A framework for assessing animal behavioural responses to wire snare poaching

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ABSTRACT

Wire snares are among the most common and widely-used techniques for illegal harvesting of terrestrial animals around the world. Recent research has documented the mortality effects of wire snare poaching on animal populations, but the indirect impacts on the behaviour of surviving individuals remain largely uninvestigated. We know little about the short- and long-term effects of snaring injury on the behaviour of animals that survive wire snares. Here, we present a framework for assessing animal behavioural responses to wire snare poaching. Via the framework, we highlight the physiological mechanisms underlying animal responses to being captured, and identify the behaviours affected when animals escape entrapment with injury. We use evidence from mammal species that commonly escape wire snares to highlight the short- and long-term effects of snaring injury on individual animal behaviour, and how they can potentially scale to have population-level consequences. The framework can be used to evaluate the nature of animal behavioural responses to being captured in snares and the resultant effects on their fitness and survival. We identify priorities for research as well as management actions to mitigate impacts of snare injury on animals that survive wire snares.

Key words: wire snares, poaching, snare injury, behaviour

1. INTRODUCTION

Trapping animals is a geographically widespread activity practiced by humans for centuries (Atkeson 1956, Lishak 1976, Englund 1982, Elbroch et al. 2013, de Araujo et al. 2021, Montgomery et al. 2022). People trap animals for several reasons including harvest for food, trophies, or medicament (Proulx et al. 2012, Montgomery 2020), as a means of population control (Quiatt et al. 2002, Mijele et al. 2013), or for research and management purposes (McCarthy et al. 2013, de Araujo et al. 2021). Research and management trapping often intends to live capture animals for scientific data collection, monitoring, or relocation (Mowat et al. 1994, Logan 1999, Gompper et al. 2006, Sawaya et al. 2011, Breed et al. 2019, de Araujo et al. 2021). In contrast, trapping for possessions and consumption typically involves the lethal take of animals, and may be conducted legally or illegally. Though the consequences of widespread illegal trapping for animal conservation and population persistence have been documented (Gray et al. 2017, Gray et al. 2018, Belecky & Gray 2020, Figel et al. 2021), the life history costs for animals that escape from the traps with injury remain largely uninvestigated.

Illegal trapping is a global problem but one that is particularly intense in parts of Sub-Saharan Africa, Southeast Asia, and South America, regions collectively referred to as the Global South (Gray et al. 2017, Gray et al. 2018, Belecky & Gray 2020, Figel et al. 2021). Within these areas, snares are the most common tool used by people to illegally harvest animals (Gray et al. 2017, Gray et al. 2018, Belecky & Gray 2020, Figel et al. 2021). Snare traps can be made using a diversity of products from rope to wire (see Box 1). In any case, one end of the snare is attached to an anchor (i.e., often a tree) and the other made into a noose to capture the target animal (Mudumba et al. 2021). Even though snares are often set to capture specific species, the technology is indiscriminate and capable of capturing target and non-target species alike (Noss 1998, Gardner 2010, Becker et al. 2013, Campbell et al. 2019, Montgomery 2020). Snares are commonly deployed in large numbers, and some can remain undetected by both hunters and law enforcement patrol teams. As such, snares can be a widespread source of mortality for several species (Becker et al. 2013, Kumar 2015, Gray et al. 2017, Gray et al. 2018, Campbell et al. 2019, Belecky & Gray 2020, Figel et al. 2021). Once caught however, some species can break from the snare constriction and often sustain debilitating injuries in the process (Berchielli & Tullar 1980, Noss 1998, Proulx et al. 2015, Proulx & Rodtka 2017).

Research on the effects of wire snare poaching has tended to focus on direct, mortality-related impacts (Aziz et al. 2017, Becker et al. 2013). Within that context, rates of animal offtake and population-level effects of illegal hunting, for example, have been documented (Fa et al. 2005, Ripple et al. 2016, Gray et al. 2017, Gray et al. 2018, Gubbi et al. 2021). Additionally, some studies have investigated effects on social organization, kinship, and genetic structure resulting from selective offtake of individuals from animal populations via poaching (Archie & Chiyo 2012). Other studies have examined the socioeconomic factors affecting why some people illegally hunt animals (Ceppi & Nielsen 2014, Cawthorn & Hawthorn 2015, Nielsen et al. 2017, Nieman et al. 2019). In contrast, few studies have examined the mechanistic links between snare entrapment and the resultant behavioural changes that shape the fitness outcomes of captured animals. In addition, the life history costs of animals with snare-related injuries have not been widely studied. Consequently, accurate estimation of population-level effects of snaring would require examination of life history costs of snaring injuries in addition to the direct mortality effects. Such knowledge would be integral for management of comparatively long lived and slow reproducing species of conservation concern that are often caught as bycatch (Loveridge et al. 2020).

