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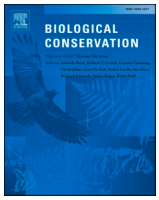

Effects of de-snaring on the demography and population dynamics of African lions

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ABSTRACT

Lions and other African large carnivores are in decline, due in part to effects of illegal hunting with snares, which can reduce prey availability and directly kill or injure carnivores. It is difficult to effectively remove snares from large ecosystems by patrolling, but an additional approach to reduce effects on large carnivores is to monitor the population closely and de-snare individuals who are found in a snare or have broken free but still carry the wire (often with serious injury). The effectiveness of de-snaring programs to reduce impacts on large carnivores has not been directly tested. Here, we used long-term demographic data from 386 individually identified lions in the Luangwa Valley Ecosystem to test the effects on population growth (λ) and population size (N) of a program to remove snares from injured lions and treat their wounds. Stochastic Leslie matrix projections for a period of five years showed that the population grew with the benefits of de-snaring, but was expected to decline without de-snaring. Mean annual growth (λ) with de-snaring was 1.037 (with growth in 70% of years), closely matching observed changes in population size. Mean annual growth was 0.99 (with growth in 47% of years) for a model that assumed snared animals would have died if not treated, and 0.95 (with growth in 37% of years) for models that also accounted for super-additive effects via the death of dependent cubs and increased infanticide with increased male mortality. De-snaring requires intensive effort, but it can appreciably reduce the effect of snaring on lion population dynamics.

Large carnivores are declining and their range is contracting worldwide due to human impacts, including prey depletion, direct persecution, human utilization and range contraction or degradation (Ripple et al., 2014; Estes et al., 2011; Ripple et al., 2015). Large carnivores depend heavily on large herbivores as prey, and large herbivores are also declining rapidly in most of Africa, primarily due to unsustainable hunting (both illegal and legal) (Creel et al., 2018: Midlane, 2014; Bolger *et al.*, 2008; Fa & Brown, 2009). Large carnivores can limit large herbivores through predation, and mesocarnivores through intraguild competition, thereby shaping ecosystems along multiple food-web pathways. These in turn influence the nature and strength of ecosystem functioning. These effects, together with their vulnerability to extinction, make large carnivores important for ecosystem conservation and management.

The bushmeat trade has had strong negative impacts on herbivores and carnivores across sub-Saharan Africa (Coad et al., 2010; Fa et al., 2002; Lindsey et al., 2013). The most common method of bushmeat poaching is with wire snares because they are inexpensive, effective and easy to obtain (Noss, 1998, Watson et al., 2013; Wittemyer et al., 2008; Brashares et al., 2004; Mudumba et al., 2021). Snares are also easy to set and conceal, and (unlike hunting with guns) they are silent. The strongest impact of bushmeat poaching for carnivores has been prey depletion, but the accidental snaring of non-target species, known as snare by-catch, is also a potentially significant impact that is poorly understood (Becker et al., 2013a, 2013b; Loveridge et al., 2020; Vinks et al., 2021). Because snares are non-selective, they can inflict significant by-catch mortality on non-target species that are of a similar size to the target species (Lindsey et al., 2011; Noss, 1998; Loveridge et al., 2020). For

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large carnivores, snaring can immediately kill a snared individual, but also can cause serious injuries when a carnivore struggles in the snare, or when they break a snare free from its anchor, usually leaving the wire deeply imbedded. These deep open wounds are prone to infection, and often lead to permanent, serious injuries such as the loss of a limb (Loveridge et al., 2020). These problems are widely recognized, and programs of two types have been developed to reduce the impact of snaring on threatened and endangered large carnivores. One approach ('patrolling') relies on law enforcement to conduct patrols to detect and remove snares from the environment (Mudumba et al., 2021), thus reducing both direct depletion of herbivore prey and incidental by-catch of carnivores. While removing snares from the landscape is an important approach, an additional strategy to reduce effects on endangered carnivores relies on close monitoring (usually using radio telemetry) to detect snared animals, removing the snares and treating the injuries ('de-snaring'). While both of these approaches to mitigate the effects of snaring on large carnivores are increasingly common, no research has directly tested how snaring and de-snaring affects the demography and population dynamics of any large carnivore. Here, we use long-term demographic data to directly evaluate the effect of a de-snaring program on the dynamics of a Zambian lion population.

Lions are Africa's largest predator and their populations are strongly correlated with prey densities (van Orsdol et al., 1985; Hatton et al., 2015, Loveridge et al., 2020). Lions have declined across their range, and prey depletion is recognized as one of the strongest threats (Ripple et al., 2014; Bauer et al., 2022). Vinks et al. (2021) recently found that prey depletion due to heavy snaring pressure caused poor cub recruitment, small average pride size and very low population density for lions in Zambia's Greater Kafue Ecosystem. However, the effects of snaring by-catch on lion demography remains poorly understood (Loveridge et al., 2020; Mudumba et al., 2021), and to our knowledge, no prior study has evaluated the effectiveness of de-snaring. Given that de-snaring is one of the most direct options to mitigate snaring by-catch and the associated mortality, it is important to assess its effectiveness at improving demography and population dynamics.

