Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Long-term reproductive costs of snare injuries in a keystone terrestrial by-catch species

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Keywords
snare injury; illegal bushmeat hunting; reproductive costs; spotted hyena; by-catch; wire snare; life history; Serengeti National Park.

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Editor: Vincenzo Penteriani
Associate Editor: Elissa Cameron

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Received 16 June 2021; accepted 29 April 2022

doi:10.1111/acv.12798

Abstract

Extensive bushmeat hunting is a major threat to wildlife conservation worldwide, particularly when unselective methods such as wire snares kill target and non-target species (by-catch). Animals that escape from snares have injuries of varying severity, with effects on performance that are largely unknown, as most studies typically focus on immediate mortality caused by snaring. Here, we assessed the life-history costs of debilitating snare injuries in individually known female spotted hyenas *Crocuta crocuta* in three clans in the Serengeti National Park, Tanzania. This keystone predator is a regular by-catch of illegal bushmeat hunting of herbivores in the Serengeti ecosystem. We monitored individuals which escaped from snares between May 1987 and March 2020 and survived long enough to return to their clan territories from commuting trips in the park and surrounding protected areas. Snares that inflicted debilitating injuries on females did not reduce longevity but did delay age at first reproduction and reduced both litter size and offspring survival to the age of 1 year. This long-term decrease in reproductive performance likely resulted from increased inflammatory and immune responses to the snare injury and/or a decreased ability to travel the long distances necessary to feed on migratory herbivores. While our results are based on a relatively small sample of females with debilitating injuries, they suggest that the total population-level costs of wire snares in terrestrial by-catch species may be underestimated and that future studies may need to account for the potential reproductive costs of sublethal snare injuries.

Introduction

The extensive consumption of bushmeat is a major threat to wild terrestrial mammal populations, particularly for long-lived, slowly reproducing species, in parts of Africa, Southeast Asia and South America (Lindsey *et al*., 2013; Ripple *et al*., 2016; Tilker *et al*., 2019; Loveridge *et al*., 2020). Wire snares are an effective and inexpensive method used to capture bushmeat species (Hofer *et al*., 1996; Muchaal & Ngandjui, 1999; Gray *et al*., 2018; Tilker *et al*., 2019). Due to their unselective nature, snares also capture non-target species, including predators attracted to carcasses in snare lines (Wolf & Ripple, 2016), which results in substantial by-catch (Hofer, East & Campbell, 1993; Becker *et al*., 2013). For instance, a recent study revealed a high proportion of non-lethal snare injuries in several carnivore species in Zambia, with evidence of snare entanglement greatly surpassing previous estimates for these regions (White & Van Valkenburgh, 2022).

In terrestrial ecosystems, although animals caught in wire snares typically die, some may escape with injuries that vary in severity. The physiological and immunological costs of wound healing on female reproductive success, when wounds were caused by factors other than snares, have been reported from some long-term research studies (e.g. Hawaiian monk seals *Monachus schauinslandi*: Hiruki *et al*., 1993; yellow baboons *Papio cynocephalus*: Archie, Altmann & Alberts, 2014). As most studies on the consequences of bushmeat hunting on wildlife populations focused on the demographic, genetic or behavioral consequences of immediate snaring mortality (e.g. Hofer *et al*., 1993; Kenney *et al*., 1995; Sukumar, Ramakrishnan & Santosh, 1998; Archie & Chiyo, 2012), virtually nothing is known about the outcome, in terms of longevity and reproductive success, for individuals that escape from snares. Any potential negative fitness consequences of injuries in animals that escaped from snares may thus constitute additional population-level costs that have been largely neglected. Such costs may be relevant for the viability of long-lived, slowly reproducing mammals (Loveridge *et al*., 2020).

In the Serengeti National Park (NP) in Tanzania, numerous by-catch species are injured or killed by illegal bushmeat hunting. Snares are hand-made from several strands of more or less tightly entwined wires and are typically set in areas containing large aggregations of migratory ungulates by people living near the western boundary of the Serengeti NP (Arcese, Hando & Campbell, 1995; Campbell & Hofer, 1995; Hofer *et al*., 1996; Nyahongo *et al*., 2005). Even in protected areas such as in the Serengeti NP (and others, see Loveridge *et al*., 2020), spotted hyenas *Crocuta crocuta* (hereafter 'hyenas') are vulnerable to snares (Hofer *et al*., 1993). This is because their main prey is migratory herbivores (Hofer & East, 1993*a*,*b*) and hyenas throughout the park regularly travel long distances from their clan territories to forage in areas containing large aggregations of migratory herbivores before returning to their territory (Hofer & East, 1993*a*,*b*). Some of these areas have a high density of snares, particularly in the west and north-west of the Serengeti NP and associated protected areas, where the hunting areas used by bushmeat hunters and hyenas converge (Hofer *et al*., 1993, 1996). As a result, even hyenas from clans in the center of the Serengeti NP have an estimated 8% annual risk of dying in a snare (Hofer *et al*., 1993). The Serengeti NP authority directs considerable effort to prevent illegal bushmeat hunting and when animals with snares are seen, efforts are made to remove these snares.