Injuries sustained when animals escape snare traps can include soft tissue lacerations, joint dislocations, haemorrhages, severe internal organ damage, broken teeth or amputated limbs (Kuehn et al. 1986, Olsen et al. 1986, Olsen et al. 1988, Phillips et al. 1996, Obanda et al. 2008, Proulx & Rodtka 2017; White & Valkenburgh 2022; Bernstein-Kurtycz et al. 2023; Fig. 1). By altering the normal anatomical functioning of the animal's body, snare-related injuries may cause substantial changes to behaviour of affected animals. The extent and type of behavioural change among snare-injured animals, however, would be expected to depend on the affected body part, injury severity, environment, as well as species' trophic position (a quantitative measure of its energetic interactions) in the food web. For example, limb injuries which reduce animal movement interferes with ability to locate and compete for resources, mate, and defend against predators (Noss 1998, Cattet et al. 2008). Ultimately, the injured animal would likely die prematurely due to infection, predation or starvation (Daoust & Nicholson 2004, Proulx & Rodtka 2017). Limited empirical investigations as well as lack of synthesis of existing literature limit our understanding of the extent of behaviour change, morbidity, as well as the short- and long-term life history costs of bearing snaring injury. Without a comprehensive examination of the costs of bearing injury among snare survivors, we risk overlooking important conservation and management considerations that might be useful for population persistence, especially for species of conservation concern, amidst the increasing the snaring pressure.

In this paper, we present a novel framework for assessing animal behavioural responses to wire snare poaching. By synthesizing broad literature and theory, we outline the mechanisms that underpin animal behavioural responses to snaring, from capture to death or escape with injury. We then discuss the behavioural pathways through which snaring injuries affect the life history strategies of affected animals. We link the documented animal behaviour changes due to snare-related injury to established or hypothesized individual-level survival costs and population-level consequences. Finally, we explore the conservation and management implications and discuss the important research gaps in this area of study that need to be filled.

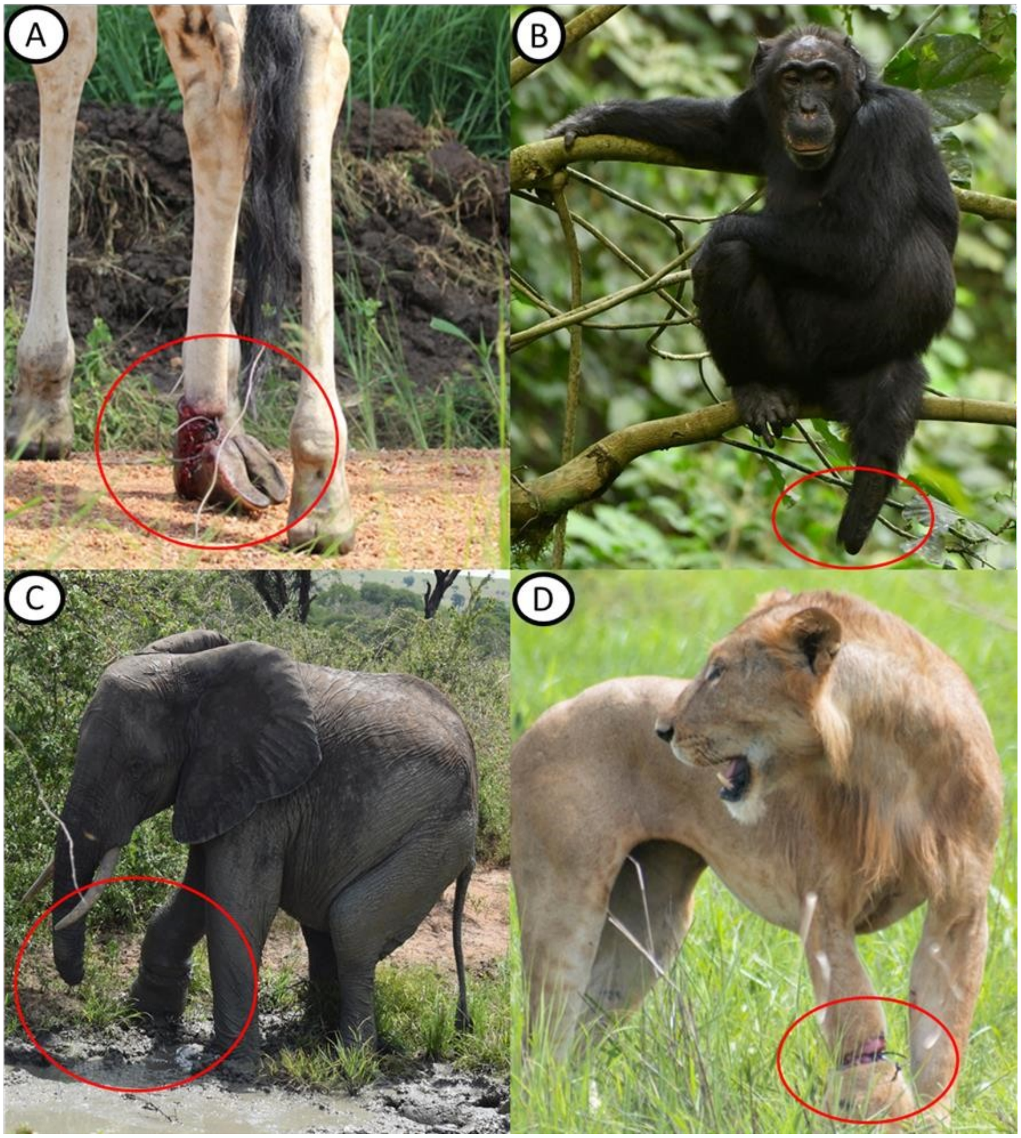

Figure 1. Limb injuries sustained by animals when escaping snare entrapment including a) Rothschild's giraffe (*Giraffa camelopardalis*) b) Chimpanzee (*Pan troglodytes*) c) African savanna elephant (*Loxodonta africana*) and d) African lion (*Panthera leo*).

