

Threat analysis for more effective lion conservation

HANS BAUER, AMY DICKMAN, GUILLAUME CHAPRON, ALAYNE ORIOL-COTTERILL
SAMANTHA K. NICHOLSON, CLAUDIO SILLERO-ZUBIRI, LUKE HUNTER
PETER LINDSEY and DAVID W. MACDONALD

Abstract We use comparable 2005 and 2018 population data to assess threats driving the decline of lion *Panthera leo* populations, and review information on threats structured by problem tree and root cause analysis. We define 11 threats and rank their severity and prevalence. Two threats emerged as affecting both the number of lion populations and numbers within them: livestock depredation leading to retaliatory killing of lions, and bushmeat poaching leading to prey depletion. Our data do not allow determination of whether any specific threat drives declines faster than others. Of 20 local extirpations, most were associated with armed conflicts as a driver of proximate threats. We discuss the prevalence and severity of proximate threats and their drivers, to identify priorities for more effective conservation of lions, other carnivores and their prey.

Keywords Africa, carnivore, conflict, lion, *Panthera leo*, problem tree, ranking, root cause

Supplementary material for this article is available at doi.org/10.1017/S0030605320000253

Introduction

The lion *Panthera leo* is categorized as Vulnerable on the IUCN Red List (Bauer et al., 2016); further declines are projected across Africa, except in the southernmost countries (South Africa, Zimbabwe, Botswana and Namibia), and India (Bauer et al., 2015). The threats that drive these declines are believed to be understood, even though their relative importance is debated and may vary spatially and temporally (Dickman et al., 2011; Packer et al., 2013; Lindsey et al., 2017). Surprisingly, we found no complete formal analysis of threats that included a description of causal relations (situation or problem tree analysis; IUCN, 2008), nor a formal ranking of threats. Tranquilli et al. (2014) ranked threats for protected areas in Africa generally, but did not include threats to wildlife outside protected areas, such as so-called human-wildlife conflict. Lindsey et al. (2017) used expert ratings of threats on a five-point Likert scale to derive a ranking that provided a useful overview of the geographies in which specific threats emerge, but the data were not designed to facilitate a comparison of the intensity of each threat among sites. Here we build on existing work to analyse lion population trends and to describe and rank threats. We discuss the implications of our work for priority setting in lion conservation.

In 2005, the Wildlife Conservation Society and the IUCN held a workshop with various stakeholders and experts who listed and ranked threats by lion population (Table 1). The threats were loosely defined but here we provide a formal description for each threat. Environmental problems can often be traced back to multiple causes along causal chains; on those chains are human activities that constitute threats (Callicott et al., 1999; Salafsky et al., 2002). Problems are best defined as human activities; by influencing these activities threats become greater or lesser. Human-lion conflict, prey depletion and habitat conversion have been cited as major threats to lions (e.g. Bauer et al., 2016), which is useful in a colloquial sense, but analytically these threats are effects of multiple human activities. For a logical framework of solutions to problems in lion conservation, we need an analytical framework identifying pathways from human activities to their effects on lion distribution and abundance. Here, we use problem tree and root cause analysis to provide such a framework.

Although we focus on lions, much of our analysis is relevant to other large carnivores but we lack similar data for such analyses. As the lion is an apex predator and its status is closely related to the status of its habitat and prey, the root cause analysis is informative for African ecosystems more generally.

HANS BAUER (Corresponding author, orcid.org/0000-0001-5031-5842), AMY DICKMAN (orcid.org/0000-0002-7879-415X), ALAYNE ORIOL-COTTERILL (orcid.org/0000-0003-0049-7988), CLAUDIO SILLERO-ZUBIRI (orcid.org/0000-0003-3867-5858) and DAVID W. MACDONALD (orcid.org/0000-0003-0607-9373) Department of Zoology, Wildlife Conservation Research Unit, University of Oxford, Recanati-Kaplan Centre, Tubney, OX13 5QL, UK E-mail hans.bauer@zoo.ox.ac.uk

GUILLAUME CHAPRON (orcid.org/0000-0002-6727-1070) Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden

SAMANTHA K. NICHOLSON (orcid.org/0000-0002-9460-028X) The Endangered Wildlife Trust, Conservation Science Unit, Johannesburg, South Africa

LUKE HUNTER (orcid.org/0000-0001-9653-6544) Wildlife Conservation Society, Big Cats Program, New York, USA

PETER LINDSEY* (orcid.org/0000-0002-9197-2897) Lion Recovery Fund, Wildlife Conservation Network, Harare, Zimbabwe

*Also at: Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa; and Environmental Futures Research Institute, Griffith University, Nathan, Queensland, Australia

Received 11 December 2019. Revision requested 5 March 2020.
Accepted 27 March 2020. First published online 2 December 2020.

This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is unaltered and is properly cited. The written permission of Cambridge University Press must be obtained for commercial re-use or in order to create a derivative work.

TABLE 1 Threats to the lion *Panthera leo* identified by experts at a workshop organized by the Wildlife Conservation Society and the IUCN in 2005. These threats form the basis of a problem tree analysis (see text for details) that captures most of the terms used in the literature on lion conservation. We have not listed disease as a specific threat as it is part of natural ecological processes and only becomes problematic in populations that are affected by other threats, including increased exposure to pathogens from domestic animals; some experts listed disease and small population size as threats and therefore they appear in our ranking of threats.

