



## Predicting the consequences of subsistence poaching on the population persistence of a non-target species of conservation concern

Robert A. Montgomery<sup>a,\*</sup>, Tutilo Mudumba<sup>b</sup>, Matthew Wijers<sup>c</sup>, Lara A. Boudinot<sup>d</sup>, Andrew Loveridge<sup>c</sup>, Guillaume Chapron<sup>e</sup>, David W. Macdonald<sup>c</sup>

<sup>a</sup> Department of Biology, University of Oxford, 11a Mansfield Road, Oxford OX1 3SZ, UK

<sup>b</sup> Department of Zoology, Entomology, and Fisheries Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda

<sup>c</sup> Wildlife Conservation Research Unit, Department of Biology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon OX13 5QL, UK

<sup>d</sup> Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota Twin Cities, 2003 Upper Buford Circle, USA

<sup>e</sup> Department of Ecology, Swedish University of Agricultural Sciences, 73091 Riddarhyttan, Sweden

### ARTICLE INFO

#### Keywords:

African lions  
Conservation biology  
Illegal hunting  
Lethal pressure  
Poaching  
Population persistence

### ABSTRACT

Illegal animal hunting, a contributor to biodiversity loss, occurs along a relative selectivity spectrum from indiscriminate to highly selective. Extensive research has evaluated the impacts of selective hunting on animal populations. In contrast, the ways in which indiscriminate hunting pressure can shape populations of non-target species has not yet received comparable attention. We used empirical field data collection and simulation modelling to predict the persistence of an African lion population (*Panthera leo*) subject to indiscriminate hunting pressure from non-target subsistence poaching via wire snares in Murchison Falls National Park, Uganda. Our simulation modelling predicted lion population extirpation following a 50 % rise of lethal poaching pressure above the observed levels. When lethal poaching pressure doubled, the lion population was extirpated in ~70 % of our simulations. We then simulated reductions in lethal poaching pressure to quantify the predicted population recovery of lions. We found that the lion population increased by 40 % with reductions in lethal poaching pressure of 50 %. When we removed lethal poaching pressure entirely, the lion population nearly doubled in just 18 years. Our results demonstrate that by reducing the density of wire snares in the study area by just 2.79/km<sup>2</sup>, the lion population transitioned from being locally extirpated in 67 % of the simulations to reaching carrying capacity inside of two lion generations. We explore how vulnerable even non-target animals are to subsistence poaching and describe the types of applied practices that can be implemented to reduce wire snaring and effectively promote the population recovery of species of conservation concern.

### 1. Introduction

The world lost an estimated 68 % of terrestrial biodiversity in the latter half of the 20th century (Leclère et al., 2020) with species extinction rates occurring 100 to 1000 times higher than background conditions (Pimm et al., 2014). Many factors have contributed to these global biodiversity declines including, but certainly not limited to, habitat loss, climate change, invasive speciation, disease, human-wildlife conflict, guild disruption, and unsustainable hunting by humans (Macdonald, 2016; Montgomery et al., 2020a). These factors represent conservation threats that fuel defaunation both directly and indirectly via the reduction of animal survival and reproduction (Frid

and Dill, 2002) with effects that can rapidly scale from individuals to populations (Harris et al., 2002; Coltman et al., 2003). The loss of biodiversity can, in turn, destabilise the structure of trophic systems with subsequent implications for ecosystem services and integrity (Duffy, 2003). Consequently, biodiversity loss represents one of the most pressing global conservation challenges (Rands et al., 2010).

Given the rapid loss of biodiversity, there is a need to understand how specific conservation threats can drive animal populations to extirpation (Yackulic et al., 2011). Population modelling presents a useful tool for evaluating the effects of various threats on animal population dynamics (Wood et al., 2015). The outcomes of these predictions can then be used to design and optimise interventions that reduce the

\* Corresponding author.

E-mail address: [robert.montgomery@biology.ox.ac.uk](mailto:robert.montgomery@biology.ox.ac.uk) (R.A. Montgomery).