2. FRAMEWORK LAYOUT

The framework describes the pathway from snare capture to behavioural changes which determine fitness outcomes of affected animals. Thus, the framework is structured around four sequential dynamic events: *i)* snare capture triggers stress-induced fighting to break free; *ii)* the fighting animal either dies or escapes with injury; *iii)* the surviving animal then experiences altered behaviour; *iv)* altered behaviour has implications for its fitness and welfare (Figure 2). We discuss these events to establish a foundation for assessing capture-induced consequences for individual behaviour, fitness, and population growth. We demonstrate, with evidence from mammal species that commonly escape wire snares, how animals are affected by snaring injuries. Mammals are a taxonomic group that is mostly targeted and thus disproportionately affected by illegal snaring.

3. THE MECHANISMS OF ANIMAL BEHAVIOURAL RESPONSES TO SNARING

Getting caught in a snare could alter the affected animal's behaviour via several mechanistic pathways. When captured, animal behavioural responses are linked to increased stress levels (Lynn & Porter 2008, Dickens et al. 2009, Dickens et al. 2010, Breed et al. 2019). Restraint, fighting to break free, and resultant injuries cause physiological and psychological stress as well as extreme pain among animals captured in snares (Powell 2005, Reeder & Kramer 2005, Figs. 1, 2). Stress among vertebrates is characterized by somatic or physiological challenges to homeostasis which increase the concentration of glucocorticoid hormones (cortisol and corticosterone) produced by the adrenal cortex along the hypothalamic-pituitary-adrenal axis

(McEwen 2008, Dantzer et al. 2014, Haase et al. 2016). The rise in the concentration of glucocorticoids can drive animals into restless states when captured in snare traps (Santos et al. 2017, Figs. 1, 2). As such, captured animals often fight vigorously to break free (Frank et al. 2003, Powell 2005, Fig. 2). In the process of fighting however, the snare noose tightens and cuts into the skin and flesh of the animal. When captured by the neck, the fighting animal could die due to strangulation or survive with catastrophic injury (Benhaiem et al. 2022). When captured by the limbs, the animal could suffer dislocation, sustain fractures or break the snare with a debilitating injury. When captured by the torso, the injuries may cause disembowelment.

Stress hormones affect animal behavioural responses via signalling the upregulation or downregulation of relevant physiological systems, such as immune systems, metabolic systems, nervous systems, and others (Moore & Orchinik 1994, Windle et al. 1998, Sapolsky et al. 2000). When snaring injuries are extreme or prolonged, affected animals may become distressed with negative consequences for their health and survival (von Holst 1998, Moberg 1999). Distressed animals can deplete their energy reserves with implications for other biological functions including reproduction, tissue growth, and immune responses (Cattet et al. 2003, Reeder & Kramer 2005, Fig. 2).

In addition to physiological stress, psychological stress could be another pathway by which animal behavioural changes as a response to snaring pressure could occur (Teixeira et al. 2007, Santos et al. 2017). Snaring events could cause fear, anxiety, and frustration among injured and non-injured animals within affected populations. Among injured animals, the levels of psychological stress likely depend on the sex, age, reproductive condition or degree of sociality for the species (Reeder & Kramer 2005, Santos et al. 2017). The psychological stress of animals that escape snares could lead to increased aggression and altered movement. Additional behavioural responses induced by psychological stressors include escape or avoidance behaviours, altered cognition and attention span, stress-induced analgesia, as well as suppression of feeding and reproduction (Reeder & Kramer 2005).

Another pathway by which snaring may affect animal behaviour is via total or partial paralysis of the injured body parts. Paralysis can have negative consequences for animal activity due to nerve damage which results in the loss of voluntary control of the affected body parts (Hobaiter & Byrne 2010). In addition to paralysis, behavioural effects may manifest due to paresis, a condition in which muscular weakness leads to deficiency in the generation of gait or ability to support body weight (Crilly et al. 2015). Paresis could result from the fracture or amputation of animal body parts. Unlike paralysis, injured animals with paresis can maintain a degree of voluntary movement, albeit with extreme pain (Crilly et al. 2015). Further, body temperature and cardiac rate among captured animals have been suggested to be determined by the intensity of physical exertion caused by response to entrapment (Cattet et al. 2003). Trapped free ranging wolves (*Canis lupus*), for instance, have been found to have lower cardiac rate and rectal body temperature than normal conspecifics (Santos et al. 2017). Thus, snare-injured animals are likely to have reduced energy reserves compared to non-injured individuals.

Finally, animals may exhibit behavioural responses to snaring pressure via cognition. Given their cognitive abilities, primates for example, have been suggested to have learned the potential danger of snares and have been recorded to deactivate snares safely (Ohashi & Matsuzawa 2011, Sugiyama & Humle 2011). Particularly, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) were observed to remove snares from limbs of affected conspecifics (Amati et al. 2008, Boesch & Boesch-Achermann 2000, Tokuyama et al. 2012). In addition, mountain gorillas (*Gorilla beringei*) have been recorded to exhibit snare awareness behaviour including avoidance, displays near the traps, and biting group members who approach snares (Williamson 2005). It remains unclear, however, whether animals outside of great apes can avoid areas of intense snaring pressure.

