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Wire-snare bushmeat poaching and the large African carnivore guild: Impacts, knowledge gaps, and field-based mitigation

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ABSTRACT

Wire-snare poaching for bushmeat is increasingly recognized as a serious threat to the species comprising the large African carnivore guild (African lion, African wild dog, spotted hyena, cheetah and leopard), with impacts described primarily through prey depletion and snaring by-catch mortality or injury. However, the species-specific impacts of snaring on this guild and on intraguild dynamics are not well-understood. These guilds evolved through competition and predation and have a diverse array of behaviors, space use, movements, diet, morphology, and densities; thus, it is logical to expect snaring impacts through prey depletion and by-catch will also be variable, subtle, and complex, yet significant. Utilizing the scientific literature and ongoing, long-term research we: 1) Summarize and describe the known and potential impacts of snaring by-catch and prey depletion on specific species in the guild and on intraguild dynamics, 2) Identify knowledge gaps and propose areas of future research to better understand and address snaring threats, and 3) Describe a successful strategy collaboratively merging conservation science work with resource protection, that has been implemented across carnivore strongholds in Zambia to combat the immediate threats from snaring on large carnivore populations. Collectively, this work can help mitigate snaring impacts while longer-term community-based solutions to the bushmeat crisis are developed and implemented.

1. Introduction

Large carnivores are globally imperiled and declining across their range due to a multitude of human impacts including habitat loss, conflict, and prey depletion (Estes et al., 2011; Ripple et al., 2014; Wolf and Ripple, 2016). Inherently linked to these declines and range contractions is the global decline of large herbivores, primarily due to unsustainable bushmeat poaching and in some cases poorly managed legal meat hunting; consequently, Africa has the highest rates of herbivore declines behind Southeast Asia (Ripple et al., 2015). The illegal bushmeat trade is one of the major drivers of these trends, with severe ecological impacts across virtually every ecosystem in sub-Saharan Africa (Noss, 1998; Lindsey et al., 2013; Ripple et al., 2016; Rogan et al., 2017; Vinks et al., 2020).

The primary method of bushmeat poaching is the use of wire snares, acquired from various sources (e.g., bicycle brake cables, radial tires, electrical lines, fencing) and set either passively, or actively triggered, along game trails or water holes in areas of high encounter rates for the target herbivore species; these are usually ungulates in general and antelope species in particular (Lewis and Phiri, 1998; Mudumba et al., 2021). Snare materials are cheap, readily accessible, easy to make, set, and conceal, and carry a low risk of detection and prosecution by law enforcement relative to firearms or other methods (Lindsey et al., 2013). Snares are also typically placed in sets, often numbering in the dozens or even hundreds for small areas; mammalian herbivores have limited ability to detect and avoid snares, and thus this method of poaching can have devastating impacts on populations through individuals killed or maimed (Hofer et al., 1993, Hofer and East, 1995, Becker et al., 2013,

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Bouley et al., 2018, Loveridge et al., 2020, Mudumba et al., 2021, Kasozi et al., 2023, Montgomery et al., n.d.).

The severe impact of snaring on biodiversity in Africa was first brought to attention by the seminal studies in forest biomes of West and Central Africa (e.g. Noss, 1998, Wilkie and Carpenter, 1999). However, it was not broadly recognized as a serious threat in savanna Africa until recently, perhaps due to the abundance and diversity of mammal species still populating these landscapes relative to other areas on the continent (Lindsey et al., 2013). The large African carnivore guild (LACG) is comprised of five species: lion (*Panthera leo*), spotted hyena (*Crocuta crocuta,* hereafter hyena), wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), and leopard (*Panthera pardus*)) that primarily prey on ungulate communities (Hayward and Kerley, 2009) targeted by the majority of bushmeat poaching. The dominant LACG competitors are the lion and hyena, while the subordinate competitors are the wild dog, cheetah and leopard (Creel et al., 2019). The guild has evolved under intense competition and predation which has resulted in an array of strategies to mitigate competition and reduce predation risk (Droge et al., 2017). Given significant differences in behavior, diet, morphology, movement, space use, density, and population dynamics across species within the LACG, it is logical to expect different species to have different impacts from snaring.

Snaring by-catch of carnivores has been continuously documented in the scientific literature for decades, yet the impacts of snaring on species-specific dynamics, and on the LACG as a whole, are not well-understood. However, research has increasingly focused on understanding these impacts (Becker et al., 2013, Bouley et al., 2018, Loveridge et al., 2016, 2020, Mudumba et al., 2021, White and Van Valkenburgh, 2022, Benhaiem et al., 2022, Creel et al., 2023a, b; Banda et al., 2023, Kasozi et al., 2023, Montgomery et al., n.d.). Building upon this foundation, we utilize the scientific literature and our own collective research experience to address three main objectives in this paper: 1. Summarize and describe the known and potential impacts of snaring on the respective species comprising the LACG and on intraguild dynamics; 2. Identify knowledge gaps and propose areas of future research for better understanding and addressing the threat of snaring; 3. Describe successful field-based mitigation techniques combatting immediate threats from snaring on LACG populations.

