level of extinction and a range of anthropogenic threats (Bauer *et al.,* 2020), it is important that assessments be completed at regional levels where they are currently lacking, thus providing a more detailed understanding of the status of lions across their entire range.

A deeper and more nuanced understanding of complex threats to a species and the socio-political and ecological landscapes is required for their effective conservation

I present the first evaluation on the fragility of lions in Africa integrating both socio-political and ecological variables (Chapter 4), an approach that has not widely been done (see Dickman *et al.,* 2015; Kuiper *et al.,* 2018). By assessing the socio-political and ecological fragility of lion populations, I was able to demonstrate that a population's fragility may not always be driven by ecological factors but rather by socio-political ones (Nicholson *et al.,* 2023b). I also present an assessment of the threats impacting 132 lion subpopulations in Africa (Chapter 5). This research demonstrates the importance of understanding socio-political influences (such as governance, economics and policy), ecological variables (e.g., population isolation, small population size, fencing, area protection etc.) and anthropogenic threats (e.g., poaching, human-wildlife conflict, targeted poaching for parts etc) and how they need to be incorporated into mitigation and conservation strategies.

Together, these results allow for a clearer understanding of the drivers and causes of lion population declines and, therefore, how to implement targeted mitigation to effectively conserve lions. The importance of this approach becomes evident when assessing populations individually. For example, the results demonstrated that Yankari Game Reserve (Nigeria) experiences high socio-political fragility resulting from poor government effectiveness, high political instability, high corruption, conflict and high human population densities. This makes it far more socio-politically fragile than many other populations (Nicholson *et al.,* 2023b). A population such as this is likely to require greater financial investment to effectively manage it and governance-related issues (e.g., corruption, government effectiveness) need to be addressed (Nicholson *et al.,* 2023b). For example, political instability generally reduces the effectiveness of protected area management and diverts attention from conservation (Wright *et al.,* 2007). This can deter funders, researchers and conservation organisations from working in that country (Wright *et al.,* 2007). If the root causes contributing to increased socio-political fragility are not addressed, effective conservation is more challenging (Wright *et al.,* 2007; Irland, 2008; Nicholson *et al.,* 2023b). However, this does not mean that conservation efforts in areas like Yankari are less important but that when compared with other populations, a similar financial investment may not result in the same outcomes and different spending priorities might be needed. Funds may rather be allocated towards projects that address the socio-political landscape in these areas as opposed to addressing ecological issues.

By assessing both the socio-political and ecological landscapes, we demonstrate that resource allocation targeting one specific threat to a species might not necessarily be most suitable, but should potentially be broader socio-political or ecological focused interventions. If a triage approach to address species decline is going to be implemented (Bottrill *et al.,* 2008), it is essential to consider more than just anthropogenic threats. The solution is to implement an integrated approach that is strategic, evidence-based and tailored to the unique circumstances of each lion population, considering the specific anthropogenic threats, and socio-political and ecological factors that can influence each population. Funding for conservation is limited (Bottrill *et al.,* 2008; Hayward & Castley, 2018) and this understanding allows funds to be targeted to what will yield the biggest impact (Nicholson *et al.,* 2023b).

6.5 Opportunities for further research

Within each of my chapters, several opportunities for further research were identified. Below, I present a summary of the most urgent opportunities for research and the knowledge gaps that should be filled.

Chapter two:

- A cost benefit analysis comparing the different methods to survey lions should be undertaken, as it is lacking in the literature (but see Midlane *et al.,* 2015).

- Lion populations in East and Southern Africa have been surveyed more than those in Central or West Africa. Published lion surveys have not been done in Chad, Democratic Republic of the Congo (DRC), Malawi, Rwanda, Somalia and South Sudan. This includes large expanses of potential lion range in Chad, Democratic Republic of the Congo, and South Sudan, which have never been formally surveyed.
- The challenges around data reliability emphasises the need for harmonised survey methods that would ensure the reliability and comparability of survey results. This would allow population trends to be assessed more accurately (Elliot & Gopalaswamy, 2017; Braczkowski *et al.,* 2020a). To achieve this, I recommended that consensus surrounding more harmonised methods for surveying lions be developed. Aiding this would be a decision tool that must be developed to guide researchers and managers in selecting the most suitable method based on objectives and available resources.