Threat	Description
Bushmeat poaching	Involves a combination of hunting for subsistence & to acquire meat for sale, with relative prevalence varying among sites. In urban areas, bushmeat is sometimes considered a luxury commodity & is typically costlier than meat from livestock, whereas in rural areas close to wildlife populations, bushmeat is often the most readily available source of protein & is typically cheaper than meat from livestock (Lindsey et al., 2013a; Tranquilli et al., 2014; Mallon et al., 2015). Bushmeat hunting mostly targets ungulates, which are potential lion prey, & is the dominant factor leading to prey depletion, to which all other threats also contribute (in Fig. 2 cultural killing on the prey depletion pathway refers to killing of prey for skins, horns & other parts). Hunting of some species is legal in some areas, & therefore poaching is not always the correct term, but as restrictions on hunting apply in most lion habitat we use this term.
Cropland expansion	This is the main threat leading to encroachment on or conversion of lion habitat, & it is linked to high human population growth (Riggio et al., 2013). Cropland expansion is driven by slash-&-burn agricultural practices, human population growth, local & global growth of demand for food products, inadequate controls on human incursion into protected areas, land grabbing, & increased access to wild areas as a result of infrastructure development (e.g. access roads, irrigation systems) (Oriol-Cotterill et al., 2015).
Livestock expansion (or encroachment, when combined with mobility)	This leads to human–lion conflict (see below) & also to habitat conversion & prey depletion through overgrazing & resource competition (Fig. 2). In West & Central Africa, cattle have traditionally been herded to follow rainfall patterns, but reduced rangeland availability & increased herd sizes as a result of wealth accumulation & disease eradication have increased their range & impact. Armed conflict has fuelled abnormal transhumant migrations & resulted in increased threats to rural communities & wildlife (Louizza, 2017). Everatt et al. (2019b) demonstrated a clear threshold: lions disappeared where livestock occurred across 21% of their territory.
Resource extraction	Industrial or artisanal mining of gold, precious stones & fossil fuels, & the extraction of firewood & charcoal, occurs in various lion habitats. In Benoue National Park, Cameroon, an estimated 10,000 displaced people were panning for gold in 2016 (Benoue warden, pers. comm., 2016). These people primarily entered the Park for mining, but while there they engaged in bushmeat poaching for both consumption & commercial trade; this is an example of how the same people can exercise multiple threats.
Poor protected area management	This has been identified as a crucial catalyst of threats (Packer et al., 2013; Lindsey et al., 2017). When management of protected areas is inappropriate or insufficient, the area becomes less effective for lion conservation. Protected area management includes many activities that address threats, & poor protected area management can therefore exacerbate other threats (e.g. snares are supposed to be absent but, in the absence of de-snaring teams, snares may be present). Even though lion range includes community land, lions mostly occur in landscapes with protected areas, & where the protected area is critical to their survival lions are a conservation-dependent species. Poor management of protected areas, resulting in lower effectiveness of protection, can therefore be conceptualized as a threat.
Trophy hunting	This is practised in some protected areas, with wildlife hunted for maximum yield, & offtake keeps populations below carrying capacity to maintain productivity. Trophy hunting can generate important funds for the management of wildlife areas, but inadequate management & excessive harvests can have negative impacts (Packer et al., 2011a; Lindsey et al., 2012, 2013b; Loveridge et al., 2016; Macdonald et al., 2017). We list trophy hunting as a potential threat because of this duality (Macdonald et al., 2016), even though a discussion of its impacts is beyond our scope here.
Wildlife trade	This refers to the illegal &/or commercial trade in lion parts & derivatives (Williams et al., 2015, 2017a,b; Bauer et al., 2018a). As with trophy hunting, legal commercial trade is listed here as a potential threat because the attribution of monetary value could drive poaching (Fig. 2). It is useful to distinguish two markets for lion parts (Fig. 2): demand within Africa for decorative/ceremonial (e.g. teeth, claws, manes, skin) or zootherapeutic products (e.g. lion fat) supplying a largely informal regional economy, & global demand (primarily from East Asia) for high-value products (primarily bones & skulls) supplying a trade that is largely fraudulent & criminal. The latter threat is increasing (Everatt et al., 2019a).

Table 1 (Cont.)