2. Snaring impacts: by-catch, prey depletion, and intraguild dynamics

We propose that bushmeat snaring impacts the LACG in three main ways: 1. Snaring By-Catch 2. Prey Depletion, and 3. Intraguild Dynamics. There is a significant illegal trade in LACG species, particularly big cat skins and body parts (e.g., Everatt et al., 2019, Coals et al., 2020), that utilizes snaring (usually with baits). However, we confine our scope to bushmeat snaring where the LACG are not directly targeted, though many of these same impacts and knowledge gaps apply. By-catch—a term adopted from the fisheries literature (Hall et al., 2000) to classify incidental catch of non-target species–is the most well-documented and obvious impact of snaring. Snaring by-catch can cause mortality or severe injuries compromising fitness (Table 1, Benhaiem et al., 2022). Prey depletion is perhaps the more significant impact on carnivore demography as it can drive gradual or abrupt lowering of carrying capacity (Creel et al., 2023a). Given the diverse ecosystems and prey bases comprising the LACG's range, it is likely to be considerably more complex and variable than our current understanding. Lastly, because snaring impacts populations of predators, competitors, and prey, there are likely to be subtle, complex, and significant impacts on the intraguild dynamics of sympatric competitors in the LACG.

Table 1
Species-specific LACG life history characteristics and their potential relevance to differential impacts of snaring by-catch.

Trait	Lion	Spotted Hyena	Wild Dog	Cheetah	Leopard
Competitive rank	Dominant	Dominant	Subordinate	Subordinate	Subordinate
Significance	Dominant competitors are higher density and can displace subordinates through predation risk effects, often into more human-impacted high snare-risk areas (but see below relationship to prey density for dominant competitors). Snare injuries to subordinate carnivores are more likely to result in intraguild predation. Wild dog and cheetah are naturally lower densities than competitors, potentially making them more impacted by snaring.				
Sociality	Highly Social	Highly Social	Highly Social	Partially Social	Solitary
Significance	Highly social species can potentially support injured individuals unable to hunt. Multiple snarings in a group are likely to occur in social species. Loss or injury of high-ranking individuals can have strong demographic consequences on social groups through alpha takeovers, infanticide, loss of litters or group dissolution. Solitary hunting species incurring snare injuries are much more likely to starve with their hunting ability compromised.				
Hunting method	Ambush	Coursing	Coursing	Ambush	Ambush
Significance	Snaring injuries are likely to compromise hunting ability for coursing predators more than ambush predators. Coursing predators are likely to use game trails and linear features more and set snares at higher speeds, with higher chance of by-catch, injury/death. Ambush predators may frequent more vegetated areas, likely to have more snare sets, depending on the landscape.				
Body size	Large	Large	Small	Small	Small
Significance	Larger bodied species more likely to break/bite free from snares and avoid mortality/serious injury; smaller bodied species more likely to elude or wriggle out of larger, stiffer snares. Ability to break free from snare set also increases likelihood of being detected as snared compared to dying in snare set, potentially biasing evaluations of by-catch impacts. Juveniles of all species less likely to break free and likely underestimated as by-catch.				
Scavenging	Frequently	Frequently	Rarely	Rarely	Frequently
Significance	Snare lines often scavenged, risking snaring by-catch of scavenger.				
Relationship with prey density	Strong Positive	Strong Positive	Weak	Weak	Strong Positive
Significance	Snare sets typically target areas of high prey density on the landscape (moderated by protection status), making species that have positive relationships with prey density potentially more at risk of by-catch.				
Generation time/fecundity	7.0 Years, Mean litter size 2–4	5.7 Years, Mean litter size 1–2	5.0 Years, Mean litter size 10	4.9 Years Mean litter size 4	7.4 Years, Mean litter size 2
Significance	Long generation time requires longer recovery from snaring by-catch and prey depletion. Lower fecundity requires more recovery time.				
Dispersal	Male-Biased	Male-Biased	Both Sexes	Both Sexes	Male-Biased
Significance	Snaring by-catch can be male-biased and socially disruptive for male-dominated species such as lions. Dispersers are likely to have increased mortality rates from snaring by-catch, negatively impacting connectivity and helping create source-sink dynamics.				
Ability to move through human-impacted landscapes	Limited	Unknown	Good	Unknown	Unknown
Significance	Snaring will have differential impacts on connectivity and source-sink dynamics. Spatial avoidance of intraguild predation can be into human-impacted areas where snaring probability is higher.				

3. Species specific snaring impacts

3.1. African Lion

As the dominant species in the LACG, lions exert an array of negative impacts on their competitors from direct predation and predation risk effects. Lions are IUCN-listed as Vulnerable, with prey depletion considered the major threat to the estimated 23,000–33,000 lions remaining (Bauer et al., 2020). Lion densities are strongly positively correlated to prey density (Orsdol et al., 1985). Snaring frequently targets areas of high prey density; therefore lions can have a high risk of by-catch, and are snared throughout their range (Ogutu and Dublin, 2002, Hunter et al., 2007, Groom et al., 2014, Mweetwa et al., 2018, Loveridge et al., 2016, 2020, Mudumba et al., 2021, White and Van Valkenburgh, 2022). The impact of snaring on populations has not been well-quantified and is likely affected by sex and age characteristics within populations. For example, lion dispersal is male-biased, and dispersers are more likely to move through high-risk human-impacted landscapes. Similarly, coalition males attend 1–3 prides, and are thus potentially more apt to encounter snares within their home-range than females (Hunter et al., 2007; Becker et al., 2013), though Loveridge et al. (2020) found no difference in by-catch between sexes. If snaring by-catch mortality is sex-biased then male depletion in populations can be exacerbated, and frequent coalition male turnover can drive elevated levels of infanticide negatively impacting cub recruitment and population growth rates (Banda et al., 2023). Sex-specific snare mortality can also interact with snare type; in areas that foot-snares predominate, male lions are much less likely to survive front foot injuries given their heavier build and weight severely limits their mobility and hunting success (ZCP unpublished data).