Animals caught by a snare typically attempt to pull themselves free, thereby causing the wire noose to tighten. When the noose is around the animal's neck, death may occur through strangulation. Some hyenas free themselves by gnawing through the snare's tethering wire which is usually attached to a tree. When this is achieved without the noose tightening and cutting into the animal's flesh, wounds are non-debilitating (or not apparent) and heal swiftly, even though the animal may still carry the wire noose. By contrast, when snares slice deeply into the body, profound wounding occurs and can lead to septic and inflammatory responses, particularly when the wire is embedded in the flesh. The snare's noose may also cut a hole in the trachea or snares may amputate body parts (e.g. ear, teat, foot or part of a leg).

Using the Serengeti hyena population as a case study, we investigated the overlooked sublethal effects that snare injuries may have on the reproductive performance of females that escaped from snares and survived long enough to be resighted by us in their clan territories, following their return from long-distance foraging trips to distant migrators herbivores (Hofer & East, 1993*a*,*b*,*c*). This population inhabits a protected area and thus any negative effects of bushmeat hunting in this population are likely to also occur in hyena populations facing similar or higher anthropogenic pressures (see Loveridge *et al*., 2020). As hyenas typically have robust immune responses and tissue healing when wounded (Flies *et al*., 2016), any long-term performance costs of snare wounds in hyenas imply that such costs are also very likely to occur in more vulnerable terrestrial mammals. Focusing on hyenas that escaped alive from snares, we first describe seasonal, sex, age and social rank-specific snaring patterns. We then assess whether debilitating injuries sustained by philopatric females reduced four components of their performance – longevity, age at first reproduction, litter size and offspring survival – using snaring records and detailed life-history data from more than three decades.

Profound snare wounds that entail extensive replacement of damaged tissue and require the expenditure of additional energy for immunological responses to combat septic wounds were expected to drain body resources for weeks, months or years after a snare encounter, and thus reduce longevity, delay the start of reproduction in young females, and/or potentially cause a prenatal reduction in litter size in pregnant females. We also expected such wounds to decrease investment in milk production and thus to decrease the survival chances of both current and future litters. Second, we expected snares that caused amputations of a foot or leg to impair a female's ability to travel long distances to forage and thus to reduce female body condition and longevity, as well as the overall volume of milk transferred to offspring during their development, thereby decreasing the survival chance of both the current and future litters. Female hyenas typically have two functioning teats, thus snares that cause the amputation of one teat were expected to decrease offspring survival by increasing sibling rivalry and the likelihood of facultative siblicide in twin litters. When mothers suffered mastitis and only had one functioning teat, the incidence of facultative siblicide in twin litters sharply increased (Hofer & East, 1997). Also, when maternal milk provisioning rates were low, cub growth rates were low which resulted in reduced cub survival (Hofer & East, 2003) and an increased likelihood of facultative siblicide in twin litters (Hofer & East, 2008).

Materials and methods

Study population and standard methods

We collected data on hyenas between May 1987 and March 2020 as part of an ongoing, individual-based long-term research project on three clans located at the center of the Serengeti NP in Tanzania (Isiaka clan: monitored since 1987, Pool: since 1989, Mamba: since 1990). We observed hyenas in their clan territories at communal den sites during periods of several hours around dawn and dusk (Hofer & East, 1993*b*). During each field session, we routinely scored the presence of all clan members present within a radius of 100 m of the communal den(s). Data from all-night watches and aerial tracking demonstrated that dawn and dusk observations at communal dens missed only a small proportion of clan members present in the territory (Hofer & East, 1993*c*).

We individually recognized clan members by their spot patterns (Frank, 1986; Hofer & East, 1993*a*) and cubs by ear notches, scars or bald patches (Golla, Hofer & East, 1999). We estimated cub age ±7 days using pelage characteristics and locomotion (Golla *et al*., 1999). Individuals were called cubs when less than 1 year old, subadults when aged between 1 and 2 years and adults when older than 2 years (Hofer & East, 2003). Of the total of 928 females born in the three study clans during the study, 333 survived at least until adulthood. We could not age females which were adults at the start of the project.

The Serengeti NP is characterized by the annual migration of large herds of wildebeest *Connochaetes taurinus*, Thomson's gazelles *Eudorcas thomsonii* and zebras *Equus quagga*, the main prey of Serengeti hyenas (Hofer & East, 1993*a*). From approximately early December, when the rains start, until the end of May, which is roughly the end of the wet season period, herds are in the east and southeast of the Serengeti NP. During the dry season (early June–end of November), herds move to areas in the west and north of the NP (Hofer & East, 1993*a*), where snares are set (Arcese *et al.*, 1995; Campbell & Hofer, 1995; Hofer *et al.*, 1996; Nyahongo *et al.*, 2005). Hyenas regularly commute between clan territories and areas where migratory herbivores are located (Hofer & East, 1993*a*,*b*; Gicquel *et al.* 2022).

We determined the social rank of adult females based on their positions in the (strictly linear) adult female dominance hierarchy. For this, we recorded submissive behaviors during dyadic interactions among adult females and constructed strictly linear dominance hierarchies for each clan (e.g.Hofer & East, 2003; Marescot *et al.*, 2018). Interactions were recorded *ad libitum* during field sessions. Dominance hierarchies were adjusted after each loss or recruitment of adult females and when dyadic interaction data revealed than an individual had increased or fallen in rank. To compare ranks held by individuals within hierarchies containing different numbers of animals within and across clans, we computed standardized ranks. This measure places the ranks within a given hierarchy evenly between the highest (standardized rank: +1) and the lowest (standardized rank: −1) rank (Hofer & East, 2003; Marescot *et al.*, 2018). We classified adult females with standardized ranks within the top, middle and lower thirds of the total range as high-ranking, mid-ranking and low-ranking, respectively.