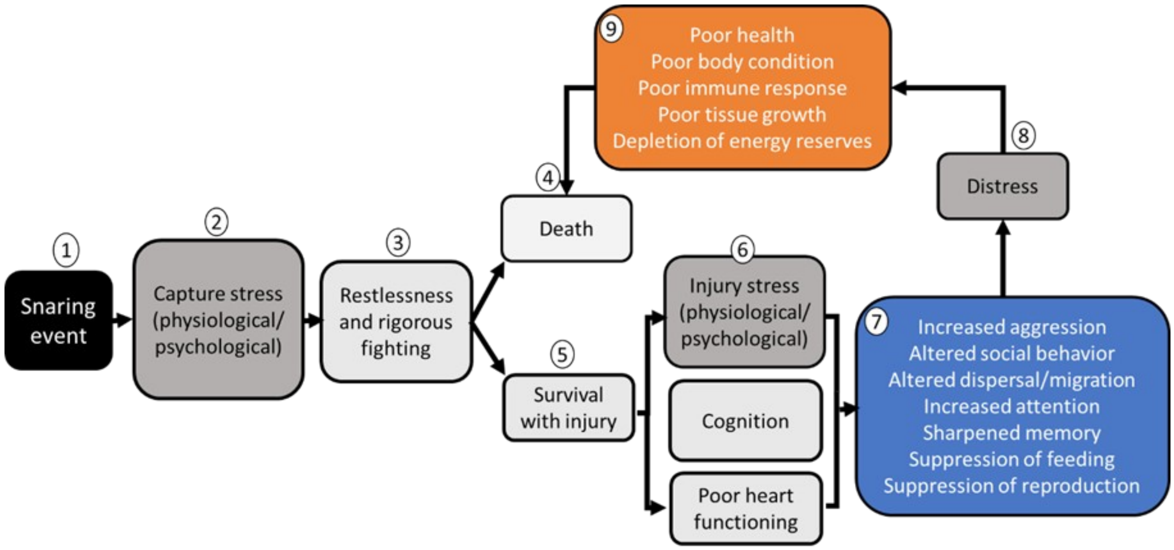

Figure 2. Mechanisms underlying animal behavioural responses to wire snare poaching. Arrows indicate progression of events. When an individual animal is caught in a snare (1), it experiences a rise in stress hormones (2) which triggers restless behavioural states and rigorous fighting (3) in attempt to escape entrapment. Captured animals could die due to strangulation or catastrophic injury (4) or break free with a non-lethal injury (5). Animals that break free with injury could experience additional stress, altered cognition or poor cardiac functioning such as bradycardia (6). The resulting behavioural responses (7) might include increased aggression, altered social behaviour, altered movement and others. Depending on the longevity of the injured animal, cumulative injury-induced stress could result into distress (8). The distressed injured animal can experience significant reduction in activity due to depletion of energy reserves, poor nutrition, and tissue growth with negative impacts on the animal’s overall health (9). Eventually, the injured individual dies.

3.1 The role of environmental context and predation risk effects

The habitat in which animals are snared may modulate their behavioural responses and fitness outcomes. For example, by avoiding areas of intense snaring pressure, some species may be forced to utilise suboptimal habitats (Williamson 2005). Further, animals with severe snare injuries may experience significant reductions in their activity (Munn 2006, Santos et al. 2017). While animals with less severe injuries may not have observable significant impacts on their movement and foraging times (Munn 2006, Stokes 1999). Thus, the injured animals could select habitats in which they do not require long distance or constant movements in pursuit of critical resources such as food and water. Ultimately, injured animals must make the critical trade-off between forage availability and quality. Among Chacma baboons (*Papio ursinus*), for example, injured individuals were observed to feed more on raided high-return foods from human habitations (Beamish & O'Riain 2014). When reduction in the ability to move occurs in areas with insufficient or low-quality resources, the body condition of animals with snare injuries is likely to deteriorate, leading to reduced fitness. Conversely, animals injured within a habitat of high resource productivity are likely to maintain healthy body condition if their feeding pattern is not altered. The type and severity of snare injury in this case would be the limiting factor to its fitness.

Similarly, to promote survival and reproductive success via maximizing nutritional intake, snare-injured animals would be expected to exhibit some control for the risk of predation in the areas and times that they choose to be active (Creel 2018). We suggest that strategies employed by snare-injured animals to minimize predation risk could be more proactive than reactive because of the handicap (Creel 2018). Based on the type and severity of the injury, as well as the level of risk of the habitat in which the animal is injured, we predict two possible strategies that injured animals may employ to reduce predation risk. We consider injuries that interfere with the injured animal's natural ability to defend against predation, such as limb injuries that diminish running and kicking. First, when injured in areas of high predation risk (i.e., with a high density of predators), the injured prey would be expected to feed during times that are less risky, maintain high levels of vigilance as well as associate closely with other conspecifics in social groups. Related to this, they may need to select areas of poorer quality nutrition-wise but are lower in predation risk. Second, when injured in habitats that are less risky (i.e., with a lower density of predators), injured animals may be less risk-averse in the times that they forage, in their amount of vigilance, as well as the degree of association with conspecifics. Lastly, when injured in areas with no predation risk, the habitat selection and use dynamics of the injured animals would be driven only by resource-related factors, such as the need to minimize competition.