Determining the impact of snaring by-catch relative to prey depletion on lions is difficult. Studies in a prey depleted system in the Greater Kafue found low density populations with poor cub recruitment but relatively high survival across subadult and adult female age classes (Vinks et al., 2021a), while Loveridge et al. (2020) found significantly higher mortality of snared lions and evidence of local extirpation. Banda et al. (2023) found lion de-snaring efforts likely enabled a stable or increasing population relative to what would have been a declining population due to snaring by-catch mortality. Similarly, Montgomery et al. (n.d.) modeled snaring by-catch impacts of lions and found significant population increases with reductions in snaring, and population decreases and even extirpation with varying levels of snaring increases.

3.2. Spotted Hyena

In contrast to other LACG species, hyenas are IUCN-listed as Least Concern (Bohm and Höner, 2015) despite exposure to the same threats, and to substantial human persecution related to witchcraft. This listing likely owes to a significant data deficiency on their status, coupled with a severe lack of public support for their conservation. As with lions, hyena densities are strongly correlated with prey density and they predate many of the same large antelope species targeted by bushmeat poaching and snares; thus, prey depletion is likely to be a significant impact (Bohm and Höner, 2015, Davis et al., 2022). Hyenas are wide-ranging, readily scavenge snare lines, and frequent areas of human development and livestock, making them extremely susceptible to snaring by-catch or retaliatory snaring after feeding off snare lines or depredating livestock (Kolowski, 2008; Gebo et al., 2022). Hyenas are typically the most common LACG species detected in snares or with snare injuries. The most comprehensive evaluations of snaring by-catch on hyenas come from the Serengeti's long-term studies, and Hofer et al. (1993) estimated approximately 400 adult hyenas died from snares in the Serengeti annually, amounting to over half the estimated adult mortality. Hofer and East (1995) estimated 8 % of the breeding females were removed annually in the ecosystem through snaring and poisoning by bushmeat poachers. Similarly, studies by Loveridge et al. (2020) found hyenas comprised 92 % of the snared LACG records in Zimbabwe's Kavango-Zambezi region, with 52–255 individuals having likely died across surveyed sites.

Their large body size and superior jaw strength likely enables hyena to break free from snares more so than subordinate species in the guild, thus a substantial number are not killed outright by the snare but are severely injured (e.g. Loveridge et al., 2020). Hofer et al., 1993 estimated 57 % of hyenas caught in snares died. Impacts of snaring likely vary among age- and sex-classes, as well as rank, for hyenas, and the impacts of by-catch mortality and prey depletion are not well-understood. For non-lethal snaring by-catch, Benhaiem et al. (2022) evaluated the fitness of snare-injured Serengeti hyenas and found no reduction in survival, but delayed age of first reproduction, reduced litter size, and reduced offspring survival to one year. This was likely due to increased immunoresponse costs and decreased mobility for long-distance commuting necessary for hunting by breeding females, and this latter cost could impose sex-biased costs (Benhaiem et al., 2022). Furthermore, given their life history characteristics, hyena populations are potentially slow to respond after negative demographic impacts due to the level of parental investment in their young and their low fecundity rates relative to sympatric carnivores.

3.3. Cheetah

Cheetahs are listed as IUCN Vulnerable with an estimated population of 6500 individuals; they are subordinate competitors, occur at naturally low densities, and are the widest-ranging species of the LACG (Durant et al., 2022). The majority of cheetah populations (91 %) number 200 or fewer individuals, and it is estimated that range-wide, more animals occur outside strictly protected areas than within them, making cheetah highly susceptible to human impacts (Durant et al., 2016).

Snaring by-catch of cheetah has been documented throughout their range (Laurenson, 1995, Buk et al., 2018, van der Meer, 2018, Gigliotti et al., 2020, Sievert et al., 2022); however, detection is infrequent, and snaring impacts are not well-evaluated. This may be because snared individuals remain undetected given their elusive nature, low density, small body size limiting their ability to break free from snares, tendency not to scavenge snare lines, and the inherent difficulties in monitoring small and declining populations. Where cheetahs are intensively monitored, snaring may have a significant impact on adult cheetah survival; for example, in the Greater Kafue Ecosystem snaring accounted for one-third of adult mortality from 2019 to 2022 and snaring by-catch is the leading cause of death in the Greater Liuwa Ecosystem for adult and dispersal-aged cheetah (ZCP Unpublished Data).

Cheetah can persist on smaller prey not as vulnerable to declines from bushmeat poaching and snaring (Vinks et al., 2020). However, snare-related injuries are likely to have severe impacts on survival, through impairment of hunting ability and success, increased susceptibility to intraguild predation, and because cheetah are not social outside of mothers with dependent cubs and male coalitions (which are unlikely to be large outside of well-protected areas). While cheetah naturally can incur high levels of juvenile mortality, it is unknown how resilient populations are to elevated levels of adult mortality from snaring by-catch, particularly in the human-impacted landscapes characterizing the majority of their remaining populations. Overall, given cheetah are characterized by naturally low densities and currently exist primarily in small, fragmented, and often declining populations (Durant et al., 2016), the impacts of snaring warrant increased attention.