Zambia's Luangwa Valley Ecosystem (LVE) is one of 10 remaining lion strongholds on the African continent (Riggio et al., 2013), but it is also an area where lions have been affected by snaring by-catch (Becker et al., 2013a, 2013b) and are the focus of long-term de-snaring efforts. Using long-term data from lions from in the LVE, we evaluated the effect on lion demography and population dynamics of a systematic program to detect snared lions, remove the snares and treat the injuries they caused. We conducted this evaluation in a population that was intensively monitored over the long term, allowing rigorous evaluation of effects on survival, reproduction and population size using methods that have been previously described (Rosenblatt et al., 2014; Creel et al., 2016; Mweetwa et al., 2018).

1. Methods

1.1. Population monitoring

Our analyses are based on data from intensive monitoring of 386 individually identified lions in 21 prides and 24 male coalitions across a study area of 2775 km^2 in the Luangwa Valley Ecosystem (LVE: 31° 50′ E–32° 5′ E, 12° 50′ S–13° 05′ S). This study area includes the eastern side of South Luangwa National Park (primarily west of the Luangwa River) and the adjacent Lupande and Lumimba Game Management Areas (east of the Luangwa River). The vegetation on both sides of the river is a mosaic of mopane woodland (dominated by *Colophospermum mopane*), scrub woodland, open grassland, and riparian woodland. Our methods for radiocollaring, individual identification and monitoring have previously been described in detail (Rosenblatt et al., 2014; Mweetwa et al., 2018). Briefly, we used a combination of VHF and satellite-GPS radiocollars to allow frequent relocation of lions for direct observation from a vehicle. Lions were individually identified using whisker-spot patterns, nose coloration patterns, scarring, and tooth breakage, using a catalog of identified lions photographed from several angles. At least one adult female lion was radio-collared in each of 19 resident prides for the duration of the study and one adult male lion in 4 resident male coalitions between 2009 and 2013. Darting and radiocollaring from 2009 to 2013 was conducted by experienced personnel authorized by the Department of Veterinary and Livestock Development and the Zambia Department of National Parks and Wildlife (DNPW), and from 2013 to 2021 by a Zambian registered veterinarian, with approval by the Montana State University Animal Care and Use Committee. We recorded all lion sightings from 2008 to 2015 to allow estimation of age-specific survival and reproduction. As has been described previously, survival rates were estimated using Cormack-Jolly-Seber models that corrected for variation among age-sex classes in detectability (Mweetwa et al., 2018; Rosenblatt et al., 2014).

1.2. De-snaring

On 22 occasions during the study period, a lion in the study population was detected carrying a wire snare. In each of these cases we immobilized the lion and removed the snare using wire cutters. We treated the snare injury by cleaning and debriding the wound, and with topical and injectable antibiotics. We darted using a Dan-Inject air rifle with continuously adjustable pressure or a Pneu-Dart cartridge-fired rifle, and immobilized lions with a combination of medetomidine and tiletamine-zolazepam, reversing the medetomidine with atipamezole.

1.3. Stochastic age-structured population projections

We estimated the effect of de-snaring on population growth using age-structured stochastic population projections, each projected 10,000 times over a period of 5 years. The baseline model used previously published estimates of age- and sex-specific survival and fecundity (Mweetwa et al., 2018; Creel et al., 2016) to build Leslie matrices for male and female lions in the LVE (Supplementary material S1). Each projection began with a population with the mean size (149 individuals) previously reported for this population for the period from 2008 to 2015 (using Huggins closed capture-mark-recapture models with individual heterogeneity in detection), and with the observed age-sex structure (Mweetwa et al., 2018). We then projected over a period of five years with a series of nested loops, tracking the number of individuals of each age and sex, drawing survival from a binomial distribution with the observed mean for each age-sex class, and drawing fecundity from a Poisson distribution with the observed mean for each age-sex class. We confirmed that this model made realistic predictions by comparing the projected final population size with the observed minimum and maximum population size from 2008 to 2015 (Mweetwa et al., 2018).

Having confirmed that the baseline demographic projection model correctly described population dynamics, we compared the distributions of population growth rates (λ) and final population size (N) for four scenarios describing snaring effects on lion dynamics:

- The *observed demography model* (A) used the observed patterns of survival and reproduction, which include all effects of de-snaring on survival and reproduction.
- The *direct mortality model* (B) reduced mean survival rates for each age-sex class by assuming that all 22 de-snared animals would have died if the snare had not been removed and the wound treated (but see the discussion for further consideration of the lethality of snares).
- The *direct mortality + infanticide model* (C) reduced survival as in (B), and reduced (female) fecundity to account for reduced cub recruitment with increased adult male mortality. To estimate this super-additive effect, we compared mean cub recruitment from 2013 to 2015 (when adult male mortality was reduced by a trophy hunting moratorium: Mweetwa et al., 2018) and 2008–2012 (when adult male mortality was higher: Mweetwa et al., 2018). We used the ratio

of change-in-cub-recruitment to change-in-male mortality from these two periods to describe the change in recruitment expected per unit change in adult male mortality, and multiplied this by the estimated change in male mortality, to obtain the super-additive effect on recruitment. We applied this reduction equally to the fecundity of all female age classes.

- The *direct mortality + infanticide + loss of dependent cubs model* (D) included all effects in (C), but also assumed that for every adult female that died, her dependent cubs would also die. We estimated this reduction in recruitment using the mean fecundity for females in that age class (rather than the specific number of cubs for each snared female), because the first measure includes less sampling error.