4. ANIMAL BEHAVIOURS AFFECTED BY SNARING INJURIES

4.1 Movement

Animals caught in snares often sustain injuries when they break the wire to escape entrapment. Injuries on the limbs pose challenges to animal movement (Figs. 3, 4). The degree of movement difficulty among injured animals, and subsequent impacts on energy expenditure, depends on the severity of the injury (Munn 2006). For example, movement within tree branches may be impaired among primates when their hands are cut off, deformed, or paralyzed by snare-related injuries (Munn 2003, Hermans 2011). However, chimpanzees with forelimb injuries have been observed to modify their locomotory techniques to navigate the canopy (Munn 2006; Qiatt

1996). Additionally, severe injuries among female chimpanzees have been found to reduce their daily travel distances (Munn 2006). Similarly, large herbivores such as giraffes (*Giraffa camelopardalis*) move with extreme difficulty when their legs have snare injuries (Kasozi et al. 2022, Bernstein-Kurtycz et al. 2023, Fig. 1). Leg-hold trapping has been found to significantly reduce the movement of wolves (Santos et al. 2017), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) (Johnson & Pelton 1980, Cattet et al. 2008). In extreme cases, self-mutilation has been recorded in captured raccoons (*Procyon lotor*), with consequences for movement and digging behaviour (Atkeson 1956, Berchielli & Tullar 1980, Proulx et al. 1993). In East Africa, limb injuries to elephants (*Loxodonta africana*) due to snares are prevalent (Fig. 1), leading to negative effects on movement (Obanda et al. 2008, Mijele et al. 2013). Movement difficulty among snare-injured animals arises from the inability of the affected limb to support the body weight of the animal and to generate a stride (Basu et al. 2019). Thus, snaring injuries on animal limbs may negatively affect locomotor dynamics via distortion of the distribution of the vertical impulse (i.e., the integral of the vertical force throughout the stride duration) (Griffin et al. 2004, Basu et al. 2019).

4.2 Feeding and Foraging

Effects of snaring injuries, and the associated infections that may arise, can be expected to alter the feeding and foraging dynamics of animals in both direct and indirect ways (Fig. 3). Direct effects of snaring injuries on feeding can occur when affected animals are caught around parts of their body that are critical for food intake. For example, carnivorous mammals have been observed to chew on the snare wire with subsequent injuries to their teeth and jaw (Kuehn et al. 1986, Benhaiem et al. 2022, White and Van Valkenburgh 2022). In such cases, the injured animals may no longer be able to consume prey (Fig. 3,4). Additionally, injuries to the neck may interfere with the ability to consume and ingest food and water. Snare injuries to elephants can include the loss of a part or whole trunk (Fig. 1), which considerably alters their ability to both handle and process food items and drink water (Obanda et al. 2008). Among primates, severed limbs as a result of escaping wire snares impair their ability to handle and process food (Byrne & Stokes 2002, Stokes & Byrne 2001). Thus, snare-injured animals may employ suboptimal techniques, such as using their mouth for food processing (Byrne & Stokes 2002). Alternatively, disabled animals may focus on high-quality foods that require less processing time from their habitat (Stokes & Byrne 2006) or food from human habitation (Beamish & O'Riain 2014). The foraging ability of animals could also be impaired by snaring pressure indirectly via reduced movement. In cases of severe injuries that completely compromise animal movement, affected individuals could be unable to access forage and water, or lose the ability to pursue, subdue and handle prey. In addition, disabled Chacma baboons (*Papio ursinus*) have been observed to spend more time travelling and resting than feeding (Beamish & O'Riain 2014). Given their inability to obtain and process high-quality forage and to pursue subdue and handle prey, the injured animals are likely to feed less effectively, possess compromised immune systems, and consequently display poorer body conditions compared to able bodied conspecifics (Yersin et al. 2017).

4.3 Anti-predator behaviours

Snaring injuries can also affect anti-predator behaviours of animals. First, by diminishing movement, snare-injured prey species can quickly succumb to the pursuit of predators (Figs. 3, 4). Additionally, reduced mobility of snare-injured animals among social species might lead to isolation from social groups, as observed among chimpanzees (Munn 2003). Given the isolation, the snare-injured animals may often not obtain the reduction in predation risk conferred by associating in groups (Kasozi & Montgomery 2020, Figs. 3, 4). Further, snaring injuries may interfere directly with the antipredator behaviours of many mammal species by disfiguring body parts critical for defence against predators. For example, snare-injured limbs may diminish the animal's ability to fight and escape predators. Among giraffes, snare injuries on the legs have been found to disproportionately affect locomotor dynamics via reducing stride length, speed, and altered gait symmetry (Bernstein-Kurtycz et al. 2023). Snaring injuries may also affect habitat use and selection dynamics of affected animals, with respect to minimising the risk of being detected by predators. To minimize the risk of predation, injured animals may select less risky times and places to engage in active behaviour such as foraging (see Section 3.1). Similarly, it is likely that species in high snare density landscapes may have higher flight distances and become more vigilant and aggressive to the presence of humans within their habitats due to the constant persecution.