Threat	Description
Cultural & political killing	The killing of lions & their prey for prestige is of marginal importance in some areas, but in others lion hunting is culturally important; in addition to the well-known lion hunts in East Africa by certain groups of Maasai as a rite of passage, these hunts also occur amongst other tribal groups (Hazzah et al., 2009; Dickman et al., 2014; Fitzherbert et al., 2014). More generally, many cultures across Africa attribute value to hunting of lions & their prey, & the spoils are often used in cultural & religious practices. Prestige hunting can also be an assertion of entitlement or anger, & may fluctuate with political circumstances, occasionally leading to eruptions of lion killing in exceptional numbers (Frank et al., 2006).
Human–lion conflict	The retaliatory or preventative killing of lions in response to livestock depredation is a major problem across Africa (Bauer et al., 2010; Dickman et al., 2014). Killing is nominally aimed at so-called problem lions, but this threat affects all lions, as people resort to revenge killing of lions, or even pre-emptive killing or poisoning (Loveridge et al., 2017). In most cases people tolerate some degree of livestock depredation before they retaliate, but tolerance is lower when lions kill people (Packer et al., 2005); this locally acute problem is limited & therefore not examined here, but the fear of lions, & the restrictions people impose on themselves to avoid risk, are widespread (Packer et al., 2011b). These so-called conflicts differ from other threats because they are not direct but rather an emergent consequence of human activity; husbandry techniques influence the extent of conflict (Oriol-Cotterill et al., 2015). Figure 2 shows this as a set of pathways centred on livestock depredation, which is fed by all other threats in various ways.
Infrastructure development	This refers to dams, highways, railways, powerlines, urban sprawl & other developments. The direct impact on land cover is multiplied by the effects of fragmentation & by increasing access into remote areas, which potentially increases the spread of other threats. Infrastructure can also affect lions by disturbance resulting from increased human presence (Oriol-Cotterill et al., 2015).
Small population	Population size is part of the extinction vortex indicated in the top left corner of Fig. 2: habitat reduction & fragmentation lead to lion populations that are so small their viability is reduced by environmental, demographic &/or genetic stochasticity, creating a vicious circle leading to extirpation (Kissui & Packer, 2004). Small population size is not necessarily a problem in itself but a consequence of the human activities described above.

Methods

The 2005 Wildlife Conservation Society and IUCN workshop brought together various stakeholders and > 50 lion experts to use an adapted version of the range-wide priority setting methodology that had previously been used for the jaguar *Panthera onca* and tiger *Panthera tigris* (Sanderson et al., 2002). Experts were asked to describe all significant Lion Conservation Units (here we use the term population) (IUCN, 2006a,b). Thirteen years later, in 2018, the IUCN compiled a status update through online consultation of the same experts and new published and unpublished sources; the 2018 dataset was more comprehensive but still included the populations assessed in 2005 (Bauer et al., 2018b). The 2018 assessment included c. 600 lions in India and c. 600 lions in small fenced South African reserves, but threats in these areas are different and therefore outside our scope. In Supplementary Table 1 we provide the 2005 and 2018 data but we refer to the original documents (IUCN, 2006a,b; Bauer et al., 2018b) for further information on methodology and information sources.

In the 2005 workshop, threats were listed and ranked per population. Experts chose from a list of threats or nominated a new threat under ‘other’. Among the threats was

the ambiguous category ‘lion killing’; the discussions at the time clearly situated it in the context of so-called human–lion conflict and that is how we report it here. We made some semantic adjustments that reflect our approach of labelling a threat by the human activity at the root, rather than by the consequences along the causal chain: ‘declining prey base’ was translated as bushmeat poaching, ‘habitat conversion’ as cropland expansion, ‘livestock encroachment’ as livestock expansion. Small population size and disease were both ranked highly by several experts; these now refer to the small population vortex but they are listed and ranked among the threats. The threats identified per population are also given in Supplementary Table 1, in the order in which they were ranked.

We used these data for three lines of investigation: (1) ranking of threats based on expert knowledge in 2005, (2) framing those threats using problem tree and root cause analysis, and (3) an analysis linking threats to population trends up to 2018.

Threat ranking Experts ranked all relevant threats; the highest number of threats listed for any population was eight. Overall ranking of threats across all populations was then ranked by assigning 8 points to a threat every time it

was scored first, 7 points for every time it was scored second, and so on, and then ranking the sums per threat. We present the score per threat as a per cent of the total number of points.

Threat analysis We constructed a problem tree, with root causes at the base as the drivers of threats; these root causes are not exhaustively listed and described here but some appear in the text below. Above the root causes are the threats described in Table 1 (nine of them appear as threats, see below for ‘conflict’ and ‘small populations’), with interactions indicated by arrows. These threats lead to various effects, often in synergistic ways, whereby primary effects lead to secondary or tertiary effects, also indicated by arrows. These effects lead to a normative problem: the decline in lion range and numbers. Human–lion conflict did not fit into the problem tree in the same way as other threats, and therefore we performed a root cause analysis (Wilson, 1993) for this. Small population size is shown as a vicious circle of negative reinforcement, as explained in Table 1.

Threat impact To assess the impact of threats on population trends, we used the 2005 and 2018 data to follow the fate of individual populations for which threats were listed. This was done to determine whether different threats had led to different population declines and whether some threats were particularly important over this period. However, the data ranked threats relative to each other within a population and not on a scale comparable among populations. For example, in one population illegal killing could be ranked the third most important threat, but still be of higher intensity than in another population where it was ranked the most important threat. We could not therefore use threats as independent variables to predict population trend. Instead, we used a linear model (analysis of variance) to determine whether population decline could be explained by the presence of threats. We also looked at these trends qualitatively to highlight apparent patterns. For one apparent pattern, we generated a list of countries that experienced armed conflict between 2005 and 2018, using Pettersson et al. (2019).

Results

In 2005, 78 lion populations assessed contained an estimated total of 33,292 lions and all were used for threat ranking. The 2018 assessment was more comprehensive and included 25,580 lions in 99 populations, and the 78 populations assessed in 2005 contained 24,480 lions. The 2018 assessment retained 2005 data for eight populations where no new information was available and these were excluded from the analysis so that matching data pairs were available for 71 populations comprising 32,237 lions in 2005 and 21,906 lions in 2018 (Supplementary Table 1).