<https://doi.org/10.1016/j.biocon.2023.110147>

Received 19 January 2023; Received in revised form 31 May 2023; Accepted 3 June 2023

Available online 16 June 2023

0006-3207/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

occurrence, likelihood, and intensity of specific conservation threats. Unsustainable human hunting of animal populations, for instance, has been a critical conservation threat both historically and presently (Gosselin et al., 2014; le Roex and Ferreira, 2020). Humans are prolific hunters with induced defaunation rates that are considerably higher than any other non-human predator (Darimont et al., 2015) and it is challenging to estimate with precision the number of animal species that humans have hunted to extinction (Ripple et al., 2016).

Unsustainable human hunting can occur legally, when sanctioned hunts are poorly managed, as well as illegally in a form that is broadly referred to as poaching (Woodroffe and Redpath, 2015; Montgomery, 2020). There are several different types of poaching differentiated by the motivations of the poachers and intended use of the animal products (Montgomery, 2020). Trophy poaching represents the pursuit of physical characteristics of animals used as possessions, whereas accessing animal parts for their purported medicinal properties is represented by medicative poaching, and consumptive poaching involves the use of animal parts for human consumption or subsistence (Montgomery, 2020). In both the legal and illegal forms, human hunting of animals occurs along a selectivity spectrum from indiscriminate to highly selective (Montgomery et al., 2020a). The precise selectivity is determined, in part, by the hunting tools and techniques that are used (Montgomery et al., 2022a). For instance, a trophy poacher using a high-powered rifle can have a high degree of selection for a specific animal target (Chiyo et al., 2015). Medicative poachers, using a wide array of tools, are often highly selective for specific species (Challender and MacMillan, 2014). The tools used in consumptive poaching however, occur across a much broader spectrum of selectivity with many tools that are often far less selective for individual animals or species (Montgomery et al., 2020a). Snare and traps, for example, are among the most common tools of subsistence poachers globally and are largely indiscriminate (Gray et al., 2018; Tilker et al., 2019; Mudumba et al., 2020). Consequently, subsistence poaching presents threats to the population persistence of target and non-target species that are trapped, often referred to as 'bycatch' (Becker et al., 2013; Bouley et al., 2018; Loveridge et al., 2020; Vinks et al., 2021).

The consequences of targeted poaching on animal populations have been widely studied (Kenny et al., 1995; Everatt et al., 2019). Less attention has been extended to indiscriminate poaching on non-target animal populations. We explored the impact of subsistence poaching on African lion (*Panthera leo*) population persistence in Murchison Falls National Park, Uganda. Murchison Falls National Park is a coupled human and natural system that experiences some of the highest rates of subsistence poaching via wire snares documented globally (Mudumba et al., 2020). Though snares are typically set to capture antelope, non-target species such as lions, can also become entrapped. Via field data collection, we recorded demographic data including the total lion population size and the number of lions caught by wire snares. We then used a lion population simulation model to predict the level of lethal poaching pressure that resulted in the extirpation of the lion population. We also predicted the recovery of the lion population from simulations in which non-target subsistence poaching was reduced and eliminated altogether as a lethal pressure. Concurrently, we conducted wire snare surveys to quantify the density of wire snares in the national park. We then quantified the linear relationship between that density and lion mortality via wire snares. We used this model to quantify the reduction in wire snares predicted as the outputs of the lion simulation models. We discuss the implications of subsistence poaching for the persistence of non-target species and explore the conservation policy and conservation practice interventions capable of promoting population recovery of species of conservation concern.