3.4. Wild dogs

Wild dogs are listed as endangered by the IUCN, with an approximate 1400 adults remaining, though as cooperative breeders their effective population size is smaller (Woodroffe and Sillero-Zubiri, 2020). Wild dogs are naturally low density compared to their dominant competitors and are strongly limited by lions (Creel and Creel, 1996). Woodroffe and

Ginsberg (1999) identified snaring as an important cause of adult mortality, and wild dog snaring by-catch has been recorded across their range (Creel and Creel, 2002, Woodroffe et al., 2007, Becker et al., 2013, Van der Meer et al., 2013, Schuette et al., 2018). The importance of snaring by-catch on wild dogs also varies regionally (Woodroffe et al., 2007), likely related to the snaring intensity and methods employed, but impacts can be severe. Long-term studies from Zimbabwe's Save Valley found that 40 % of recorded wild dog mortalities were from snaring by-catch (Rabaiotti et al., 2021), and local extirpation in multiple ecosystems has been attributed to snaring (Pole, 1999; Leigh, 2005; Loveridge et al., 2020; Bouley et al., 2021). In contrast, survival rates recorded in the heavily-snared Kafue ecosystem were comparable with those of stronghold populations (Goodheart et al., 2021). Similarly, snare density was high in the Selous Game Reserve (Creel and Creel, 2002), but snares targeted larger herbivore species such as buffalo, with dogs less susceptible to by-catch due to the larger snare size.

Wild dogs are often found more outside of strictly protected areas than inside them (Woodroffe and Sillero-Zubiri, 2020), and dogs are more adept at moving through human-impacted landscapes than other species in the LACG, likely due to their evolution as a wide-ranging subordinate competitor (Creel et al., 2019, 2020). However, this propensity and their large-scale avoidance of high lion density areas (Creel and Creel, 1996) can increase their risk of snaring by-catch by crossing gradients of protection into areas where snaring is likely to be highest near communities and on reserve boundaries (Watson et al., 2013; Creel et al., 2020). In addition, wild dogs tend to increase their movement outside of protected areas (Goodheart et al., 2022).

As a highly social species, wild dogs can ensnare multiple individuals in snare sets, either because they are simply traveling together closely, or when pack members attempt to rescue snared individuals and become snared themselves. Indeed, in several cases, across two ecosystems, multiple dogs have been found in the same snare set (ZCP, Unpublished data). The wide-ranging behavior of dogs and their propensity to use game trails and linear features likely increases snare encounter rates. As coursing predators, dogs travel at a trot or a run, possibly decreasing their ability to avoid snares and setting them at higher speeds, with unknown impacts on the likelihood and severity of by-catch. The direct effects of snaring versus the effects of prey depletion on wild dogs likely differ between ecosystems, depending on the predominant snaring methods employed and the target herbivore species. However, Creel et al. (2023a) found overall snaring by-catch mortality to be very similar for dog populations in the Luangwa Valley and Greater Kafue Ecosystems despite substantial differences in prey density and dog density. For non-lethal injuries, wild dogs are more apt to survive provided they can keep up with a pack, and numerous animals have been documented with severe snare injuries, including loss of limbs and paws (Creel et al., 2023a). These dogs may still serve important purposes as baby-sitters and sentinels for pups and the pack, despite being relatively unhelpful for hunting. However, injuries are likely to make snared dogs slower than others, so as a subordinate carnivore, these dogs can be more susceptible to predation by lions and hyenas.

The importance of prey depletion on lions is well-established (Bauer et al., 2020; Vinks et al., 2021a); yet is not currently recognized as a major threat to wild dogs rangewide (Creel et al., 2023a, b). Recent investigations into prey depletion for wild dogs found significant impacts on density, pack size, and home range size (Goodheart et al., 2021) and strong impacts on demography and source-sink dynamics of free-ranging populations (Creel et al., n.d., Reyes de Merkle et al., n.d.). Consequently, prey depletion from bushmeat poaching should be viewed as one of the most urgent threats to wild dogs rangewide (Creel et al., 2023a, b).

3.5. Leopard

Leopards are listed as IUCN Vulnerable, and despite being widespread, have experienced substantial range loss (Stein et al., 2020). A study by Jacobson et al., 2016 stated that "The leopard's (*Panthera pardus*) broad geographic range, remarkable adaptability, and secretive nature have contributed to a misconception that this species might not be severely threatened across its range." This is a suitable statement for the impact of snaring on leopard as well, given that it is very likely to be under-estimated and very difficult to evaluate. Compared to the dominant LACG species, leopards are small-bodied and less likely to break free from snares once entrapped (Loveridge et al., 2020), and their solitary and elusive nature makes it less likely to be for them to be detected with snare injuries. Studies in India by Gubbi et al. (2021) indicate snaring can significantly impact leopards through by-catch. Snared leopards have been documented across much of Africa (Jorge et al., 2013; Swanepoel et al., 2015) and snaring has contributed to regional population declines (Naude et al., 2020, Power et al., 2021).

Studies across protection gradients found severe declines in leopard density between a national park and its surrounding buffer zones where prey densities were orders of magnitude lower (Rosenblatt et al., 2016, 2019) and where the probability of encountering a snare was five times higher (Watson et al., 2013), though survival between the two regions was found to be comparable (see below). Snaring was the major cause of illegal mortality of leopards in protected areas of southern Africa (Swanepoel et al., 2015).