For each of these scenarios, we projected 10,000 iterations of population growth over five years to determine the distribution of stochastic population growth rates (λ) and population sizes (N). For both λ and N, we used the *hdrcde* package in R to determine the highest probability density regions (Hyndman, 1996) shown in Figs. 3 & 4.

2. Results

2.1. Observed injuries due to snaring

Snares are anchored when they are set, so that they tighten as the snared animal struggles. The herbivores that are the intended targets of snaring typically do not break free, but lions and other large carnivores can break or chew through the wire to free themselves. Because of their size and strength, adult lions are particularly able to break snares from their anchor point, but the snare often becomes deeply embedded during this struggle. Because snares typically continue to tighten over time, the injuries that they produce are often severe, including loss of one or more limbs, severed trachea, esophagus or penis, or broken teeth (Fig. 1). On 22 occasions between 2008 and 2015, we detected a snared lion and immobilized it so that the snare could be removed and the wounds treated. In all 22 cases the animal recovered and survived at least to the end of the field year (March – December) in which it was de-snared (Fig. 1).

2.2. Effects of age and sex on snaring

Between 2008 and 2015, an average of 3.5 lions per year (3.0 % of a mean of 116 known individuals, minimum = 0, maximum = 4) were found to be carrying a snare and immobilized to remove the snare and treat the wound. If an individual's age and sex did not affect the likelihood of carrying a snare, adult females would constitute the largest proportion of de-snared individuals because they were the largest segment of the population (30.8 %, 95 % CI = 24.3–38.2 %: Fig. 2A). In line with this expectation, 31.8 % of de-snared lions were adult females (95 % CI = 7.7–72.2 %: Fig. 2B). Uncertainty about the estimated proportion of snared individuals in each age-sex class is large because the number of snared individuals is much smaller than the population as a whole. While adult females carried snares at the rate expected by chance, cubs of both sexes tended to carry snares less often than expected by chance (Fig. 2) (*population*: male cubs = 15.2 % [10.5–21.5],