## 2. Material and methods

### 2.1. Study area

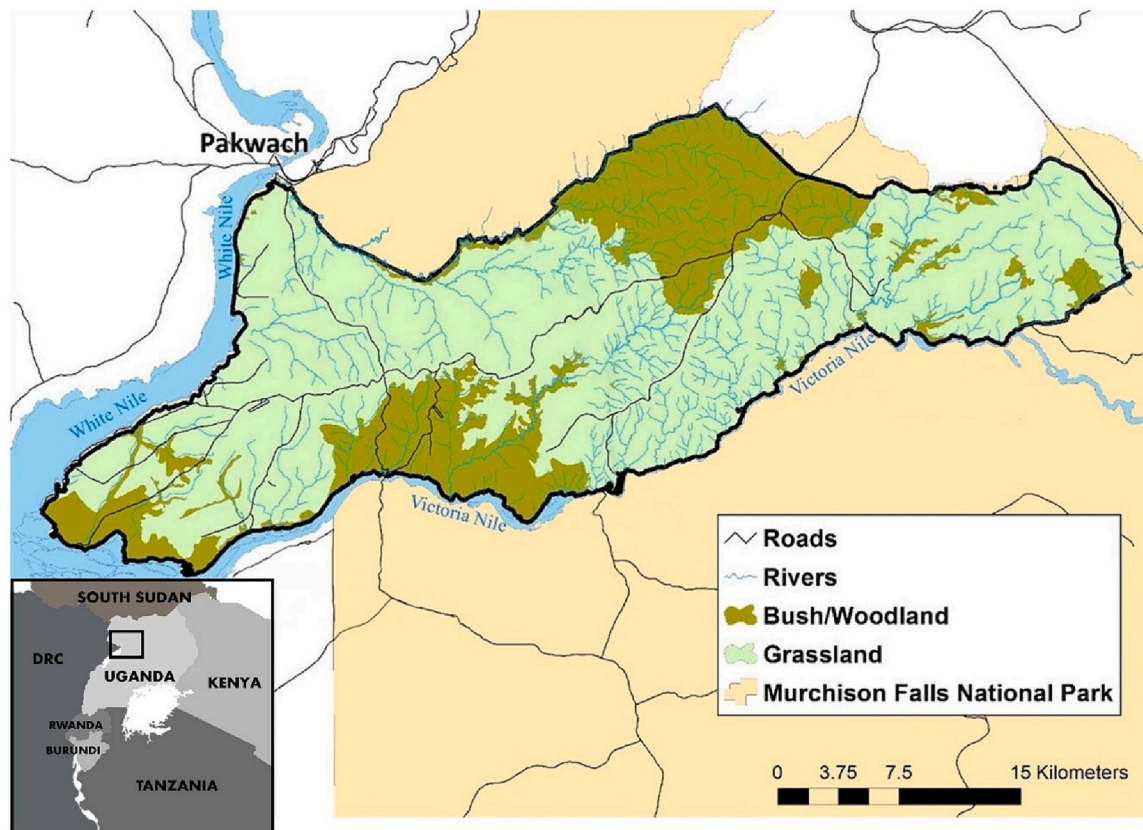
We positioned our study in Murchison Falls National Park, located in the Northwest region of Uganda (Fig. 1). Split into two portions, referred to as the Northern and Southern Banks, by the Victoria Nile River, Murchison Falls has a range of habitat types from closed forest to woodland thickets and open grasslands (Nangendo et al., 2005; Fig. 1). In the Northern Bank, we maintain a ~ 1000 km<sup>2</sup> study area within which we monitor several faunal species of conservation concern, including African lions (Montgomery et al., 2020b). Given a history of civil war and displacement, the human communities bordering the national park are among the poorest in Uganda with an average income of USD\$85 per annum (Mudumba, 2011). These realities, coupled with the abundant animal populations residing in the national park, have led many members of the local community to poach (Mudumba et al., 2020). The predominant form of poaching is subsistence-based as the meat is largely consumed within the poacher's family, and not distributed more broadly, or sold for modest financial gains.

As a by-product of the low economic status of the subsistence poachers, the tools that are commonly used in this illegal activity are comprised of freely-available materials. For these reasons, wire snares in this part of Uganda are typically built from the internal wire framework of radial vehicle tires or from motorcycle brake cables (Mudumba et al., 2020). One end of the wire is tied to an anchor, typically a tree or sturdy bush, and the loop of the snare is suspended above the ground with reed string (Mudumba et al., 2020). Animals can be captured when they walk through the loop whereupon the wire constricts around the trapped body part (e.g., head, torso, or limb) and their movement pulls pressure against the anchor. The poachers revisit the snare locations, kill animals that are caught, and field butcher the meat. The target species of subsistence poachers in Murchison Falls include Ugandan kob (*Kobus kob thomasi*), Lelwel hartebeest (*Alcelaphus buselaphus lelwel*), Bohor reedbuck (*Redunca redunca*), Cape buffalo (*Syncerus caffer caffer*), and waterbuck (*Kobus ellipsiprymnus*; Mudumba and Jingo, 2015; Mudumba et al., 2020). However, many other non-target species, including sympatric large carnivores, are vulnerable to being trapped. Lions, for instance, are a species that are regularly ensnared (Mudumba et al., 2020). Given that lion meat is not conventionally pursued for subsistence poaching and there is not a strong demand for lion parts as part of medicative poaching in this area, lions are most often left in the trap. There they either die or are subsequently rescued by interventions conducted by the Uganda Wildlife Authority.