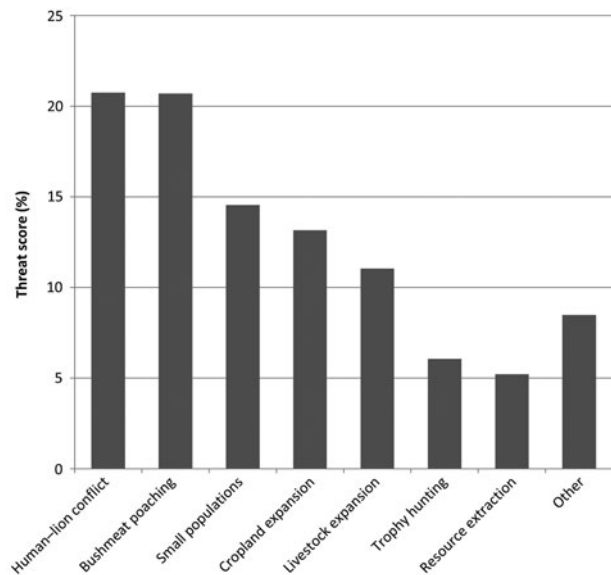


FIG. 1 Ranking of threats to lion *Panthera leo* populations, attributed by experts in the Wildlife Conservation Society/IUCN workshop in 2005. The score for each threat is presented as a per cent of the total number of ranking points (see text for details).

Threat ranking Seven threats were ranked, and there was a category of other threats comprising those mentioned only a few times: problem animal control, bush fire, lake fluctuation and armed conflict (Supplementary Table 1). Figure 1 shows the threat ranking across populations; human–lion conflict and prey depletion emerge as the two threats that, almost equally, affect most populations and most lions.

Threat analysis Figure 2 presents the problem tree, Fig. 3 the root cause analysis. Both figures are generic in that they are constructed from labels used by experts across Africa, using labels most commonly occurring in the literature. They are neither exhaustive nor tailored to specific sites, and different factors may be identified for particular sites or research interests.

Threat impact The linear model showed no significant relation between population trends and threats. Nevertheless, we observed an apparent pattern: the 20 populations extirpated, excluding two outliers with high but uncertain estimates (northern Guinea, Luzaches in Angola), were small populations with a mean of 28 lions, and 14 of these extirpations occurred in countries with armed conflict (Supplementary Table 1).

Discussion

Expert panel data can potentially be misleading, and we urge caution in the interpretation of subsets of the data presented

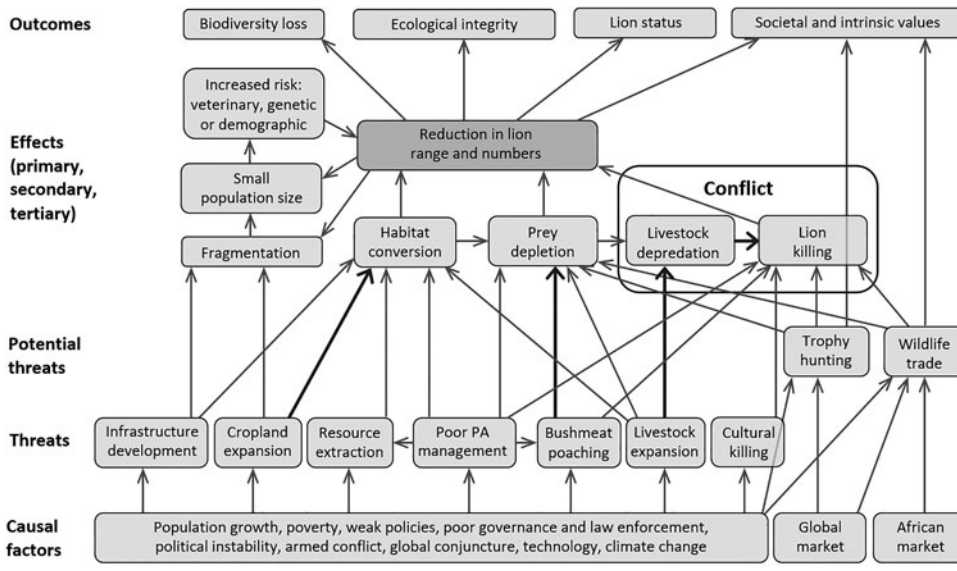


FIG. 2 Problem tree model of threats (Table 1) to African lions; note that nine threats are listed horizontally above the bottom row, and small population size and human–lion conflict appear higher up (see text for explanation). Arrows represent causal links (with single arrowheads to stress the flow, although many links are in fact bidirectional; particularly important links are displayed with heavy lines and arrows, for emphasis). PA, protected area.