We conducted this study under research permits from the Tanzania Commission for Science and Technology and permission from the Tanzanian National Parks Authority and Tanzanian Wildlife Research Institute. All procedures were performed in accordance with the Leibniz Institute for Zoo and Wildlife Research Ethics Committee on Animal Welfare (permit number: 2016-11-02).

Snaring events

As part of our health monitoring of study clans (Marescot *et al.*, 2018), during our field sessions at clan communal dens, we recorded all hyenas observed alive with a snare still attached to their bodies, and those with snare-specific injuries, including fresh wounds and scars, plus individual identity, sex and clan affiliation, the estimated date of snaring and the location of the snare on the body and its consequences, if any, for movement and behavior. Scars indicated healed wounds, that is tissues were not inflamed, swollen or bleeding. We recorded similar information for any other snared non-study clan hyena observed opportunistically within or outside our study clan territories).

To assess the consequences of snare injuries on female performance in our study clans we monitored the long-term consequences of snare injuries to females. We categorized snaring events as non-debilitating, when the snares were loose or wounds healed without evidence of septic infection, and debilitating, when the snares caused persistent septic wounds or permanent injuries (i.e. the animal was permanently maimed even when the snare was removed), including the amputation of teats, feet or a section of leg, permanent mutilation of feet, permanent openings sliced into the esophagus or trachea (Fig. 1).

Offspring development and classification

Female hyenas reproduce throughout the year and give birth to litters of mostly one or two offspring, rarely three (Holekamp, Smale & Szykman, 1996; Hofer & East, 2008). In our study population, we have never observed a female successfully raising a triplet litter. To determine whether debilitating snare injuries in adult female clan members reduced litter size and offspring survival, we categorized offspring in two main categories as illustrated Fig. 2. For the analysis of litter size, the category *offspring_control* (the control group) included offspring of non-snared females (i.e. females lacking evidence of being snared) and offspring born prior to a non-debilitating snaring event (Fig. 2a). The category *offspring_snared* (the group of interest) included all offspring born after their mothers experienced a debilitating snare injury.

For those adult females snared on more than one occasion with non-debilitating snaring events during their lifetimes, we classified all offspring born prior to the first event as *offspring_control*. We classified other offspring as follows: For adult females that experienced (1) a debilitating snare followed by a non-debilitating one, we classified offspring born after the first snare as *offspring_snared*, (2) a non-debilitating snare followed by a debilitating one, we classified offspring born after the second snare as *offspring_snared*, (3) two non-debilitating snaring events followed by a debilitating one, we classified offspring born after the third snare as *offspring_snared*.

For the analyses of offspring survival, we kept the same classification except that we excluded offspring born less than 20 months prior to a non-debilitating snaring event from the control group (Fig. 2b). We used 20 months as it is the oldest age at which weaning was observed (Hofer *et al.*, 2016). The category *offspring_snared* also included dependent offspring, that is cubs aged 6 months or less when their mother experienced a debilitating snare injury, as we expected the survival of the current litter at the time of snaring to be affected by its mother's injury. We chose 6 months as cubs are entirely dependent on highly nutritious maternal milk during their first 6 months of life (Hofer & East, 1993*c*, 1995; Hofer *et al.*, 2016). We only considered mothers and their genetic offspring and excluded offspring adopted by a surrogate female or jointly raised by their genetic mother and a surrogate mother (East *et al.*, 2009).