4.4 Mating and reproduction

The reproductive ability of animals may be affected in both direct and indirect ways due to snaring injury. For example, being rescued or breaking free from a wire snare, with physical injury and associated ill health, can lead to the loss of social rank of affected animals by reducing their ability to compete for mates (Lovell 1991, Fig. 3). Snaring injuries could not only affect an animal's capacity to pursue mates, but also diminish the ability of males to mount females. Females could also lose their ability to support mounting males during copulation. Furthermore, the impact of snare injuries on reproductive success may manifest through restriction of female ability to care for their offspring (Lovell 1991; Munn 2003). Among hyenas (*Crocuta crocuta*), a long-term study found that debilitating snaring injuries among females that had not yet given birth to litter delayed age at first reproduction by ~0.74 years (Benhaiem et al. 2022). In addition, the injured females tended to have fewer offspring which had a lower probability of survival to one year compared to litter of able-bodied females (Benhaiem et al. 2022). The energetic costs of tissue repair and immune responses to morbidity resulting from snaring injuries divert resources from reproductive functions when female animals prioritize their own survival (Festa-Bianchet et al. 2019). Snaring injuries have been recorded to cause foetus mortality among leopards (*Panthera pardus*) rescued from snare traps in India (Kumar 2015). The age at which animals obtain injuries likely determines the impact on their survival and reproduction. Among hyenas in Serengeti National Park, subadult females are more likely to die shortly after escaping snares than adults (Benhaiem et al. 2022). High levels of stress hormones over extended periods have the potential to diminish reproductive function, decrease immunity and muscle function, and increase mortality risk (Wingfield & Sapolsky 1999, Saplosky et al. 2000, Reeder & Kramer 2005). A study of African elephants found that long term stress related impacts of poaching persist among matriarchs and have long term impacts on their reproductive output (Gobush et al. 2008). It remains to be established whether such effects manifest in other long lived large mammals. Overall, consistent with life history theory, we predict that snare-injured animals would allocate their limited resources (time, effort and energy) more to activities that promote survival (such as feeding and evading predation) than mating, with implications for population dynamics.

4.5 Group association

Snaring injuries can also impact the social behaviour of affected animals. Research on this topic has been explored among primates, particularly chimpanzees. For instance, snare-injured female chimpanzees have been recorded to associate in smaller groups than non-injured females (Munn 2003, Hermans 2011). These observations have been interpreted to reflect amelioration of food competition associated with larger groups (Hermans 2011). Similarly, snare injuries have also been found to negatively affect chimpanzee mothers' ability to carry their offspring (Munn 2003, 2006). Among male chimpanzees, snare injuries have been found to alter ability to compete for higher social ranks and to defend territory from rival chimpanzees (Smith 1995). We suspect that similar behavioural impacts are relevant among non-primate social species, but additional research is required to quantify such effects.

4.6 Grooming

Finally, snaring injuries can also impact grooming and body maintenance. Animals with disfigured, injured, or paralyzed body parts lose their ability to clean or maintain their own and/or conspecific's bodies. By disrupting body grooming capabilities, snaring injuries may indirectly break social bonds and disrupt social structure and family links (Munn 2003). When wire snares cut off elephant trunks, they affect trunk functions useful in body maintenance such as siphoning and spraying water and sprinkling dust. The application of water and dust is an important thermoregulatory behaviour that enables elephants to cope with environmental temperatures that exceed their body temperature (Mole et al. 2016). Similarly, primates with injured or paralyzed hands lose their ability for body grooming and scratching (Hobaiter &

Byrne 2010), behaviours that are critical for managing external parasites and skin irritation (Nakamura et al. 2000). The inability to auto groom their body coupled with the tendency to reuse old nests expose injured chimpanzees to build up of both internal and external parasites with negative consequences for their immune function (Plumptre & Reynolds 1997, Sadd & Schmid-Hempel 2009, Hobaiter & Byrne 2010, Strait et al. 2012, Yersin et al. 2017). Additional research is required to quantify the impacts of snaring injuries on grooming and body maintenance behaviours across mammals.

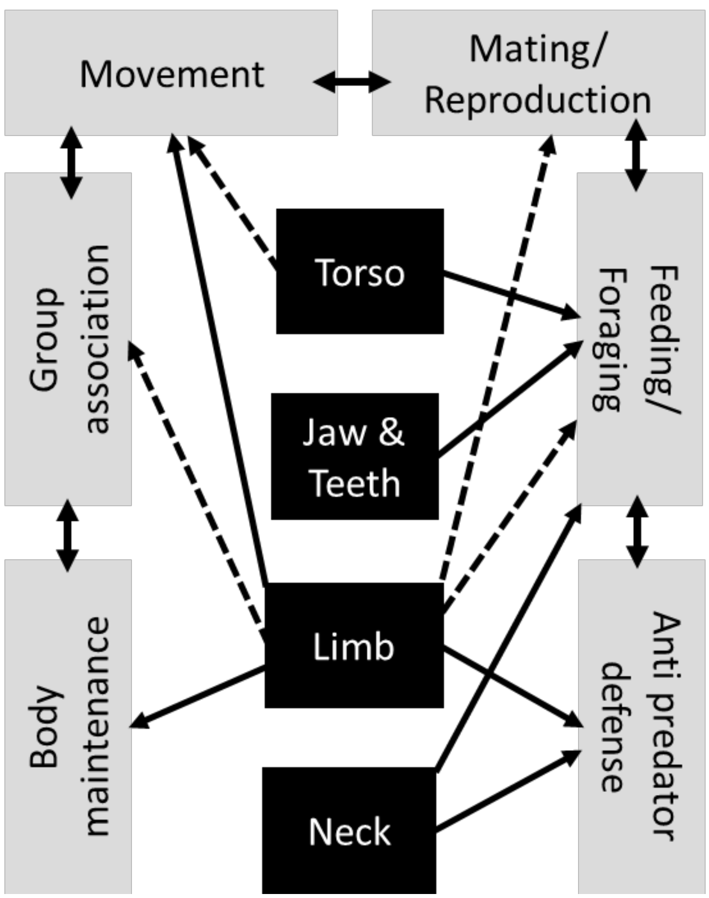

Figure 3. Animals can sustain snaring-related injuries to a number of body parts (black) with subsequent behavioural impacts (gray). These behavioural impacts will vary according to the