Given they are solitary, a snare-injured leopard can be extremely compromised for avoiding intraguild predation and for hunting, despite their catholic diet allowing for broad dietary options beyond ungulates. In general, little is known about snaring by-catch and studies have found variable impacts of prey depletion, ranging from stable survival rates and density estimates when prey depletion reduced lion density and the larger prey species preferred by lions (Vinks et al., 2022), to severe impacts of reduced prey from snaring (Stein et al., 2020).

4. Prey depletion from snaring, impacts on carnivore guild dynamics, and knowledge gaps

The LACG has evolved through competition and intraguild predation and this is reflected in the diverse behavior, morphology, sociality, movements, space use, and diet of each of these species (Droge et al., 2017). These dynamics, coupled with the dynamics of predators and prey in some of the most diverse carnivore and herbivore communities on the planet (Ripple et al., 2015) make African ecosystems extremely complex. It is logical then to expect that prey depletion from snaring is likely to impact these systems in similarly complex and variable ways.

Prey depletion is widely recognized as a threat for large carnivores (Wolf and Ripple, 2016), and as the primary threat for lions (Bauer et al., 2020). The specific impacts of prey depletion, particularly on the more subordinate species in the guild, are not well-evaluated (Creel et al., 2018, Goodheart et al., 2021, Vinks et al., 2021a, 2022) but are likely to be significant and variable (Creel et al., 2023a, b). Long-term studies of LACG dynamics and herbivore demography in snaring-impacted systems are rare to our knowledge, and studies in the Kavango-Zambezi's (KAZA) Greater Kafue Ecosystem (GKE) and Luangwa Valley Ecosystem (LVE) in Zambia provide a number of insights and predictions related to what we consider to be key knowledge gaps in understanding and addressing snaring impacts on the LACG (Tables 1, 2). However, the generalizability of these findings to the diversity of snaring-impacted LACG populations across Africa remains unknown and in need of additional research.

Predictions:

1. ***Prey depletion is not uniform and likely to impact larger herbivore species disproportionately.*** Prey depletion generally impacts the larger, preferred bushmeat species first, particularly the large antelope species, which also comprise the preferred species for the dominant lion and hyena competitors (Creel et al., 2018; Vinks et al., 2020). Metanalyses across Africa support this general pattern, and it is likely driven by the slow recovery potential of the larger species, as

Table 2
Knowledge gaps and proposed areas of research on snaring impacts in relation to the large African carnivore guild.

Knowledge gaps on snaring in the large African carnivore guild	Conservation significance	Relevant references
Demography of snaring-impacted populations	Both snaring by-catch and prey depletion can impact the density and vital rates of populations, as well as drive source-sink dynamics and create attractive sinks and ecological traps.	Hofer et al., 1993, Banda et al., 2023, Becker et al., 2013, Goodheart et al., 2021, Loveridge et al., 2016, 2020, Montgomery et al., n.d., Mudumba et al., 2021, Rosenblatt et al., 2016, van der Meer, 2018, Creel et al., 2023a, b, n.d., Reyes de Merkle et al., n.d
Demography and dynamics of herbivore prey communities in snaring-impacted populations	Prey depletion is widely viewed as a primary, if not the primary, threat to large carnivores; yet few studies have accompanying herbivore data to evaluate this threat, and even less to understand and address both the threat and restoration.	Creel et al., 2018, Rosenblatt et al., 2016, Vinks et al., 2020,
Dynamics of intraguild competition in snaring-impacted populations	Alteration of herbivore species composition, abundance, and relative abundance can alter interguild competition through preybase homogenization and niche compression, potentially increasing impacts of dominant competitors (lion, hyena) on subordinate competitors (wild dog, cheetah, leopard) through both direct and risk effects.	Creel et al., 2018, Vinks et al., 2020, Vinks et al., 2021a, 2022, Goodheart et al., 2021, Rosenblatt et al., 2016
Impacts of snaring on connectivity and dispersal success	The impact of prey depletion and snaring risk can create islands of low-density populations surrounded by high-risk sinks.	Creel et al., 2019, 2020, Loveridge et al., 2020, Naude et al., 2020, Kendon et al., 2022
The relative impact of direct mortality from snaring versus prey depletion	Direct mortality from snaring by-catch is usually the more obvious demographic impact on carnivore populations, but the relative importance of by-catch versus prey depletion is not well-understood.	Creel et al., 2023a
Relationships between snaring, human-wildlife conflict, and the illegal wildlife trade	The links between snaring and human-wildlife conflict are not well-understood; similarly, how by-catch can create markets that can change to target species are also not understood.	None
The extent and impact of non-lethal snaring injuries	Significant proportions of large carnivores escape mortality from snares but can still incur significant and often severe injuries. The impacts of non-lethal by-catch on carnivore dynamics are poorly understood.	Banda et al., 2023, Benhaiem et al., 2022, Kasozi et al., 2023, Loveridge et al., 2020, Mudumba et al., 2021, White and Van Valkenburgh, 2022

well as by poaching preference for high-value species (Rija et al., 2020). In the GKE, bushmeat poaching has depleted the larger herbivores more severely, to the extent that species such as buffalo (preferred prey of lions) are no longer available in many areas, and the prey base is largely comprised of small to mid-sized antelope (Creel et al., 2018; Schuette et al., 2018; Vinks et al., 2020). In the LVE, prey depletion is not as widespread, but is pronounced across gradients of protection, with densities declining several orders of magnitude from strictly protected areas to adjacent Game Management Areas (Rosenblatt et al., 2019), a pattern likely to characterize most protected area networks and creating distinct patterns of source-sink dynamics across the landscape for carnivores (see below, Creel et al., n.d.). Prey depletion of large species can increase snaring by-catch of carnivores, as snare sizes decrease to reflect the smaller size of target herbivores available. In our experience the materials and diameters of snares set for small to mid-size antelope pose the greatest risk of by-catch injury and mortality for large carnivores. Data on the abundance, distribution and diversity of the prey base and its potential impact on LACG dynamics under snaring threat is important in understanding and addressing these impacts.