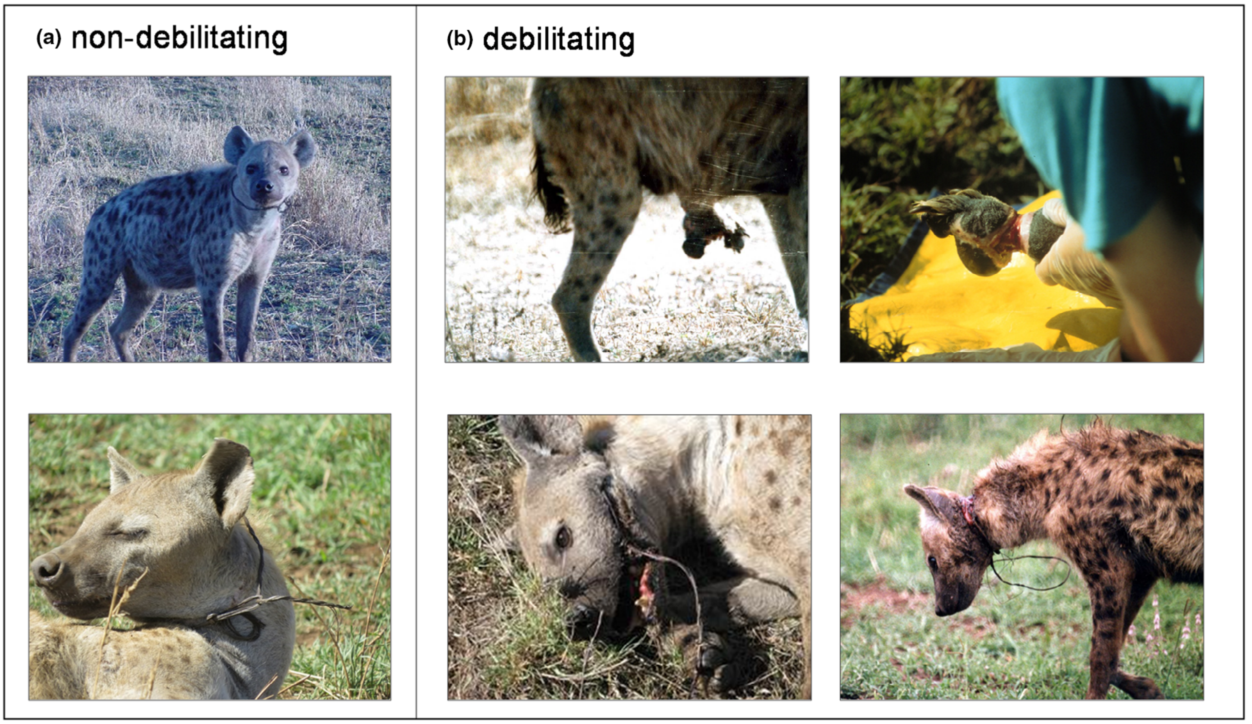

Figure 1 Snares on individuals in study clans illustrating (a) non-debilitating wire snare injuries around the neck and (b) debilitating snare injuries in various body locations. Photo credits: M. L. East & H. Hofer.

Statistical analyses

We conducted all analyses in R 4.1.2 (R Core Team, 2021). The threshold for significance was set at 5% and tests were two-tailed. Figures were done using *ggplot2* version 3.3.5 (Wickham, 2016), *ggeffects* version 1.1.1 (Lüdecke, 2018) and *survminer* version 0.4.9 (Kassambra, Kosinski & Biecek, 2021).

Survival analysis

To assess whether female longevity (the number of days between the female's date of birth and the date she was last observed alive) was reduced after debilitating snare injuries, we fitted a Cox-proportional hazards model using the package *survival* version 3.1.13 (Therneau & Grambsch, 2000; Therneau, 2021), including 'snare' (i.e. debilitating snare injury vs. no snare injury) and the average lifetime social rank as predictors. Because the dataset of females with debilitating snare injuries included females that lived long enough to be snared, whereas the dataset of females with no snare injury contained a large proportion of females that died before reaching adulthood, we first processed the data into a 'start-stop' format, that is the time data for hyenas who experienced a debilitating snare injury was divided into two periods, one before snaring and one after, and specified the predictor snare as a time-dependent variable following the procedure described in Moore (2016).

We tested the assumption of proportional hazards by using the function cox.zph in the package *survival* and used ggcoxzph in *survminer* to produce for each covariate a graph of the scaled Schoenfeld residuals against time. We checked for outliers using the function ggcoxdiagnostics in *survminer*.

Mixed-effects logistic regression models

To test whether debilitating snare injuries reduced female reproductive success in terms of litter size (noted on date of first litter observation), we fitted a mixed-effects logistic regression model with litter size (singleton, twin) as response variable, offspring type (*offspring_control*, *offspring_snared*, Fig. 2a), maternal social rank and maternal age (modeled using both a linear and a quadratic term) at the date of litter birth, as fixed effects, and maternal identity as a random effect (on the intercept). For simplicity, we excluded all cubs from triplet litters (1.1% of the dataset).

To test whether debilitating snare injuries reduced female reproductive success in terms of offspring survival, we fitted a similar mixed-effects logistic regression model with offspring survival to 1 year (survived, died) as a response variable.

We fitted both models using the function glmer in the package *lme4* version 1.1-28 (Bates *et al*., 2015). We used log-likelihood ratio tests to calculate *P*-values. The absence of multi-collinearity was verified by calculating variance inflation factors with the package *performance* version 0.8.0 (Lüdecke *et al*., 2021). Model assumptions were verified with the package *DHARMa* version 0.4.5 (Hartig, 2022).