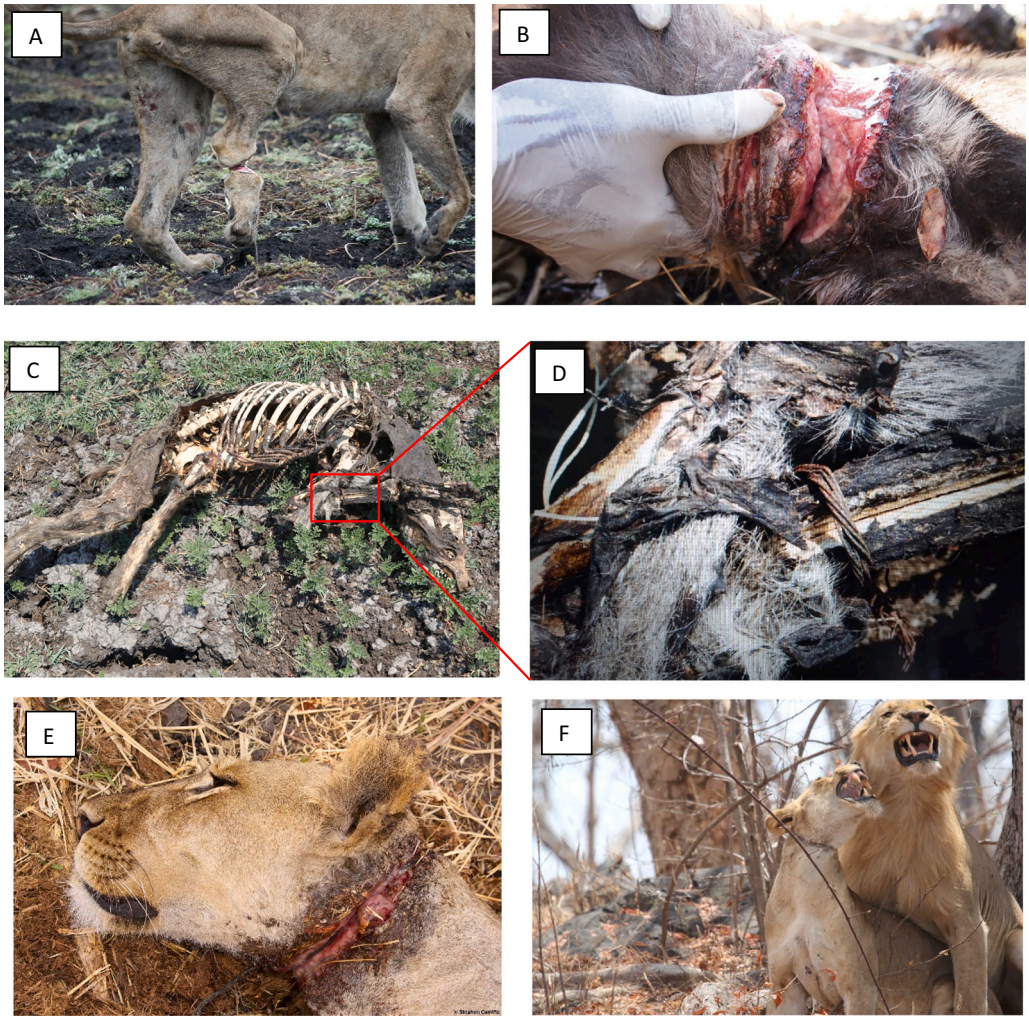

Fig. 1. Examples of injuries to large carnivores from wire snares. Snares are anchored when they are set, but lions and other large carnivores are capable of breaking free by chewing through the wire. While the snare is anchored it often causes serious injury, and snares continue to tighten even after the animal has broken free, deepening the wound. As shown, snares are most often found on the neck or legs, but they are sometimes around the entire torso. (A) A snare that has cut to the bone on the hind leg of a lion. The wire is still embedded deep in the wound. (B) A snare deeply embedded in the neck of an African wild dog. The wire is still present deep in the wound, and the trachea and esophagus can be severed by such wounds. (C) A spotted hyena who has died with a snare embedded in its foreleg. The snare is shown more closely in (D), revealing a common twisted wire structure to increase the snare's strength. (E) A female lion immobilized to remove a neck snare (which is still present) and treat the wound. (F) The same female as in (E) showing the healed injury after de-snaring.

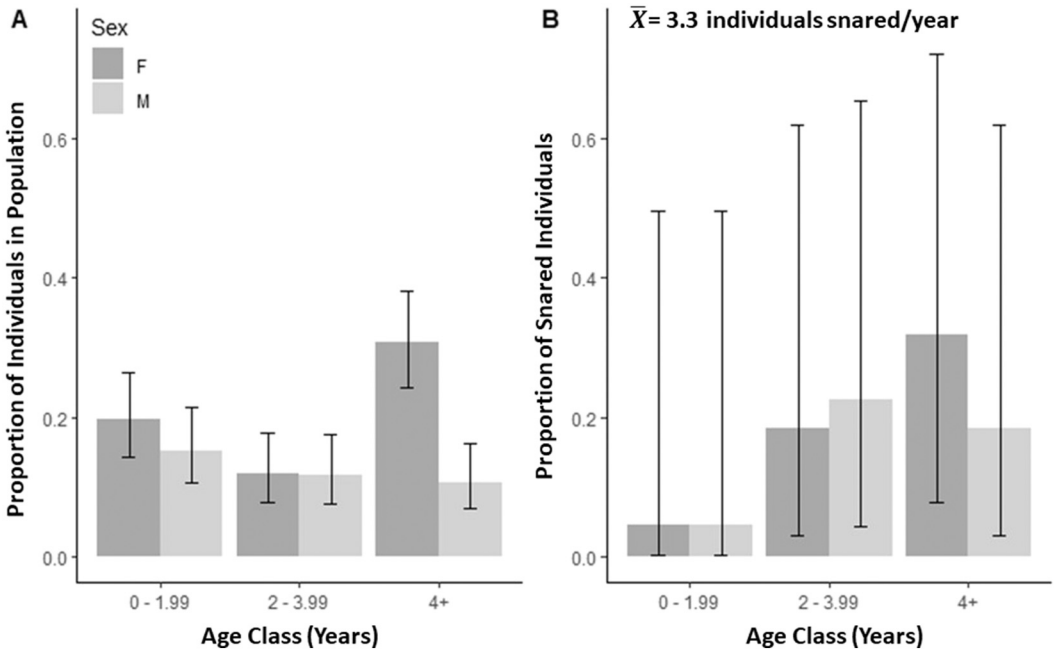

Fig. 2. (A) The proportion of lion population in each age-sex class. (B) The proportion of snared lions in each age-sex class. In both panels, error bars show 95 % binomial confidence limits. Cubs tended to carry snares less often than expected at random. Males (both sub-adults and adults) tended to carry snares more often than expected by chance. Females (both sub-adults and adults) carried snares as often as expected by chance. Because snared individuals are a relatively small subset of the population, confidence limits on the proportion of snared individuals in each age-sex class were broad.