2. ***Alteration of the prey base composition by snaring is likely to increase intraguild competition and predation by decreasing dietary niche partitioning and increasing prey base homogenization.*** The diversity of diets across the LACG helps mitigate intraguild competition and predation, as different species predate different prey types and exhibit variable patterns of activity, movement, and space use (Droge et al., 2017). Prey depletion results in prey base homogenization and niche compression, with the potential result that dominant and subordinate competitors are necessarily focused on the same suite of prey (Creel et al., 2018), increasing the likelihood of intraguild predation for subordinate species such as wild dog and cheetah that adjust their patterns of space use, movement, and activity periods to avoid predation risk and kleptoparasitism from dominant lion and hyena competitors (Creel and Creel, 1996; Droge et al., 2017; Goodheart et al., 2022). The impact on prey depletion of the entire LACG feeding on a suite of smaller herbivore species is also not understood but potentially significant.
3. ***Prey depletion will result in smaller group sizes, larger home ranges, and substantially lower densities than expected for LACG species, with corresponding impacts on demographics.*** For lions, depletion of preferred large prey results in smaller prides, reduced energy intakes, reduced cub recruitment, and substantially lower lion densities than what would be expected in comparable ecosystems (Vinks et al., 2021a). Similarly prey depletion reduces wild dog density to some of the lowest density populations recorded, with very large home-ranges and small pack sizes (Goodheart et al., 2021). Interestingly, survival rates of carnivores in the core populations of prey-depleted systems are comparable to those of less-affected populations (Rosenblatt et al., 2016; Goodheart et al., 2021; Vinks et al., 2021a, 2022), making survival rates potentially not as useful for assessing prey depletion compared to such metrics as recruitment (Vinks et al., 2021a). While the nature of these impacts likely varies across species and systems (Vinks et al., 2022, Creel et al., 2023a, b), prey depletion probably impacts dynamics of all LACG species, altering intraguild dynamics considerably.
4. ***Prey depletion impacts will vary considerably across gradients of protection and create patterns of source-sink dynamics, attractive sinks and ecological traps affecting population viability, dispersal, and connectivity.*** Snaring patterns and trends are often linked to areas of human development, which corresponds to protection levels (Watson et al., 2013). Boundaries and buffer zones surrounding parks and reserves typically have lower levels of protection, higher human impacts, and often ecological differences. These in turn can drive variability in snaring and prey depletion that can drive significant differences in prey density, diversity, intraguild dynamics,

and subsequent source-sink dynamics for LACG species (Creel et al., n.d.).

5. Merging conservation science with resource protection to mitigate snaring impacts: an example from collaborative anti-snaring work across Zambia

The drivers, trends, and patterns of snaring are complex and dynamic (Montgomery, 2020). We recognize and strongly endorse the urgent need for long-term, community-based and policy-based solutions to address the ultimate drivers of the bushmeat trade (Lindsey et al., 2013; Masolele, 2018). However, the time scales, political will, and resources required to effectively change policies and implement solutions are very significant, and severe declines and extirpations of LACG populations can occur in the interim. We thus describe a field-based mitigation method merging research and law enforcement, and benefitting from collaborations between government, conservation organizations and research projects. While intensive, this method effectively leverages scarce resources to promote population recovery and mitigate immediate threats from snaring by-catch and prey depletion, while sustainable, longer-term, community-based solutions are developed and implemented.

It is extremely difficult to conduct conservation science work in snaring-impacted landscapes given they are usually prey-depleted, LACG carrying capacity is low, and populations are wide-ranging, elusive, and often declining (Rosenblatt et al., 2014). The use of radio collars is important to gather adequate demographic data, but populations are also continually subject to snaring by-catch mortality and injury that makes turnover of packs, prides, and clans significantly elevated relative to natural systems, and results in extreme challenges to effective research. Research and monitoring work on the species in the LACG typically is conducted in isolation from law enforcement efforts, and funding for both is extremely limited. However, in many landscapes–perhaps most– snaring comprises one of the most significant threats to the viability of carnivore populations. In addition, many of these species are rarely seen, such that it is extremely difficult to detect, much less relocate, a snared carnivore.