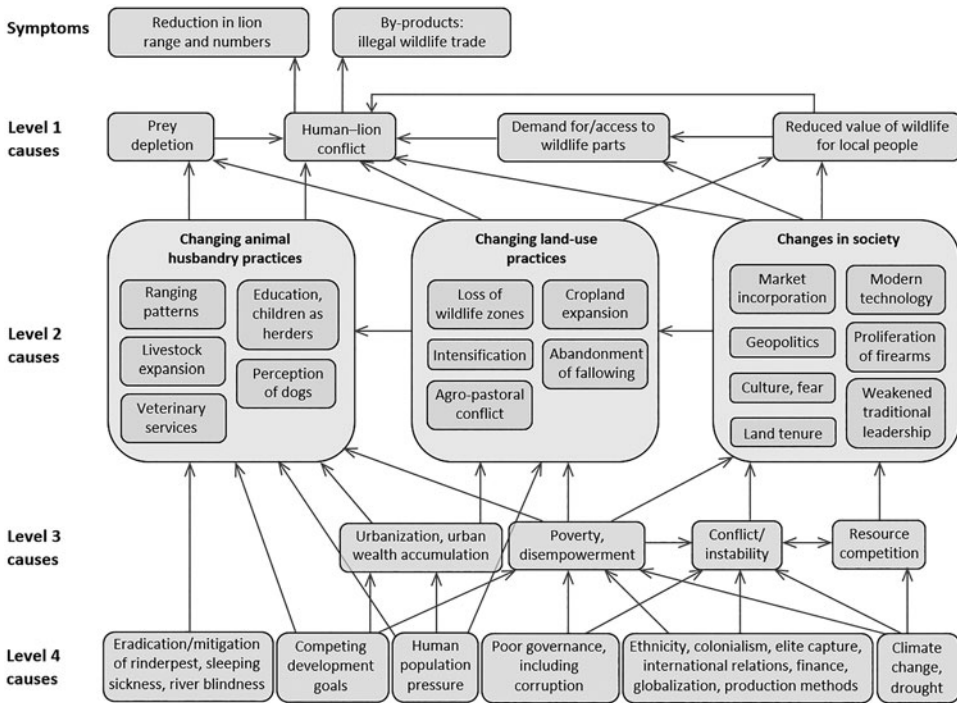


FIG. 3 Root cause analysis of human–lion conflict.

here, especially with respect to the numbers of lions. However, despite the fact that the 2005 data are from an interactive workshop and the 2018 data from online consultations, there were comparable data pairs giving changes over time that suffer less from bias than absolute numbers. The 2005 data identified human–lion conflict and bushmeat poaching as the main threats, but we failed to identify differential impact of threats on population declines. Our analysis reveals a multitude of threats stemming from a complex web of drivers; this may explain why we did not find a significant relation between population trajectories and individual threats. We infer that the prevalence of

threats is more important than the nature of those threats in driving population declines. By extension, our ranking analysis provides empirical evidence for the contention that human–lion conflict and prey depletion are the most serious threats to lions, and our problem analyses deconstruct these terms to show the underlying causes.

Because of the complexity of human–lion conflict, and to show how multiple threats occur concurrently and interact, we illustrate the use of our root cause analysis (Fig. 3) with a recent example from northern Kenya. The Laikipia–Samburu region is home to several pastoralist and crop-farming ethnic groups, commercial ranchers and private

conservancies. Lions occur throughout the landscape; they thrive best on those commercial ranches and private conservancies with good livestock husbandry and abundant wild prey, leading to low livestock depredation. Long-term viability probably depends on this source population, as other land-use types are primarily sinks for lions (Oriol-Cotterill et al., 2015). Long-standing tensions between ethnic groups (Level 4 in Fig. 3) lead to regular periods of instability in the region (Level 3) compounded by a proliferation of firearms (Level 2). Human population growth (Level 4) and dependence of pastoralists on livestock directly result in increased livestock numbers, as does accumulated wealth amongst the pastoralist elite, such that large prestige herds of livestock are owned by a few individuals (livestock expansion, Level 2). Livestock expansion puts pressure on resources and aggravates poverty amongst pastoralists (Level 3), because land tenure is communal (Level 2). Traditional boundaries between grazing lands are regularly disputed, and individual ownership of land is often not recognized by pastoralists, exacerbating instability. A drought in 2017 (climate change, Level 4) forced many traditional pastoralists to move their livestock (ranging patterns, Level 2). During the general election in the same year there was rhetoric from politically motivated individuals encouraging people to appropriate commercial ranch land, private conservancies and protected areas. The widespread use of mobile phones and social media (modern technology, Level 2) facilitated this political incitement and the coordinated movement of large numbers of warriors and their livestock, bypassing traditional decision-making processes (weakening traditional leadership, Level 2). The resultant mass movement of livestock and people caused the effective loss of some wildlife areas (Level 1) and the increase in availability of weak and poorly guarded livestock induced large carnivores to switch from wild prey to livestock, further compounded by drought-induced prey declines (Level 1), disease transmitted from domestic livestock and dogs, and hunting by armed livestock herders.

Kenya is a relatively stable country, although human conflicts also played a role in these changes. Recent extirpations of lions have often occurred in areas with armed conflict; this factor was mentioned as one of many root causes but emerged in our analysis, especially for fragile populations (e.g. Comoé, Cote d'Ivoire: Henschel et al., 2014) but also for larger populations (Angola: Funston et al., 2017; Central African Republic: Bouché et al., 2012). This underscores the impact of war on wildlife (Daskin & Pringle, 2018), with chaos in society leading to increased levels of all threats, including anarchic livestock movements and killing of lion prey and lions facilitated by proliferation of firearms. In the context of lion conservation, war has hitherto received little attention, possibly because no work with a species focus is being done in war zones (Hickisch et al., 2019). There has been debate regarding the effects of conflict on biodiversity, focusing on the myth of poachers as

terrorists (Duffy, 2016) and the resultant militarization of conservation (Büscher & Fletcher, 2018). In our analysis, armed conflict is a higher level cause, and Fig. 3 and provides insight into possible pathways by which it specifically affects lions.