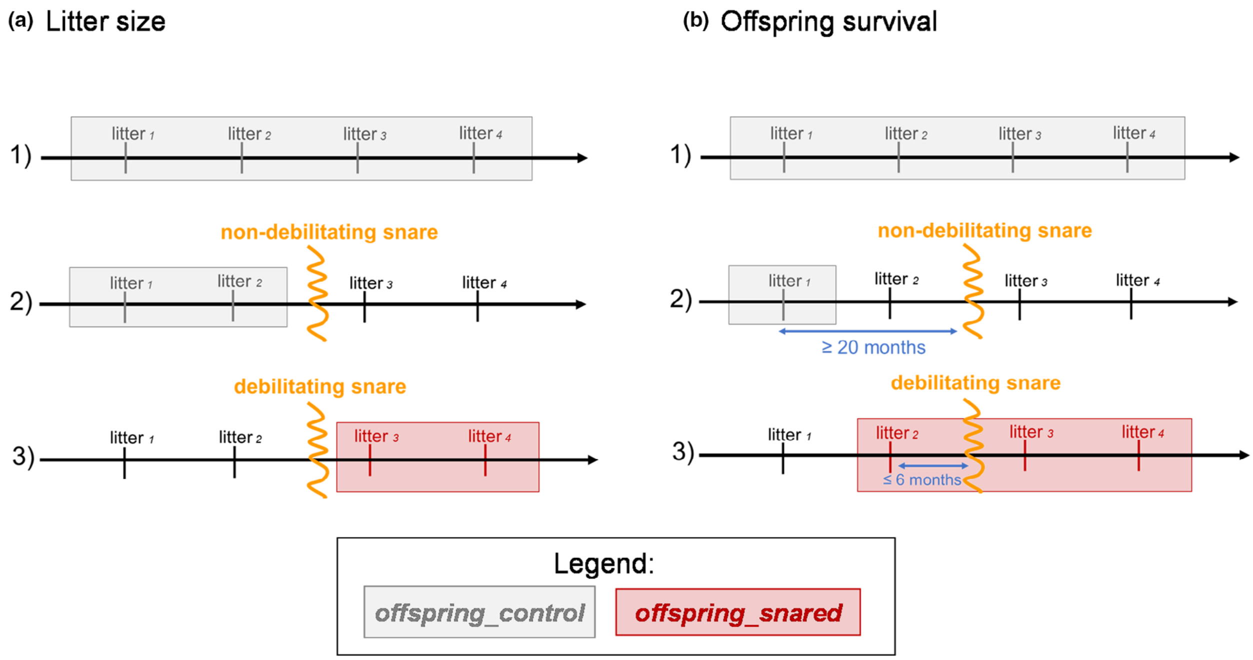

Figure 2 Classification of offspring for (a) litter size and (b) offspring survival analyses. In both panels, the three horizontal black arrows illustrate adult female spotted hyenas (1) which were not snared, and those that at some point during their lifetimes experienced (2) a non-debilitating snare, or (3) a debilitating snare. The vertical lines represent the birth of a litter (singleton or twin). We compared (a) litter size for offspring reared by mothers unaffected by a snare or born before their mother experienced a non-debilitating snare (gray boxes, *offspring_control*) and those born after their mother experienced a debilitating snare (red boxes, *offspring_snared*). In the analysis of (b) offspring survival, we excluded offspring born at least 20 months prior to their mother experiencing a non-debilitating snare from *offspring_control* (as such offspring may have been affected by maternal snaring and 20 months is the oldest age at weaning reported) and we included offspring born less than 6 months prior to a debilitating snaring event in *offspring_snared* because these were entirely dependent on maternal milk when snaring occurred and we expected the survival of the current litter at time of snaring to be affected by its mother's injury. For an alternative representation of how we classified offspring see Supporting Information Figure S1.

Results

We observed a total of 208 incidences of 193 hyenas with snares, snare-specific injuries or scars between 1987 and 2020 in the Serengeti NP. Most snares were located in the neck region (62.5%, 130 of 208; Supporting Information Figure S2).

Snaring patterns in study clans

The majority of snare incidences were observed in study clans during our systematic monitoring of hyenas at clan communal dens: we recorded 148 incidences involving 133 clan members observed with snares, snare-specific injuries or scars (Table 1). Among these, 14 (10.5%) hyenas escaped after being caught by a snare on two or more occasions. We observed more snared animals in the Pool clan than in the Mamba or Isiaka clans (Table 1). There was considerable variation between years in the number of snared clan members and no obvious temporal trend (Supporting Information Figure S3). The majority of clan members were snared during the dry season (Table 1). Most clan members were snared as adults, no clan member was observed with a snare or snare-specific injury as a cub (Table 1). Among subadult and adult females and males, females were more often snared than males (Table 1). Low-ranking ($n = 21$ snaring events), mid-ranking ($n = 21$ snaring events) and high-ranking ($n = 20$ snaring events) adult females were equally likely to be snared. The social rank of adult females at the date of snare observation was -0.01 on average (median = -0.04, min = -1, max = 1, $n = 57$ individuals, 62 snaring events).

Of the total of 95 snaring events in 84 female clan members, 68 (71.5%) were classified as non-debilitating, 24 (25.3%) as debilitating and three could not be scored. In the following analyses, we focused on the life-history consequences of debilitating snare injuries in female clan members.

Effect of debilitating snare injuries on female longevity

Females with debilitating snare injuries, a known date of birth and an estimated date of snaring ($n = 18$) and non-snared ($n = 844$) females did not differ in their longevity (Cox-proportional hazards model, log-likelihood ratio test, $G = 0.92$, d.f. = 1, exact $P = 0.34$). Average lifetime social rank did not influence longevity ($G = 1.24$, d.f. = 1, exact

Table 1 Number of spotted hyenas observed on one or more occasions with snares, snare-specific injuries or scars in three clans at the centre of the Serengeti National Park between 1987 and 2020

	Clan				Season[a]			Age class and sex ratio[a]				
								Subadult		Adult		
	Isiaka	Mamba	Pool	Total	Wet	Dry	Total	♀	♂	♀	♂	Total
Individuals	33	37	63	133	22	64	84[b]	8	2	57	17	84
Snaring events	35	42	71	148	22	67	89	8	2	62	17	89

[a] Based on cases for which a date of snaring could be estimated.
[b] Two individuals were snared once during the dry season and once during the wet season. The total number of individuals is thus 84 and not 86.

$P = 0.27$). Of the 12 females with debilitating snare injuries that had died by the end of the study, most did not die shortly after this experience; the mean number of years between snaring and death was 5 years and the average age at death of those females was 11 years (Supporting Information Figures S4 and S5).