Our interest here was to assess the vulnerability of the lion population to non-target subsistence poaching via wire snares. This lethal pressure accounts for the highest proportion of mortality for lions in Murchison Falls (Mudumba and Jingo, 2015). Given that the study area is surrounded by waterways (see Fig. 1), rates of human-lion conflict are comparatively low. Furthermore, though disease has affected other populations of lions in Uganda, across the study period no disease outbreaks were recorded (Mudumba et al., n.d.). Finally, several of the primary prey species of lions are the main targets of subsistence poachers and thus, vulnerable to lethal poaching pressure. Nevertheless, the densities of prey species in Murchison Falls remain high. Ugandan kob, for instance, occur at a density of 245.9/km<sup>2</sup> which is among the highest recorded across the species range (Mudumba et al., n.d.). Predictions of the population size of lions in Murchison Falls as a function of prey density demonstrate that the lion population is presently well below the size that would be expected (Mudumba et al., n.d.). Thus, prey depletion does not appear to be a limiting factor on the lion population.

Lion Population Monitoring and Snare Density Surveys.

From June 2016 to December 2021, we conducted vehicle-based surveys across seasons to identify and track individual lions among five prides in the study area and quantify the density of prey species preferred by lions. Then in 2018, we also recorded data on the incidence



**Fig. 1.** The northern bank of Murchison Falls National Park, Uganda where we maintain a ~1000 km<sup>2</sup> study area to study the dynamics of the African lion (*Panthera leo*) population. This lion population is subject to non-target subsistence poaching pressure via wire snaring. People participating in subsistence poaching, many of which reside in the neighbouring town of Pakwach, typically access the national park via the waterways along the western boundary.

of lions being caught, injured, and killed by wire snares, and quantified the density of wire snares. We collected data on each of these four categories to develop the parameter values needed to simulate lion population dynamics under different snaring intensity scenarios. Via the vehicle-based photographic surveys we calculated the total counts of individual lions observed (see [Mudumba et al., n.d.](#) for full methodological details). We tracked lions among each pride and recorded right-side photos to individually identify lions via their whisker spot patterns and facial features ([Bertram, 1975](#)). We photographed all lions and maintained an image database to distinguish among individual animals using body marks and whisker spot patterns ([Pennycuik and Rudnai, 1970](#)). In instances in which we could not find lions, we used reports from the Uganda Wildlife Authority to relocate the prides. We continued our search efforts until no new lions were added to our database. That is how we calculated the minimum number of known individual lions in the study area to be 139.

Next, we conducted transect surveys to predict the density of preferred lion prey needed to calculate carrying capacity for the lion population in the study area. In doing so, we developed a network of transects plotted randomly and positioned in a north-south direction in each vegetation type ([Buckland and Turnock, 1992](#)). Elevation change throughout the study area is minimal and so we were not concerned about positioning transects perpendicular to the contours. We conducted a pilot survey in each vegetation type to estimate survey effort required to give reliable density estimate ([Marques et al., 2001](#)). We determined preferred prey according to their frequency in lion kill sites using techniques outlined by [Bouley et al. \(2018, see Mudumba et al., n.d.\)](#). Thereby, the prey species preferred by lions included Ugandan kob, oribi (*Ourebia ourebi*), Cape buffalo, hartebeest, common warthog (*Phacochoerus aethiopicus*), and waterbuck. We calculated the preferred prey biomass to be 10,844 kg/km<sup>2</sup> ([Mudumba et al., n.d.](#)) and predicted

a lion carrying capacity estimate of 253. This calculation was based on the [Hayward et al. \(2007\)](#) equation for preferred prey:  $y = 10^{(-2.158+0.377x)}$ , where  $y$  = lion density in km<sup>2</sup> and  $x$  =  $\log_{10}$ (prey biomass in kg/km<sup>2</sup>). [Hayward et al. \(2007\)](#) derived this equation from lion densities and prey abundances at sites within savanna ecosystems across southern and eastern Africa.