Several cases suggest a successional pattern of synergistic threats leading to decline and finally extirpation. An illustrative example is that of the lion population in Waza National Park, Cameroon, historically part of a major population in northern Cameroon and southern Chad. The demise of this lion population occurred in phases; although not limited to human–lion conflict we refer to cause levels of Fig. 3 where relevant. This landscape was fragmented in the 1970s and 1980s, with the eradication of rinderpest and sleeping sickness facilitating human settlement (Level 4). In the 1990s, there was intense conflict over livestock outside Waza National Park (Level 1; Bauer, 2003). In the 2000s, declines inside the Park were a result of decreased park management effectiveness (Level 2; Tumenta et al., 2010) along with falling prey densities (Scholte, 2014). In the 2010s, the Boko Haram group intensified the already existing armed conflicts in the region (Level 3), indirectly leading to almost complete degradation of the Park (Pennaz et al., 2018), with few lions remaining (P. Tumenta, pers. comm., 2017). The nature of the threats varies, but a succession of threats, first affecting the periphery and then the core of protected areas, is a pattern that led to major declines and extirpations. The height of this decline across West Africa may have been in the 1990s (Henschel et al., 2014), in Central Africa a decade later (Bouché et al., 2012; Brugiere et al., 2015), and in East Africa in the 2010s, whereas southern Africa is less affected (Bauer et al., 2015). Little is known about the impact of climate change (Level 4), but this could exacerbate root causes and threats (Tuqa et al., 2014; Carter et al., 2018).

Our analyses can help lion conservationists define more clearly all the issues relevant to achieve management objectives before they address threats to local lion populations. They can implement tried and tested activities such as de-snaring, patrolling, building bomas or collaring but, whatever activity they consider most suitable under local circumstances, it is most likely to be effective if it is informed by a thorough understanding of the threats. The complexity and scale of problems in biodiversity conservation transcends the traditional skills of conservation biologists. Our findings demonstrate that the conservation of lions, as with the conservation of other species, requires a holistic approach involving the natural and social sciences, and higher level policy and international relations (Pooley et al., 2017; Montgomery et al., 2018; Beck et al., 2019). What may seem a problem preoccupying biologists may actually be framed by matters such as war or poverty that biologists cannot presume to resolve alone. Lion conservationists must engage with organizations that are more qualified, experienced and resourced to address such matters, to increase

their effectiveness. The first step is to frame the problems of and solutions to lion conservation in wider societal contexts.

Acknowledgements The data used here came from IUCN (2006a,b) and Bauer et al. (2018b); we acknowledge the many contributors listed in these documents.

Author contributions Problem tree and root cause analyses: HB, AD, AO-C; quantitative analysis: HB, SN, GC; writing: all authors.

Conflicts of interest None.

Ethical standards This research complied with the *Oryx* guidelines on ethical standards.