Field-based protection (FBP), also known as the “Halo Approach”, adaptively merges anti-poaching, intensive research and monitoring, and veterinary rescue of LACG species (Figs. 1 & 2). To our knowledge this concept was developed by K. Leigh in the LVE for wild dogs and has since been adopted into the country’s LACG strongholds in the Greater Liuwa (2010) and Greater Kafue (2011) Ecosystems. Figs. 1 and 2 describe the FBP method in detail. Fieldwork relies fundamentally on year-round field teams conducting ground-based intensive monitoring of collared groups using GPS/satellite and VHF collar technology. When located, animals are individually identified, and checked for snares. When snared carnivores are detected, a local field-based veterinarian is available to immobilize, de-snare and treat the animals (Banda et al., 2023). Locations and relevant behaviors (e.g., denning) are then regularly provided to anti-poaching patrols who adaptively target areas that are of high carnivore use and of high snaring risk. The advent of Earth Ranger software has enabled both research and law enforcement teams to have a more real-time and holistic understanding of carnivore movements and areas of high risk.

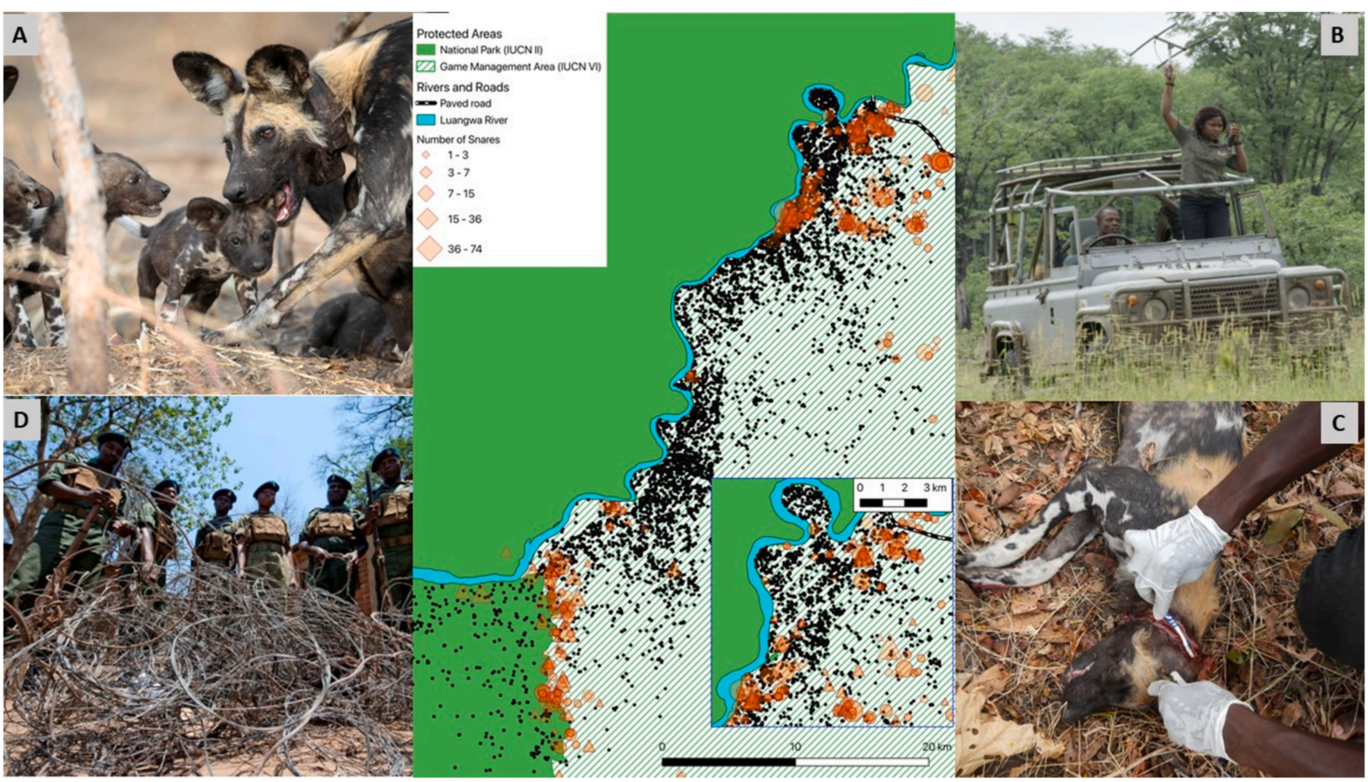

Fig. 1. Field-based protection (FBP) or the “halo effect” originated in the South Luangwa Valley with Conservation South Luangwa, Zambia DNPW, and ZCP, and later expanded into the Greater Liuwa and Greater Kafue Ecosystems with collaborating partners DNPW, African Parks, Panthera, Musekese Conservation, and Mushingashi Conservancy. FBP fundamentally relies on intensively monitored study populations using radio telemetry, Satellite/GPS collar technology (A), and a continual field presence (B) to check for and remove snares. (C) Collar locations (center) are provided to law enforcement to direct patrols into areas of high-use/high-risk for snares (D). While carnivores such as wild dogs frequent areas of severe snaring risk (center, black circles denote dog locations, red denotes snares), FBP work has helped to mitigate snaring by-catch mortality across ecosystems in Zambia, and has assisted in promoting stable and increasing populations negatively impacted by bushmeat poaching (Banda et al., 2023; Creel et al., 2023a). In 2022, these collective efforts enabled intensive monitoring of 1131 wild dogs, lions, cheetah, and hyena in 116 groups (typically 1–2 collars/group) and 13 populations across three ecosystems. This enabled 10,417 snare checks, and 8 successful de-snarings over 33,000 km^2, all while removing snares in high risk areas, providing strong presence and poaching deterrence, and conducting research on snaring and bushmeat impacts. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