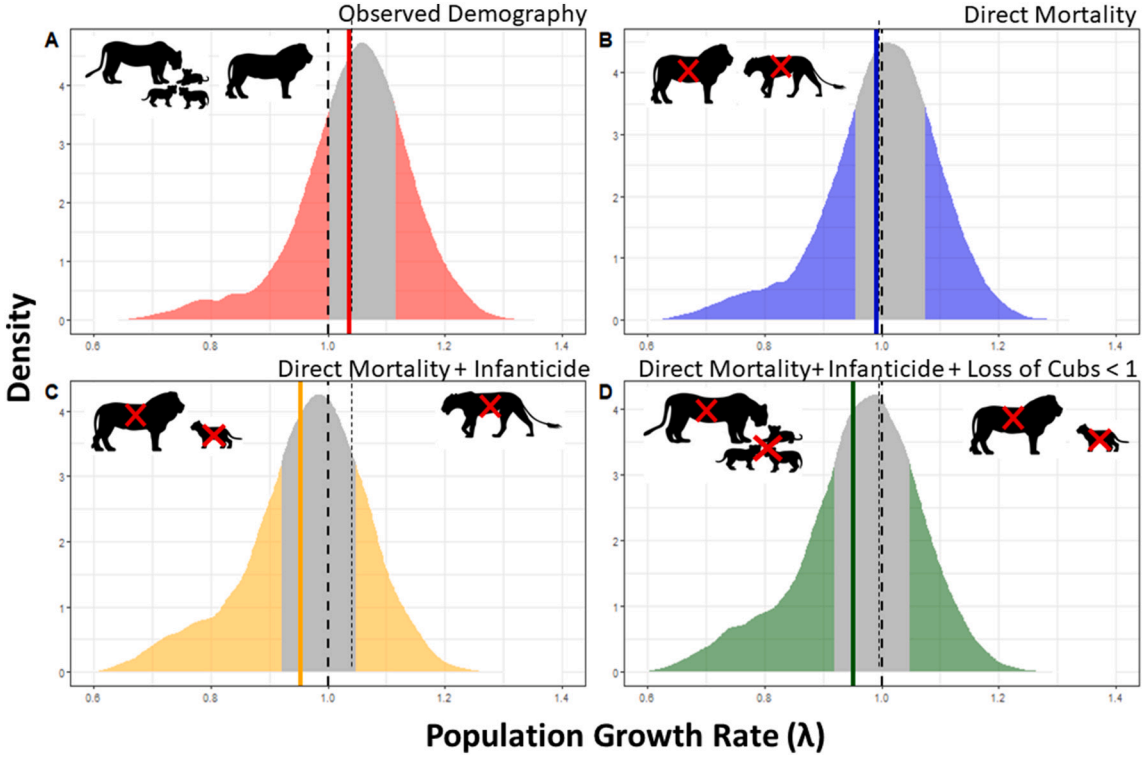

Fig. 3. The distribution of population growth rates (λ) from 10,000 stochastic projections of Luangwa lion dynamics over five years under four different scenarios. In each panel, the grey-shaded area shows the 50 % highest probability density region, and the vertical line shows the geometric mean growth rate. (A) Projection using the observed demography of Luangwa lions from 2008 to 2015. This projection implicitly includes all of the direct and indirect effects of de-snaring on survival and reproduction. The geometric mean growth rate was positive, consistent with a previously described increase in population size (Mweetwa et al., 2018) (also see Fig. 4). (B) Projection removing the direct benefit of de-snaring on survival of both males and females, assuming that snared individuals would have died if the snare had not been removed and the wound treated. The geometric mean growth rate is slightly negative. (C) Projection removing the direct benefit of de-snaring for male and female survival as in part B, but also removing the indirect benefit of better cub recruitment due to reduced male mortality. The geometric mean growth rate is appreciably negative. (D) Projection removing all the direct and indirect benefits of de-snaring in part C, but also assuming dependent cubs of de-snared adult females would have died if the female had not been de-snared. The geometric mean growth rate is appreciably negative and similar to that in part C.

female cubs = 19.7 % [14.3–26.4], *snared individuals*: male cubs = 4.5 % [2.3–49.6], female cubs = 4.5 % [2.3–49.6]). Both sub-adult and adult males tended to carry snares more often (by a factor of two) than expected by chance, probably because they range more widely than females (Fig. 2) (*population*: sub-adult males = 11.% [7.6–17.5 %], adult males = 10.6 % [6.8–16.3 %], *snared individuals*: sub-adult males = 22.5 % [4.3–65.4 %], adult males = 18.3 % [2.9–62.1 %]). Because snared animals may die without being detected, it is likely that these snaring rates are underestimates, particularly for males, despite intensive monitoring.

2.3. Effects of de-snaring on population growth

2.3.1. Observed demography model

This model projected population growth with the observed demography, including all effects of de-snaring on the survival and reproduction of both sexes and all age-classes. The geometric mean stochastic growth rate was 1.037, the mode was 1.059, and probability that λ would fall above one was 77 % (Fig. 3A). The mean population size after five years was 163.8 (9.9 % larger than the initial population of 149), the mode was 158.7, and the population was projected to grow in 70 % of the iterations (Fig. 4A). The distribution of projected population sizes aligned well with the observed range of estimated population sizes from Huggins closed capture-mark-recapture models fit to data from this population over the same period (Mweetwa et al., 2018).

2.3.2. Direct mortality model

This model projected population growth with the assumption that animals who were de-snared would otherwise have died. As expected for the patterns of snaring reported above, this had a small effect on the survival rate (s) of cubs (females: $\Delta s = -0.010$, males: $\Delta s = -0.008$), but larger effects for sub-adults (females: $\Delta s = -0.053$, males: $\Delta s = -0.057$) and adults, particularly males (females: $\Delta s = -0.028$, males: $\Delta s = -0.063$). With these reductions in age- and sex-specific survival, the geometric mean stochastic growth rate was 0.991, the mode was 1.010, and probability that λ would fall above one was 47 % (Fig. 3B).

2.3.3. Direct mortality + infanticide model

This model projected population growth with the assumption that animals who were de-snared would otherwise have died, and that the recruitment of cubs would consequently have declined due to increased male turnover and infanticide. Recall that adult males were snared at higher rates than all other age-sex classes, so their survival can be substantially improved by de-snaring ($\Delta s = -0.063$). Published data from this lion population (Mweetwa et al., 2018) show that when adult male mortality decreased by 0.14 during a three year moratorium on trophy hunting, reduced turnover among pride-resident males cause cub recruitment to increase by 0.48 cubs per adult female. Thus, an increase in male mortality of 0.063 (assuming that de-snared males would have died) would be expected to reduce cub recruitment by 0.22 cubs per adult female (i.e., 0.48 * 0.063/0.14). Combining this effect on cub recruitment with the direct mortality described for the previous model, the geometric mean stochastic growth rate was 0.953, the mode was 0.984, and probability that λ would fall above one was 38 % (Fig. 3C).