Chapter three:

- Large areas, many of which are within lion population strongholds (Riggio *et al.,* 2013) are lacking reliable, up-to-date population estimates. Some areas still require surveys to confirm the presence or absence of lions. These are critical data gaps that should be completed before the next RLA to ensure the most reliable and accurate information is used.
- The Regional Red List for lions in West Africa was last published in 2015 (Henschel *et al.,* 2015) and requires updating.
- To date, a Green List assessment for the species, which assesses recovery (Akçakaya *et al.,* 2018), has not been completed. To understand the impact conservation has had on the species and identify areas of further needed recovery, it is recommended that a Green List assessment be completed for lions.

Chapter four:

- A novel approach to assess the fragility of lion populations was carried out. This approach has applicability for many other taxa, as remaining wildlife populations are also subject to increasing anthropogenic threats from both an ecological and socio-political perspective. It is recommended that this assessment be carried out for other African carnivores of concern, such as cheetah (*Acinonyx jubatus*), leopard, African wild dog (*Lycaon pictus*), Ethiopian wolf (*Canis simensis*) and potentially the hyena species. Furthermore, a comparison of these results across species would highlight whether fragility is site or species specific. Identifying populations where multiple species may be fragile will aid in conservation planning and prioritisation.

- Further studies are required to reveal what level of fragility is sustainable for populations across Africa. Currently, there is no basis to determine or measure this and a process to identify a threshold for acceptable (or non-detrimental) fragility needs to be done.

Chapter five:

- I presented the perceptions of one expert (manager or researcher) for each subpopulation regarding whether sufficient resources were available to effectively reduce illegal lion killings (Chapter 5). A more data driven assessment of resource allocation and availability should be explored, thus enabling the identification of lion populations that are under-resourced and require urgent funding.
- Assessing how resource allocation influences the perceived threat severity of a population should be explored.

Exploring the relationship between fragility and anthropogenic threat severity:

- In this chapter, I provide a preliminary assessment of the association between fragility and threat severity of lion populations. I suggest this the approach and methodology be developed further with a larger sample size.
- This is an important topic and would benefit from an increased understanding of why the threat severity is high or low relative to socio-political or ecological fragility.

6.6 Conclusions

The results of this thesis have offered insights into the current global status of lions, the threats they face in Africa, and I provided recommendations that could enhance the management and conservation of lions across their African range. I have highlighted the need for minimum standards for harmonised survey methods and emphasised the limitations of some older methods (predominantly index-based methods). Accurate data gathered with reliable survey methods are essential to generate RLAs that are a critical tool in policy and decision making for conservation of the species. Using a decline in range, and therefore population, along with my co-assessors, I updated the RLA for lions and found that while they have experienced population declines, those declines are insufficient for an Endangered listing and as such, lions remain as Vulnerable (under Criteria A2abcd).

Using the best available data, I identified populations that were more fragile to extinction than others and demonstrated that fragility can be driven by both socio-political and ecological factors. These factors are important to understand how to implement targeted conservation interventions that address the causes of population declines. Through a structured questionnaire survey, I was able to demonstrate that the anthropogenic threats to lions not only differed among populations, but also across regions, thereby supporting the need for robust regional strategies. I also identified priorities for the most urgent opportunities for addressing research and knowledge gaps to enable future status assessments and effective conservation of lion populations on the ground. The most critical being: a) develop harmonised methods to survey lions to gather more robust and reliable data to guide RLA and conservation planning, b) fill data gaps where survey data are lacking for lions in their African range, c) assess what levels of fragility are sustainable or acceptable and 4) analyse further the complex relationships between socio-political and ecological fragility and threat severity.

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