Effect of debilitating snare injuries on female reproductive success

Age at first reproduction

Six females experienced a debilitating snare injury before giving birth to any litter. Among these, four were snared as adults (mean age at snaring was 3 years), two others were snared as subadults (at 391 and 573 days of age). The subadult female snared at 391 days of age died shortly after snaring and did not give birth to any litter. The mean age at which the other five females gave birth to their first litter was 4.58 ± 0.72 years (median = 4.63, min = 3.73, max = 5.61). This is a significantly older age at first reproduction than that of non-snared females (3.84 ± 0.71 years; median = 3.78, 95% CI: 3.75–3.93, $n = 235$; Mann–Whitney U test = 254, $P = 0.03$, Fig. 3). For all five snared females, the first litter did not survive until adulthood; for three females, the litter (one or two cubs) was lost at birth, for the two others, the singleton cubs died at 195 and 220 days of age. The mean social rank of these females at the birth date of their first litter was 0.032 (median = 0.10, min = −0.94, max = 0.82), and thus close to the median rank.

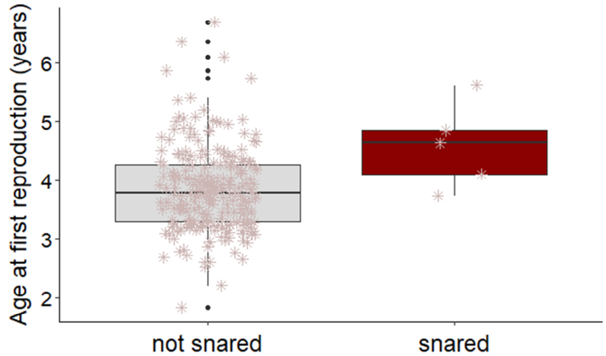

Figure 3 Age at first reproduction (in years) for non-snared females (gray, $n = 235$) and females with debilitating snare injuries (red, $n = 5$). The upper and lower hinges correspond to the first and third quartiles and the horizontal black line corresponds to the median. The upper whisker extends from the hinge to the highest value that is within 1.5 × inter-quartile range (IQR) of the hinge, or the distance between the first and third quartiles. The lower whisker extends from the hinge to the lowest value within 1.5 × IQR of the hinge. Data beyond the end of the whiskers are plotted as black dots (outliers as specified by Tukey). Pink stars indicate individual data points.

Litter size

In the absence of being snared (i.e. females before acquiring non-debilitating snare injuries and non-snared females), females ($n = 245$) gave birth mostly to twin litters ($n_{\text{singleton litters}} = 401$, $n_{\text{twin litters}} = 514$; 56.2% were twins). After a debilitating snare injury, females ($n = 18$ females with a debilitating snare injury, a known date of birth and an estimated date of snaring) gave birth to significantly smaller litters (mixed-effects logistic regression, log-likelihood ratio test, $G = 11.36$, d.f. = 1, $P = 0.0008$; $n_{\text{singleton litters}} = 45$, $n_{\text{twin litters}} = 25$; 35.7% were twins, Fig. 4a). Maternal injuries decreased the odds of producing a twin litter by 0.38 (or increased the odds of producing a singleton 2.65-fold). Litter size was also strongly influenced by maternal age (modeled as a second-order polynomial term, $G = 23.25$, d.f. = 2, $P < 0.0001$, Fig. 4b). Maternal social rank did not influence litter size ($G = 1.69$, d.f. = 1, $P = 0.19$).

Offspring survival

The percentage of offspring surviving to 1 year in the group *offspring_control* was 50.8% (712 survived, 690 died, $n = 246$ mothers), whereas in the group of interest (*offspring_snared*), the percentage of offspring surviving to 1 year was 41.9% (44 survived, 61 died). Offspring survival to 1 year was significantly reduced in litters of mothers with debilitating snare injuries (mixed-effects logistic regression, $G = 4.33$, d.f. = 1, $P = 0.037$). Snare injuries decreased the odds of the offspring surviving before reaching 1 year by 0.58 (or, snare injuries increased the odds of the offspring dying by 1.72, Fig. 5a). Offspring survival to 1 year was also influenced by maternal age (modeled as a second-order polynomial term, $G = 50.54$, d.f. = 2, $P < 0.0001$, Fig. 5b)

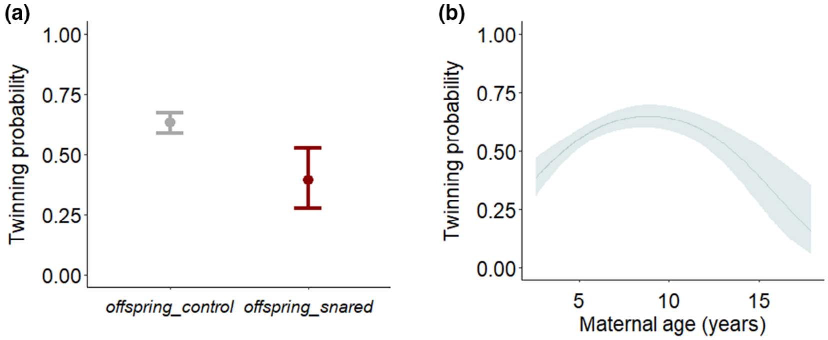

Figure 4 Predicted probabilities of giving birth to a twin litter as a function of (a) the type of offspring, that is offspring not affected by maternal snaring (*offspring_control*, gray), or offspring of mothers with debilitating snare injuries (*offspring_snared*, red) and (b) maternal age at litter birth in years. Error bars and ribbons represent 95% confidence intervals.