2.3.4. Direct mortality + infanticide + loss of dependent cubs model

This model projected population growth with the assumption that animals who were de-snared would otherwise have died, that the recruitment of cubs would consequently have declined due to both increased male turnover and infanticide and the death of dependent cubs of snared mothers. Thus, this model included all of the effects described above, and then reduced the fecundity of adult females by a factor of 0.972 (i.e., $1 - \Delta s$ for adult females). Under these conditions, the geometric mean stochastic growth rate was 0.951, the mode was 0.987, and probability that λ would fall above one was 37 % (Fig. 3D). For this model incorporating all effects of de-snaring, mean population size after five years was 115.4 (23 % smaller than the initial population of 149), the mode was 113.0, and the population was projected to grow in only 6 % of the iterations (Fig. 4B).

To summarize, with the observed demography (which includes all of the benefits of de-snaring) the population showed slow growth, with growth expected in 77 % of years and 70 % of five year windows. This pattern of growth aligned well with previously reported dynamics from direct estimates of population size for these LVE lions using capture-mark-recapture models (Mweetwa et al., 2018). In contrast, projection assuming that de-snared animals would have died (i.e., removing only the direct benefit of de-snaring) predicted population growth in only 47 % of years. Projection removing all of the demographic effects of de-snaring predicted growth in only 37 % of years and 6 % of five year periods.

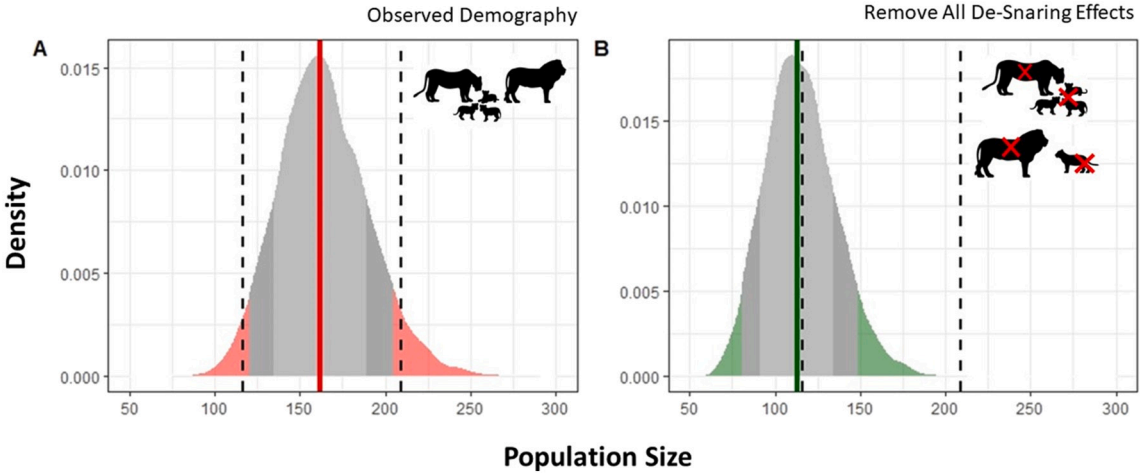

Fig. 4. Projected population size after 5 years from 10,000 stochastic projections, for a population starting with the observed mean population size on the study site (149 individuals) and the observed age-sex structure (shown in Fig. 1A). In both panels, the light and dark grey shading show the 70 % and 90 % highest probability density regions, the heavy vertical line shows the mean projected population size, and the dashed vertical lines show the largest and smallest direct capture-mark-recapture estimates of population size between 2008 and 2015 from Mweetwa et al. (2018). (A) Projection using the observed demography, which includes all of the direct and indirect benefits of de-snaring. Projected population sizes align well with observed population sizes, and slight growth is expected, as was observed (Mweetwa et al., 2018). (B) Projection removing all of the direct and indirect benefits of de-snaring (as in Fig. 3 part D). Population decline would have been expected in the absence of de-snaring.

3. Discussion

It is well established that excessive bushmeat hunting, often using snares, is driving widespread declines of large herbivore populations across Africa (Lindsey et al., 2013; Lindsey et al., 2011; Watson et al., 2013; Bolger et al., 2008). Across sub-Saharan Africa, the density of lions depends strongly on the density of large herbivore prey (Hatton et al., 2015; van Orsdol et al., 1985), so prey depletion due to snaring is an important driver of lion dynamics (Vinks et al., 2021). Several studies have also found that direct snaring can also affect the survival and reproduction of lions (Becker et al., 2013a; Becker et al., 2013b; Loveridge et al., 2020) and other large carnivores (Kenney et al., 1995; Benhaiem et al., 2022; Loveridge et al., 2020), but to our knowledge, no prior studies have evaluated whether a de-snaring program can achieve the goal of improving population growth. For an eight year period in the LVE, we found that de-snaring 3 % of the population annually appreciably improved population growth. The population grew over this period (Mweetwa et al., 2018), but stochastic age-structured projection models show that the population would have been expected to shrink in the absence of de-snaring (Figs. 3 & 4).