References

- BAUER, H. (2003) *Lion Conservation in West and Central Africa—Integrating Social and Natural Science for Wildlife Conflict Resolution Around Waza National Park, Cameroon*. PhD thesis. University of Leiden, Leiden, The Netherlands.
- BAUER, H., CHAPRON, G., NOWELL, K., HENSCHER, P., FUNSTON, P., HUNTER, L.T.B. et al. (2015) Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 14894–14899.
- BAUER, H., DE IONGH, H. & SOGBOHOSSOU, E. (2010) Assessment and mitigation of human–lion conflict in West and Central Africa. *Mammalia*, 74, 363–367.
- BAUER, H., NOWELL, K., SILLERO-ZUBIRI, C. & MACDONALD, D.W. (2018a) Lions in the modern arena of CITES. *Conservation Letters*, 11, e12444.
- BAUER, H., PACKER, C., FUNSTON, P., HENSCHER, P. & NOWELL, K. (2016) Panthera leo (errata version published in 2017). *The IUCN Red List of Threatened Species* 2016: e.T15951A115130419. dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en [accessed 26 June 2020].
- BAUER, H., PAGE-NICHOLSON, S., HINKS, A.E. & DICKMAN, A. (2018b) Status of the lion in sub-Saharan Africa. In *Guidelines for the Conservation of Lions in Africa*. Unpublished report. IUCN Cat Specialist Group, Muri bei Bern, Switzerland.
- BECK, J.M., LOPEZ, M.C., MUDUMBA, T. & MONTGOMERY, R.A. (2019) Improving human–lion conflict research through interdisciplinarity. *Frontiers in Ecology and Evolution*, 7, 243.
- BOUCHÉ, P., MANGE, R.N.M., TANKALET, F., ZOWOYA, F., LEJEUNE, P. & VERMEULEN, C. (2012) Game over! Wildlife collapse in northern Central African Republic. *Environmental Monitoring and Assessment*, 184, 7001–7011.
- BRUGIERE, D., CHARDONNET, B. & SCHOLTE, P. (2015) Large-scale extinction of large carnivores (lion *Panthera leo*, cheetah *Acinonyx jubatus* and wild dog *Lycan pictus*) in protected areas of West and Central Africa. *Tropical Conservation Science*, 8, 513–527.
- BÜSCHER, B. & FLETCHER, R. (2018) Under pressure: conceptualising political ecologies of green wars. *Conservation and Society*, 16, 105–113.
- CALLICOTT, J.B., CROWDER, L.B. & MUMFORD, K. (1999) Current normative concepts in conservation. *Conservation Biology*, 13, 22–35.
- CARTER, N.H., BOULEY, P., MOORE, S., POULOS, M., BOUYER, J. & PIMM, S. (2018) Climate change, disease range shifts, and the future of the Africa lion. *Conservation Biology*, 32, 1207–1210.
- DASKIN, J.H. & PRINGLE, R.M. (2018) Warfare and wildlife declines in Africa's protected areas. *Nature*, 553, 328.
- DICKMAN, A.J., HAZZAH, L., CARBONE, C. & DURANT, S.M. (2014) Carnivores, culture and 'contagious conflict': multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biological Conservation*, 178, 19–27.
- DICKMAN, A.J., MACDONALD, E.A. & MACDONALD, D.W. (2011) A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 13937–13944.
- DUFFY, R. (2016) War, by conservation. *Geoforum: Journal of Physical, Human, and Regional Geosciences*, 69, 238–248.
- EVERATT, K., KOKES, R. & PEREIRA, C.L. (2019a) Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, 28, 4099–4114.
- EVERATT, K.T., MOORE, J.F. & KERLEY, G.I. (2019b) Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. *Global Ecology and Conservation*, 20, e00758.
- FITZHERBERT, E., CARO, T., JOHNSON, P.J., MACDONALD, D.W. & MULDER, M.B. (2014) From avengers to hunters: leveraging collective action for the conservation of endangered lions. *Biological Conservation*, 174, 84–92.
- FRANK, L., MACLENNAN, S., HAZZAH, L., BONHAM, R. & HILL, T. (2006) *Lion Killing in the Amboseli-Tsavo Ecosystem, 2001–2006, and its Implications for Kenya's Lion Population*. Living with Lions, Nairobi, Kenya.
- FUNSTON, P., HENSCHER, P., PETRACCA, L., MACLENNAN, S., WHITESSELL, C., FABIANO, E. & CASTRO, I. (2017) *The Distribution and Status of Lions and Other Large Carnivores in Luengue-Luiana and Mavinga National Parks, Angola*. Unpublished report. Secretariat Kavango-Zambezi Transfrontier Conservation Area, Kasane, Botswana.
- HAZZAH, L., BORGERHOFF MULDER, M. & FRANK, L. (2009) Lions and Warriors: social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biological Conservation*, 142, 2428–2437.
- HENSCHER, P., COAD, L., BURTON, C., CHATAIGNER, B., DUNN, A., MACDONALD, D. et al. (2014) The lion in West Africa is Critically Endangered. *PLOS ONE*, 9, e83500.
- HICKISCH, R., HODGETTS, T., JOHNSON, P., SILLERO, C., TOCKNER, K. & MACDONALD, D. (2019) Effects of publication bias on conservation planning. *Conservation Biology*, 33, 1151–1163.
- IUCN (2006a) *Conservation Strategy for the Lion in Eastern and Southern Africa*. IUCN/Species Survival Commission Cat Specialist Group, Muri bei Bern, Switzerland.
- IUCN (2006b) *Conservation Strategy for the Lion in West and Central Africa*. IUCN/Species Survival Commission Cat Specialist Group, Muri bei Bern, Switzerland.
- IUCN (2008) *Strategic Planning for Species Conservation: A Handbook*. IUCN/Species Survival Commission, Gland, Switzerland.
- KISSUI, B.M. & PACKER, C. (2004) Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London Biological Sciences*, 271, 1867–1874.
- LINDSEY, P.A., BALME, G., BECKER, M., BEGG, C., BENTO, C., BOCCHINO, C. et al. (2013a) The bushmeat trade in African savannas: impacts, drivers, and possible solutions. *Biological Conservation*, 160, 80–96.
- LINDSEY, P.A., BALME, G.A., BOOTH, V.R. & MIDLANE, N. (2012) The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. *PLOS ONE*, 7, e29332.
- LINDSEY, P.A., BALME, G.A., FUNSTON, P., HENSCHER, P., HUNTER, L., MADZIKANDA, H. et al. (2013b) The trophy hunting of African lions: scale, current management practices and factors undermining sustainability. *PLOS ONE*, 8, 1–11.