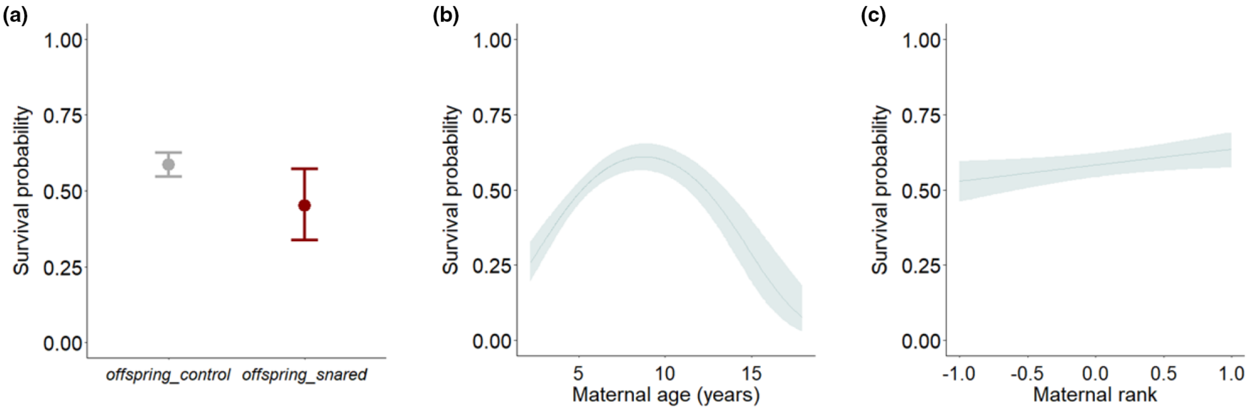

Figure 5 Predicted probabilities of offspring survival to 1 year as a function of (a) the type of offspring, that is offspring not affected by maternal snaring (*offspring_control*, gray), or offspring of mothers with debilitating snare injuries (*offspring_snared*, red), (b) maternal age at litter birth in years and (c) maternal rank. Error bars and ribbons represent 95% confidence intervals.

and increased with increasing maternal social status ($G = 4.37$, d.f. = 1, $P = 0.037$, Fig. 5c).

Discussion

Our study revealed that debilitating injuries inflicted by snares delayed female spotted hyena age at first reproduction and reduced both their litter size and offspring survival, but not their own longevity. The severity of injuries was critical, as non-debilitating snare injuries did not reduce female performance (see Supporting Information Appendix S1). We describe seasonal, sex, age and social status specific snaring patterns spanning three decades in Serengeti hyenas. These patterns should be interpreted cautiously as they do not include the unknown number of individuals that died when caught by a snare. Significantly higher rates of hyena disappearances have previously been reported during the dry than wet season, which is when hunting areas of illegal bushmeat hunters and hyenas converge (Hofer *et al.*, 1993). In line with these findings, hyenas returned to their clan territories with snares or snare wounds predominantly during the dry season. This suggests that the number of hyenas with evidence of snaring observed at communal dens during a given period might be a good index of snared-induced hyena mortality. The youngest age at which hyenas were observed with snares matched the age (1 year) at which subadults start accompanying their mothers on commuting trips (Hofer & East, 1993*c*). This suggests that snaring occurs predominantly outside clan territories when subadults and adults travel to feed on migratory herds. The higher incidence of snaring events in adult females than adult males may be caused by the more frequent commuting trips of lactating females (Hofer & East, 1993*b*,*c*) and the higher detectability of adult females at communal dens inside clan territories (Marescot *et al.*, 2018). A potential sex difference in adult mortality caused by snaring could bias the adult sex ratio, with possible consequences for demography or behavior (e.g. Regan *et al.*, 2020).

In accordance with life-history theory (Stearns, 1989, 1992), mounting an immune response, including acute inflammatory processes, is energetically costly and may compete with other life-history events for limited body resources (Lochmiller & Deerenberg, 2000). In long-lived, slowly reproducing species such as bighorn sheep *Ovis canadensis* and mountain goats *Oreamnos americanus*, females only allocated resources to reproduction when this did not compromise their own growth and survival (Festa-Bianchet *et al*., 2019). Similarly, female hyenas with debilitating snare injuries likely allocated a considerable amount of resources to repairing damaged tissues and fighting potential infections. These costly energetic processes may have caused females to prioritize their own body maintenance and survival. Consequently, snare-injured female hyenas may have delayed their first reproduction (Fig. 3). Similarly, in wild rodents, virus-infected females were more likely than uninfected females to delay maturation and therefore their age at first reproduction (Telfer *et al*., 2005). Injured hyenas may also have resorted to selective abortion, resulting in decreased litter size (Fig. 4a).

The energetic cost of tissue repair and immune responses required to tackle snare wound infection may also have reduced the long-term quality and/or quantity of milk produced by females and thus offspring survival to the age of 1 year (Fig. 5a). The high energetic cost of lactation in hyenas (highly nutritious milk produced throughout a long lactation period) is associated with increased gastro-intestinal parasite infection loads indicative of reduced resource allocation to immune processes (East *et al*., 2015; Hofer *et al*., 2016). Reduced investment in immune processes during lactation has been reported in the great mouse-eared bat *Myotis myotis* (Christe, Arlettaz & Vogel, 2000), red flying fox *Pteropus scapulatus* (Plowright *et al*., 2008) and springbok *Antidorcas marsupialis* (Turner *et al*., 2012). In yellow baboons, slower wound healing rates in lactating females suggest that lactation also may reduce the allocation of resources to wound healing (Archie *et al*., 2014). In chimpanzees *Pan troglodytes*, the prevalence of helminth parasites was significantly higher in snare-injured than in control individuals, suggesting that snare injuries might result in higher exposure and/or a decreased ability to prevent infections (Yersin *et al*., 2017). In a study of the impact of non-human related injuries in Hawaiian monk seals, pups of females with severe injuries were less likely to survive than those of uninjured females (Hiruki *et al*., 1993).