Our stochastic projection models assumed that lions who were de-snared would have died if they had not been immobilized to allow removal of the snare and treatment of the wound, but we have no way to directly test what each animal's fate would have been, if it had not been de-snared. Many of the injuries observed were severe, and because of their high body mass and method of hunting, lions are greatly impaired by the loss of a limb. Nonetheless, it is likely that some individuals would have survived, as is confirmed by anecdotal observations of individuals with healed snare wounds (who were not de-snared). On the other hand, periodic observation of individuals that have lost a limb to snaring does not establish that their survival was not compromised (perhaps substantially), or that they would reproduce (Benhaiem et al., 2022). We are not aware of any data that would allow us to quantify these possibilities. Because other studies suggest that mortality due to snaring is severe for lions (Loveridge et al., 2020), we believed the simplest and best assumption was that de-snared individuals would have died without reproducing. Many snare injuries are obviously severe at the time of de-snaring (Fig. 1), and because snares usually tighten over time, it is likely that a snare that had not yet caused a severe wound would eventually do so if it was not removed. Moreover, our methods underestimate snaring mortality, because many individuals disappear without a known cause of death, and it is likely that some of these individuals die in snares. Rather than repeating the population projections to address these uncertainties by making a weaker assumption about the consequence of leaving a snare in place, we simply note that one could devalue the differences between scenarios in Figs. 3 & 4 by a desired factor.

Relevant to the assumption that snared animals are likely to die, 29 % of adult male lions killed by trophy hunters in the Luangwa ecosystem had damage on the back of their canines that is diagnostic of chewing through a wire snare (White and Van Valkenburgh, 2022). This 29 % cumulative risk of snaring equates to an 8.2 % annual risk of snaring. In our intensive monitoring of radio-collared lions, 4.9 % of adult males were observed with a snare each year. We hypothesize that higher proportion of males with tooth damage includes animals who succeeded in removing the snare immediately, before it tightened in a manner that would produce injuries of the type shown in Fig. 1 (though tooth damage itself may compromise survival). On the other hand, Becker et al. (2013a) found that 11.5 % of adult and subadult lions in Luangwa, and 20 % of adult (>4 years) males carried snares over a period of 18 months between 2009 and 2011, so it is also reasonable to simply hypothesize that the intensity of snaring varies over time.

Differences among age-sex classes in the frequency of snaring were probably driven by two mechanisms. Males, especially sub-adults, move over larger areas than females (both in resident male coalitions and in nomadic or dispersing groups) and consequently are more likely to encounter snares. Cubs not only move less, but are probably less likely to break a snare from its anchor if they are caught, and therefore more likely to die without being observed carrying a snare.

A substantial portion of the effect of de-snaring on population growth was due to improved recruitment with reduced male mortality (Figs. 3 & 4). This effect arose partly because males were more likely than females to be snared, and partly because reducing adult male mortality appreciably increased cub recruitment in this population (Mweetwa et al., 2018). To estimate this effect, our models took advantage of unique data (Mweetwa et al., 2018) comparing cub recruitment for five years with trophy hunting of adult males and three years with a moratorium on hunting. These data allowed direct estimation of the proportion by which cub recruitment rose for a given decrease in the adult male mortality rate, and confirm prior conclusions that sexually selected infanticide by males is a strong driver of lion dynamics (Packer and Pusey, 1983). To our knowledge this is the first direct estimate of this super-additive effect of anthropogenic mortality. The manner in which we used this estimate requires an assumption that changes in adult male mortality have the same consequences for cub recruitment whether they are driven by trophy hunting or by snaring. We consider this assumption plausible because most males that were snared or killed by trophy hunters in the LVE came from the same pool of male coalitions. In some populations, trophy males are less likely to be young or old, relative to the population at large, but depletion of trophy males in the South Luangwa population by excessive hunting (under policies that have been replaced) caused the age distribution of hunted males to mirror the population at large during the years of this study (Creel et al., 2016; Mweetwa et al., 2018).

The direct and indirect threat to large carnivores due to intensive bush meat hunting is well established (Lindsey et al., 2013). Efforts to mitigate the effects of snaring are widespread, including efforts to target patrols that remove snare sets in the places that have the greatest benefit for threatened and endangered carnivore populations (Watson et al., 2013). However, we are not aware of prior research that tests whether a de-snaring program can alter the dynamics of a large carnivore population. Data from lions in the Luangwa Valley suggest that de-snaring is a direct and effective way to shift a population from decline to growth. If combined with directed patrols to remove snares from the environment, and particularly in ecosystems where snaring is more intense than in the LVE, it is likely that de-snaring could be even more effective than our results showed.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110273.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

The data and R code are provided in the supplementary material.

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References

Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S.K., Sillero-Zubiri, C., Hunter, L., Lindsey, P., MacDonald, D.W., 2022. Threat analysis for more effective lion conservation. Oryx 56 (1), 108–115.

Becker, M., McRobb, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J., Kakumbi, C., 2013a. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biol. Conserv. 158, 26–36.