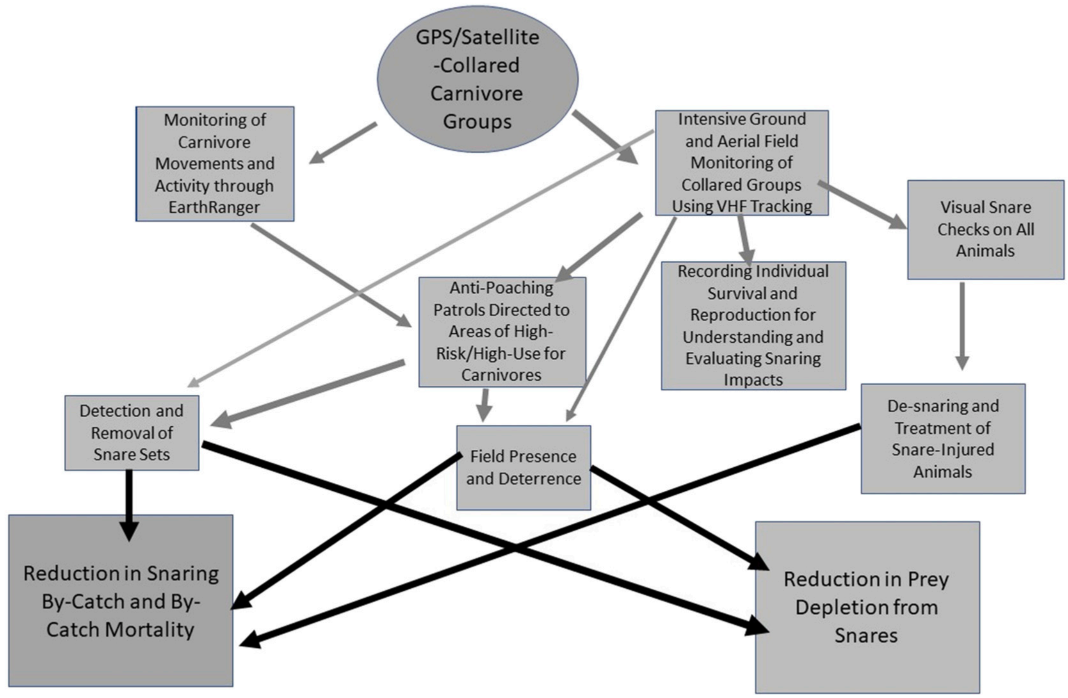

Fig. 2. Conceptual diagram of Field-Based Protection (FBP) method merging intensive research and monitoring with anti-snaring work. This model can be applied to ecosystems heavily impacted by snaring and integrates ongoing research, monitoring, and anti-poaching work.

Because all these species save for leopard are social (to varying degrees), all uncollared individuals in a group can be monitored regularly through the deployment of a single collar on a pack, pride, or clan, and we typically maintained 1–2 collars in a group depending on the species, number of individuals, and snaring risk. Intensive fieldwork and monitoring of these collared individuals and groups using VHF telemetry then provides high-quality, long-term data on snaring and large carnivore dynamics (that form much of the basis of this paper). In 2022, collaborative teams from the Zambian Carnivore Programme, Zambia Department of National Parks and Wildlife, Conservation South Luangwa, African Parks, Musekese Conservation, Frankfurt Zoological Society, Panthera, and Mushingashi Conservancy intensively monitored 1131 individual wild dogs, lions, hyena, and cheetahs in 116 groups across three ecosystems and over 33,000 km^2, collectively conducted 10,417 snare checks on animals, and successfully de-snared eight carnivores – all while collecting important long-term data on 13 LACG populations.

Recent evaluations of this method demonstrate its effectiveness in mitigating snaring threats to carnivore populations. Banda et al. (2023) found that de-snaring LVE lions through FBP resulted in a positive net growth rate for a population that would otherwise decline from by-catch. Similarly, LVE wild dog densities are some of the highest recorded, with the highest recorded for free-ranging populations of the species in South Luangwa National Park (Creel et al., 2023a, In Review, Reyes de Merkle et al., n.d.); a marked difference from prior years in which snaring impacts were greater and wild dog densities were significantly lower (Becker et al., 2013). The combined effect of directed law enforcement patrols in concert with intensive carnivore monitoring and de-snaring efforts helped result in no snared lions detected in 2020, and no snared wild dogs detected in 2021 — the first time this has occurred in over 20 years and 15 years, respectively. Collectively, FBP provides a significant mitigation method that is suitable for an array of snaring-impacted ecosystems rangewide, and can be an impactful system to implement while longer-term sustainable solutions addressing the core drivers of snaring are developed and implemented.

6. Conclusion

The impacts of wire snare poaching on prey depletion, snaring by-catch, and intraguild dynamics are significant and complex, and likely to pose some of the most serious threats to the viability of LACG populations rangewide. Understanding and evaluating the impacts of snaring and how these differ across species and drive changes in intraguild dynamics is important to effectively address the threats of snaring. Significant knowledge gaps and research needs exist to better evaluate and address the severe threat that snaring poses to large carnivores in Africa. Merging conservation science work with resource protection, through such methods as FBP can effectively leverage scarce conservation funding to both provide critical data on these species and mitigate the threats of snaring on large carnivores and their prey.

Declaration of competing interest

The authors have no conflict of interest with this manuscript.

Data availability

No data was used for the research described in the article.

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