As another mechanism, decreased litter size and offspring survival after snaring may also have resulted from maternal amputations of a foot, leg or teat, thereby directly impairing the female's ability to travel long distances, forage and transfer milk to offspring (Figs 4a and 5a). In chacma baboons *Papio ursinus* human-induced injuries, including snares, caused individuals to increase their resting time and decrease their traveling and feeding time (Beamish & O'Riain, 2014). In Serengeti hyenas, the periods between maternal nursing visits when lactating females commute are likely to be prolonged when snares amputate a foot or leg (Fig. 1b), thereby ultimately decreasing the amount of milk transferred to offspring and offspring survival (Fig. 5a; Hofer & East, 2003), and in twin litters, increasing post-natal sibling rivalry for access to maternal milk and facultative siblicide (Fig. 4a; Golla *et al*., 1999; Hofer & East, 1997, 2008).

Litter size and offspring survival increased with maternal age before reaching a plateau, followed by a decrease in older females (Figs 4b and 5b) – a pattern akin to many other mammals, such as polar bears *Ursus maritimus* (Folio *et al*., 2019). This quadratic pattern corroborates previous findings on the impact of maternal experience on offspring survival in hyenas, as offspring survival is typically low in the first two litters produced by a young adult female (Hofer & East, 2003). The decline of female reproductive success with increasing age may be indicative of reproductive senescence (Nussey *et al*., 2006; Greiner *et al*., 2014; Folio *et al*., 2019).

Wire snares are a long-term threat to wildlife because hunters may leave them behind when they shift their hunting activities to a new area (Muchaal & Ngandjui, 1999). Similarly, discarded fishing tackle persists in the environment and has sublethal effects in a wide range of marine species (Wilson *et al*., 2014). From a conservation management perspective, injuries to animals caused by human activities become relevant if they lead to mortality or interfere with reproduction. Future research could focus on assessing the total population-level costs of snares, that is the costs of immediate mortality of individuals that do not survive snaring in the first place, plus the potential sublethal fitness costs for those individuals that manage to escape from snares, and on comparing these direct and indirect effects of snaring on populations. In the Serengeti NP, an estimated 57% of hyenas caught in snares died (see Hofer *et al*., 1993). This suggests that the direct effect of snaring on population growth rate may outweigh the reduction in reproductive success which we identified in the current study. As the cause of death in adults is often difficult to identify, indirect methods based on analyzing patterns of disappearances of individuals, for example during specific seasons associated with specific spatio-temporal risks, or forensic examinations based on snare damage to teeth (White & Van Valkenburgh, 2022), may prove useful for estimating the direct population-level effects of snaring.

Acknowledgments

We thank Matt Rogan and two anonymous reviewers for their very helpful comments. We thank the Commission for Science and Technology of Tanzania (COSTECH), the Tanzania Wildlife Research Institute (TAWIRI) and Tanzania National Parks (TANAPA) for their support. We thank the Deutsche Forschungsgemeinschaft DFG (grants EA 5/3-1, KR 4266/2-1, DFG-Grako 1121, 2046), the Leibniz-Gemeinschaft (grant SAW-2018-IZW-3-EpiRank), the Leibniz-Institute for Zoo and Wildlife Research, the Fritz-Thyssen-Stiftung, the Stifterverband der deutschen Wissenschaft and the Max-Planck-Gesellschaft for financial assistance. We thank D. Thierer, S. Karl and S. Metzger for assistance in compiling the list of snaring events. We thank the IZW statistical group for statistical and programming advice, as well as R. Fyumagwa, R. Hoare, M. Jago, T. Melengye, M. Roelke-Parker, J. Schamanche and H. Wiik for snare removals, A. Francis, S. Ferreira, T. Shabani, M. Andris, N. Boyer, T. Golla, K. Goller, N. Gusset-Burgener, K. Hönig, B. Kostka, M. Lindson, S. Metzger, M. Roelke-Parker, D. Thierer, A. Türk and K.Wilhelm for field assistance. The publication of this article was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – project number 491292795. Open Access funding enabled and organized by Projekt DEAL.

Authors' contributions

M.L.E, H.H. and S.B. collected data and formulated research questions. S.K. curated snaring events and conducted preliminary analyses. Final analyses were conducted by S.B. S.B. wrote the paper and M.L.E., S.K. and H.H. revised it extensively. All authors contributed substantially to this study.

Data availability statement

Data (Benhaiem *et al*., 2022) are available from Figshare: 10.6084/m9.figshare.19747492.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Alternative representative of offspring classification.

Figure S2. Body location of snare injuries.

Figure S3. Number of snaring events per year of the study period.

Figure S4. Empirical cumulative distribution function of the time to live.

Figure S5. Empirical cumulative distribution function of longevity. Alternative representative of offspring classification.

Appendix S1. Supplementary results.