Becker, M.S., Watson, F.G., Droge, E., Leigh, K., Carlson, R.S., Carlson, A.A., 2013b. Estimating past and future male loss in three Zambian lion populations. J. Wildl. Manag. 77, 128–142.

Benhaiem, S., Kaidatzi, S., Hofer, H., East, M., 2022. Long-term reproductive costs of snare injuries in a keystone terrestrial by-catch species. Anim. Conserv. 26, 61–71.

Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecol. Lett. 11, 63–77.

Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R., Balmford, A., 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306, 1180–1183.

Coad, L., Abernethy, K., Balmford, A., Manica, A., Airey, L., Milner-Gulland, E.J., 2010. Distribution and use of income from bushmeat in a rural village, central Gabon. Conserv. Biol. 24, 1510–1518.

Creel, S., M'soka, J., Droge, E., Rosenblatt, E., Becker, M., Matandiko, W., Simpamba, T., 2016. Assessing the sustainability of African lion trophy hunting, with recommendations for policy. Ecol. Appl. 6, 2347–2357.

Creel, S., Matandiko, W., Schuette, P., Rosenblatt, E., Sanguinetti, C., Banda, K., Vinks, M., Becker, M.S., 2018. Changes in Zambian large carnivore diets over the past half century reveal the loss of large prey. J. Appl. Ecol. 55, 2908–2916.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., 2011. Trophic downgrading of planet earth. Science 333, 301.

Fa, J.E., Brown, D., 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. Mammal Rev. 39, 231–264.

Fa, J.E., Peres, C.A., Meeuwig, J., 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conserv. Biol. 16 (1), 232–237.

Hatton, I.A., McCann, K.S., Fryxell, J.M., Davies, T.J., Smerlak, M., Sinclair, A.R.E., Loreau, M., 2015. The predator-prey power law: biomass scaling across terrestrial and aquatic biomes. Science 349, aac6284.

Hyndman, R.J., 1996. Computing and graphing highest density regions. Am. Stat. 50, 120–126.

Kenney, J.S., Smith, J.L., Starfield, A.M., McDougal, C.W., 1995. The long-term effects of tiger poaching on population viability. Conserv. Biol. 9, 1127–1133.

Lindsey, P.A., Romanach, S.S., Tambling, C.J., Chartier, K., Groom, R., 2011. Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. Oryx 45, 96–111.

Lindsey, P.A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., Dickman, A., Diggle, R.W., Eves, H., Henschel, P., 2013. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. Biol. Conserv. 160, 80–96.

Loveridge, A., Sousa, L., Seymour-Smith, J., Hunt, J., Coals, P., O'Donnell, H., Lindsey, P., Mandisodza-Chikerema, R., MacDonald, D., 2020. Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. Biol. Conserv. 244, 108504.

Midlane, N., 2014. The Conservation Status and Dynamics of a Protected African Lion *Panthera leo* Population in Kafue National Park, Zambia (Ph. D. thesis). University of Cape Town, Cape Town.

Mudumba, T., Jingo, S., Heit, D., Montgomery, R.A., 2021. The landscape configuration and lethality of snare poaching of sympatric guilds of large carnivores and ungulates. Afr. J. Ecol. 59 (1), 51–62.

Mweetwa, T., Christianson, D., Becker, M., Creel, S., Rosenblatt, E., Merkle, J., Droge, E., Mwape, H., M'soka, J., Simpamba, T., Masonde, J., 2018. Quantifying demographic recovery in lions during a three-year moratorium on trophy hunting. PLoS One 13 (5), e0197030.

Noss, A.J., 1998. The impacts of cable snare hunting on wildlife populations in the forests of the Central African Republic. Conserv. Biol. 12, 390–398.

Packer, C., Pusey, A.E., 1983. Adaptations of female lions to infanticide by incoming males (*Panthera leo*). Am. Nat. 121, 716–728.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. Biodivers. Conserv. 22, 17–35.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M. W., Kerley, G.I., Levi, T., Lindsey, P.A., 2015. Collapse of the world's largest herbivores. Sci. Adv. 1, e1400103.

Rosenblatt, E., Becker, M.S., Creel, S., Droge, E., Mweetwa, T., Schuette, P.A., Watson, F., Merkle, J., Mwape, H., 2014. Detecting declines of apex carnivores and evaluating their causes: an example with Zambian lions. Biol. Conserv. 180, 176–186.

van Orsdol, K.G., Hanby, J.P., Bygott, J.D., 1985. Ecological correlates of lion social organization (*Panthera leo*). J. Zool. 206, 97–112.

Vinks, M.A., Creel, S., Schuette, P., Becker, M.S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., 2021. Response of lion demography and dynamics to the loss of preferred larger prey. Ecol. Appl. 31, e02298.

Watson, F., Becker, M.S., Mcrobb, R., Kanyembo, B., 2013. Spatial patterns of wire-snare poaching: implications for community conservation in buffer zones around National Parks. Biol. Conserv. 168, 1–9.

White, P.A., Van Valkenburgh, B., 2022. Low-cost forensics reveal high rates of non-lethal snaring and shotgun injuries in Zambia's large carnivores. Front. Conserv. Sci. 3, 803381.

Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C., Brashares, J.S., 2008. Accelerated human population growth at protected area edges. Science 321, 123–126.