- LINDSEY, P., PETRACCA, L., FUNSTON, P., BAUER, H., DICKMAN, A., EVERATT, K. et al. (2017) The performance of African protected areas for lions and their prey. *Biological Conservation*, 209, 137–149.
- LOUIZZA, M. (2017) *Transhumant Pastoralism in Central Africa: Emerging Impacts on Conservation and Security*. Unpublished report. U.S. Fish & Wildlife Service, Washington, DC, USA.
- LOVERIDGE, A., VALEIX, M., CHAPRON, G., DAVIDSON, Z., MTARE, G. & MACDONALD, D. (2016) Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. *Biological Conservation*, 204, 247–254.
- LOVERIDGE, A.J., VALEIX, M., ELLIOT, N.B. & MACDONALD, D.W. (2017) The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, 54, 815–825.
- MACDONALD, D.W., JOHNSON, P.J., LOVERIDGE, A.J., BURNHAM, D. & DICKMAN, A.J. (2016) Conservation or the moral high ground: siding with Bentham or Kant. *Conservation Letters*, 9, 307–308.
- MACDONALD, D.W., LOVERIDGE, A.J., DICKMAN, A., JOHNSON, P.J., JACOBSEN, K.S. & DU PREEZ, B. (2017) Lions, trophy hunting and beyond: knowledge gaps and why they matter. *Mammal Review*, 47, 247–253.
- MALLON, D.P., HOFFMANN, M. & MCGOWAN, P.J.K. (2015) *An IUCN Situation Analysis of Terrestrial and Freshwater Fauna in West and Central Africa*. IUCN, Gland, Switzerland, and Cambridge, UK.
- MONTGOMERY, R.A., ELLIOTT, K., HAYWARD, M., GRAY, S.M., MILLSPAUGH, J.J., RILEY, S.J. et al. (2018) Examining evident interdisciplinarity among prides of lion researchers. *Frontiers in Ecology and Evolution*, 6, 49.
- ORIOLO-COTTERILL, A., MACDONALD, D.W., VALEIX, M., EKWANGA, S. & FRANK, L.G. (2015) Spatiotemporal patterns of lion space use in a human-dominated landscape. *Animal Behaviour*, 101, 27–39.
- ORIOLO-COTTERILL, A., VALEIX, M., FRANK, L.G., RIGINOS, C. & MACDONALD, D.W. (2015) Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, 124, 1263–1273.
- PACKER, C., BRINK, H., KISSUI, B.M., MALITI, H., KUSHNIR, H. & CARO, T. (2011a) Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*, 25, 142–153.
- PACKER, C., IKANDA, D., KISSUI, B. & KUSHNIR, H. (2005) Lion attacks on humans in Tanzania. *Nature*, 436, 927–928.
- PACKER, C., LOVERIDGE, A., CANNEY, S., CARO, T., GARNETT, S.T., PFEIFER, M. et al. (2013) Conserving large carnivores: dollars and fence. *Ecology Letters*, 16, 635–641.
- PACKER, C., SWANSON, A., IKANDA, D. & KUSHNIR, H. (2011b) Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLOS ONE*, 6, 1–4.
- PENNAZ, A.K., AHMADOU, M., MORITZ, M. & SCHOLTE, P. (2018) Not seeing the cattle for the elephants: the implications of discursive linkages between boko haram and wildlife poaching in Waza National Park, Cameroon. *Conservation and Society*, 16, 125–135.
- PETTERSSON, T., HÖGBLADH, S. & ÖBERG, M. (2019) Organized violence, 1989–2018 and peace agreements. *Journal of Peace Research*, 56, 589–603.
- POOLEY, S., BARUA, M., BEINART, W., DICKMAN, A., HOLMES, G., LORIMER, J. et al. (2017) An interdisciplinary review of current and future approaches to improving human–predator relations. *Conservation Biology*, 31, 513–523.
- RIGGIO, J., JACOBSON, A., DOLLAR, L., BAUER, H., BECKER, M., DICKMAN, A. et al. (2013) The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*, 22, 17–35.
- SALAFSKY, N., MARGOLUIS, R., REDFORD, K.H. & ROBINSON, J.G. (2002) Improving the practice of conservation: a conceptual framework and research agenda for conservation science. *Conservation Biology*, 16, 1469–1479.
- SANDERSON, E.W., REDFORD, K.H., CHETKIEWICZ, C.L.B., MEDELLIN, R.A., RABINOWITZ, A.R., ROBINSON, J.G. & TABER, A.B. (2002) Planning to save a species: the jaguar as a model. *Conservation Biology*, 16, 58–72.
- SCHOLTE, P. (2014) Population trends of antelopes in Waza National Park (Cameroon) show escalating effects of poaching and livestock intrusion. *African Journal of Ecology*, 52, 370–374.
- TRANQUILLI, S., ABEDI-LARTEY, M., ABERNETHY, K., AMSINI, F., ASAMOAH, A., BALANGTAA, C. et al. (2014) Protected areas in tropical Africa: assessing threats and conservation activities. *PLOS ONE*, 9, e114154.
- TUMENTA, P., KOK, J., VAN RIJSSEL, J., BUIJ, R., CROES, B., FUNSTON, P. et al. (2010) Threat of rapid extermination of the lion (*Panthera leo leo*) in Waza National Park, Northern Cameroon. *African Journal of Ecology*, 48, 888–894.
- TUQA, J.H., FUNSTON, P., MUSYOKI, C., OJWANG, G.O., GICHUKI, N.N., BAUER, H. et al. (2014) Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*, 2, 1–10.
- WILLIAMS, V.L., LOVERIDGE, A.J., NEWTON, D.J. & MACDONALD, D.W. (2017a) Questionnaire survey of the pan-African trade in lion body parts. *PLOS ONE*, 12, e0187060.
- WILLIAMS, V.L., LOVERIDGE, A.J., NEWTON, D.J. & MACDONALD, D.W. (2017b) A roaring trade? The legal trade in *Panthera leo* bones from Africa to East-Southeast Asia. *PLOS ONE*, 12, e0185996.
- WILLIAMS, V., NEWTON, D., LOVERIDGE, A. & MACDONALD, D. (2015) *Bones of Contention. An Assessment of the South African Trade in African Lion Panthera leo Bones and Other Body Parts*. TRAFFIC, Cambridge, UK, and WildCRU, Oxford, UK.
- WILSON, P.F. (1993) *Root Cause Analysis: A Tool for Total Quality Management*. William C. Brown Publishers, Dubuque, USA.