body part affected and the severity of the injury. The solid arrows represent direct links between injured body part and affected behaviour whereas the dotted arrows indicate indirect links.

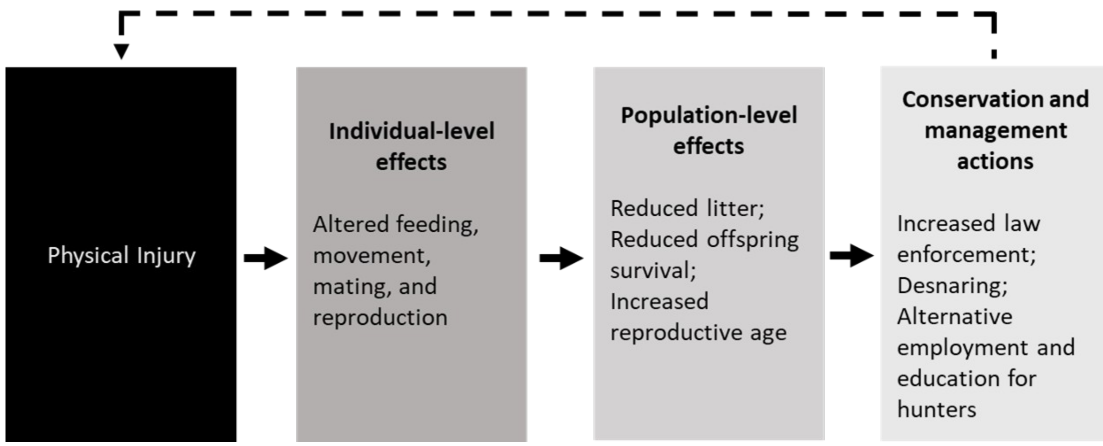

Figure 4. Consequences of snaring injuries for affected individual animals and populations. The short arrows indicate progression of events. Conservation and management interventions are needed not only to mitigate the impacts of wire snare poaching, but also bring it to an end.

5. IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Integrating information about how animals change their behaviour due to wire snare poaching into management programmes hinges on proper evaluation of the physiological, reproductive, welfare, and mortality effects on snare survivors. To compensate for effects of snare injuries, animals may respond by feeding on high quality foods that require less processing and handling time, and may obtain these from human habitation or agricultural farms (Beamish & O'Riain 2014). In effect, this may accelerate human wildlife conflict and expose animals to additional human persecution (Beamish & O'Riain 2014). Such conflicts pose challenges to the management of snare injured individuals. On the other hand, evaluating the physiological effects of snare injuries may provide useful insights on animal performance which may not be apparent through behavioural observations or injury scores (Proulx et al. 2022). Monitoring snare-injured animals post rescue and treatment is needed to examine whether immediate release was a wise option for the welfare of the animal as well as for the possibility of injured animals raiding crops or depredating livestock. Information such as this is needed to inform future decisions on what is survivable, especially among species of conservation concern where every individual is important for population persistence. In addition to the physiological costs of wound healing, there may be external interference to wound healing by factors such as birds (Weeks 2000, Diplock et al. 2018). Extended exposure of open wounds could cause additional infections to the affected animal, with implications for reproductive performance and offspring care (Benhaiem et al. 2022). As illegal animal harvest increases in many landscapes across the Global South, additional resources need to be directed to snare removal programmes to mitigate mortality and sublethal effects of wire snares. While snare removal programmes are useful, they remain a temporary solution that may not be sustainable in the long term. Perhaps the best strategies to mitigate snaring effects on animal populations are those that address the underlying drivers of poaching. While discussing these strategies lies outside the scope of the present paper, we encourage increased collaboration among researchers, managers as well as political officers to create opportunities that address the underlying causes of poaching.

6. Implications for future research

A significant limitation in existing literature relates to the unquantified life history costs of surviving snaring with an injury across different species. At the same time, we know little about associated changes in the ecological function of communities and ecosystems when several individuals of different species are killed or injured by wire snares. Measuring the consequences of wire snare poaching on animal populations presents challenges associated with quantifying the mortality of both target and non-target species and the long-term life history costs among individual animals that escape snares with injuries. In any case, poachers harvest the majority of the snared animals before they are detected by management and researchers. Furthermore, few individual animals which escape snares with injuries survive long enough to be detected by managers and scientists. Such challenges complicate efforts to accurately assess the full extent of damage caused by snares.

Our framework emphasizes the need for investigations of behavioural responses and fitness costs for animals that survive snaring with injuries. While the physiological mechanisms linking behavioural effects of capture to death or escape with injury may seem complex and difficult to measure (Figure 2), our framework outlines pathways that can facilitate predictive modelling of fitness outcomes. We encourage the development of modelling frameworks for estimating relationships among animal behaviours and fitness outcomes of snare-injured animals. To predict the fitness outcomes of bearing injury, such models would require empirical measurements of different animal behaviours and ecological functions affected by snaring injury. As such, we suggest sustained monitoring of the movements of injured animals using GPS telemetry techniques as well as collecting data on animal health using suitable sensors. The sensors and GPS tags could be conveniently deployed on the animals during rescue and veterinary treatment. Accurate measurement of behaviour of injured animals is critical to estimating and predicting health implications as well as fitness costs of bearing injury.

Thus far, studies have measured the reproductive costs of bearing snaring injuries (Benhaiem et al. 2022), the impacts of injuries on movement (Bernstein-Kurtycz et al. 2023), forensic examination of carnivore skulls and teeth (White & Valkenburgh 2022) in a few species. A key step in progressing research examining the effects of wire snare poaching is to broaden the range of behaviours that are monitored and assessed across several affected species. Future research may compare the social behaviour and movements of animals in areas of high poaching activity to that in areas with less poaching. We argue that the type and severity of injuries might determine the level of activity of affected animals, and influence the types of interactions with both conspecifics and heterospecifics. Additional research may consider examining activity budgets, foraging strategies, and trophic interactions of animals rescued from wire snares with injuries of varied levels of severity. Such research might also provide insights into the energetic costs of bearing injury. Further studies may also consider specifically investigating the ecological consequences of losing keystone species to illegal poaching as these are more likely to result in detectable ecological change. Additionally, these could provide an upper bound in terms of anticipated outcomes for other species.

Overall, a major factor hindering the progress of research on the impacts of wire snare poaching on animals relates to the lack of data. We appreciate that data on animals that are killed and those that escape wire snares are hard to obtain. Because animals may be harvested before being detected or because of the lack of capacity and resources needed to conduct field monitoring. The lack of data limits our ability to analyse and uncover patterns and trends in animal responses to wire snare poaching. We encourage researchers and managers to collect and curate long-term datasets on snare locations, demographic patterns of detected animals that are killed or rescued from snares, as well as individual and population-level behavioral responses to wire snare poaching.

7. CONCLUSION

Our synthesis highlights consequences of snaring injuries for animal behaviour. Snaring injuries can substantially change the behaviour of snare survivors, via alteration of movement (Kasozi et al. 2022, Bernstein-Kurtycz et al. 2023), feeding (Byrne & Stokes 2002, Stokes & Byrne 2001), mating (Benhaiem et al. 2022) and social interactions (Archie & Chiyo 2012, Munn 2003, Hermans 2011). In turn, the snaring injuries supplement the mortality effects of wire snare poaching and translate into long term physiological, behavioural and welfare effects that are currently unmeasured for many species. Given the potential for the sublethal effects of snare related injuries to interfere with reproduction due to heightened physiological stress, poaching has additional indirect effects that may limit expansion of the surviving wildlife populations. These impacts are relevant to the conservation and population persistence of long-lived and slowly reproducing species of conservation concern. Thus, accurate examination of the population-level effects of wire snare poaching among such species would require quantifying both direct lethal and indirect sublethal effects on individuals that escape wire snares. We encourage novel research that empirically examines both the short-term and long-term impacts of snare related injuries on the performance of snare survivors. Specifically, the effect of snaring injuries as a limiting factor for animal reproduction requires further investigation. Outputs from this research will be useful for determining how these effects might scale to have population-level ramifications additive to the mortality effects. Overall, research examining animal behavioural responses to wire snare poaching may provide important additional information on the ways in which humans as super predators shape animal populations for both target and bycatch species.

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Box 1: Evolution of snare technology for animal trapping

Snares are commonly used to illegally trap animals because they are cheap to produce, simple to set in large numbers, and can capture a diverse range of animals (Proulx et al. 2019, Belecky & Gray 2020). Snare traps are anchored to trees with a free end formed into a flexible noose held off the ground at the approximate height of the animal target (Fig. 1.1). The noose captures animals around the neck, body, or leg when triggered (Fig. 1.1). Earliest snare traps were made from plant or animal sources such as bark, lianas, rattan, rawhide, or hair cords (Phillips et al. 1990, Belecky & Gray 2020). Given their organic nature, these snares lacked the flexibility and strength required to restrain or kill animals (Phillips et al. 1990). Consequently, trappers frequently checked the snares to harvest captured animals before they chewed or broke the organic loops. In addition, the organic loops would sometimes decay or get weakened by arthropods which fed on them before they captured animals (Phillips et al. 1990). Given these deficiencies, snares today are typically made of metal components (e.g., wires from radial vehicle tires, motorcycle brake cables, locks, swivels, fences and powerlines). The wire snares are more efficient and versatile than those made from organic materials. The availability of metal components for making wire snares may be linked to increasing development in society.

Figure 1.1. a) Wire snare trap set to capture animals, b) Deactivated and confiscated wire snare traps, c) Rescuing a waterbuck (*Kobus ellipsiprymnus*) from a wire snare, d) A Uganda Kob (*Kobus kob*) killed in a wire snare. All images taken in Murchison Falls National Park, Uganda, a system experiencing high rates of wire snare poaching.