To quantify the proportion of the population caught in wire snares, we surveyed the lion prides for snare-injured lions and recorded the number of lions that the Uganda Wildlife Authority veterinary unit had rescued from snares when they had not been identified among those in our field survey. Concurrently, we quantified the density of wire snares, again using vehicle-based surveys. To do so, we used the grid overlay method (see [Mudumba et al., 2020](#) for full methodological details). We placed a 6 × 6 km grid over our study area and then sectioned the gridded area into two categories, snare and no-snare areas, using previously collected data from Uganda Wildlife Authority ranger patrols. We then randomly selected five grid cells from each category (snare and no-snare), and five random grid cells from the two categories. Each selected grid cell was further divided into 600 m × 6 km transects, of which three were selected to be surveyed. To estimate snare density, observers scanning for snares from each side of the vehicle surveyed a 100 m × 6 km transect (sectioned from the 600 m × 6 km transects), and the total snares found per transect were summed (see [Mudumba et al., 2020](#)).

Via these surveys, we found the wire snares to be highly detectable from the vehicles. To examine this contention however, we conducted two experiments to test for the detection probability of snares. The first was predicated upon the distribution of dummy snares and the second estimate derived from repeat surveys. First, two observers distributed 20 dummy snares randomly across the study area. These dummy snares took the same form as a conventional snare, but the wire was non-



functioning given that the lasso end was taped rather than fixed. Thus, if an animal were to walk through, the wire would break at the taped end, rather than constrict. Two surveyors, unaware of the location of the snares, then initiated the snare survey. Here the detection probability was 1.00 as the surveyors detected all 20 of the dummy snares. Secondly, a repeat survey of randomly-sampled grids throughout the study area was implemented. The detection probability of wire snares in this repeat survey was 0.83. These two separate detection surveys demonstrate that wire snares are conspicuous given the open and flat savanna system in the study area and the reality that snares tend to be connected to large trees capable of holding an animal once it is caught. At the conclusion of each of these experiments, all snares were removed from the landscape.

## 2.2. Lion population simulations

Next, we used an individual-based model available in the package *pop.lion* (Loveridge et al., 2023) in R (version 4.2.3; R Core Team, 2019) to simulate the impact of varying levels of lethal non-target poaching pressure on lion population dynamics (see Table 1 for model parameters). As we had relatively little data on baseline survival and litter size distribution of the lion population in Murchison Falls, we imputed starting values of these parameters from a long-term study of lions in Hwange National Park, Zimbabwe (see Loveridge et al., 2023; Table 1). Next, we calculated the annual lethal poaching pressure from the data deriving from our vehicle-based surveys. We found that, on average, 9.7 lions are killed each year from subsistence poaching via wire snares. We assumed that all individual lions were vulnerable to snaring and did not consider there to be a threshold age. Thus, we calculated the annual lethal poaching pressure to be 0.07 (i.e., = 9.7 / 139 lions). We then input this lethal poaching pressure as a parameter in the model and functioned by removing a random proportion of the population corresponding to the set mortality rate. Furthermore, the model inherently accounts for infanticide that can occur when a resident pride male is killed and the pride subsequently taken over by a new male coalition (see Loveridge et al., 2023).

In addition to carrying capacity, the *pop.lion* model requires an estimate of the maximum number of prides to determine space availability for new prides to settle. We estimated a maximum number of 19 prides could occupy the study area at carrying capacity. This estimate equates to an average home range size of ~58 km<sup>2</sup>, which is within the range reported by Mudumba and Jingo (2015) for lion prides in Murchison Falls National Park. We initiated all simulations with these initial parameter estimates (Table 1) and let the model run to the population asymptotic state. We visually assessed this as being the point at which oscillations caused by the non-asymptotic initial population structure fade out. We then applied variations in the lethal poaching pressure at 25 %, 50 %, 75 %, and 100 % increases and decreases relative to the current rate. We simulated 1000 iterations for each snaring scenario with the mean and quantile range between 0.025 and 0.975 calculated

**Table 1**

Parameter values used to simulate lion population dynamics under different snaring mortality rates in the northern bank of Murchison Falls National Park, Uganda.

Parameter	Value
Baseline survival	See Loveridge et al. (2023)
Litter size distribution	1 (12 %); 2 (30 %); 3 (35 %); 4 (19 %); 5 (4 %)
Initial population	5 prides
Lethal poaching pressure age threshold	0
Lethal poaching pressure (annual)	0.07
Carrying capacity	253
Maximum prides	19
Maximum coalitions	19

and plotted.

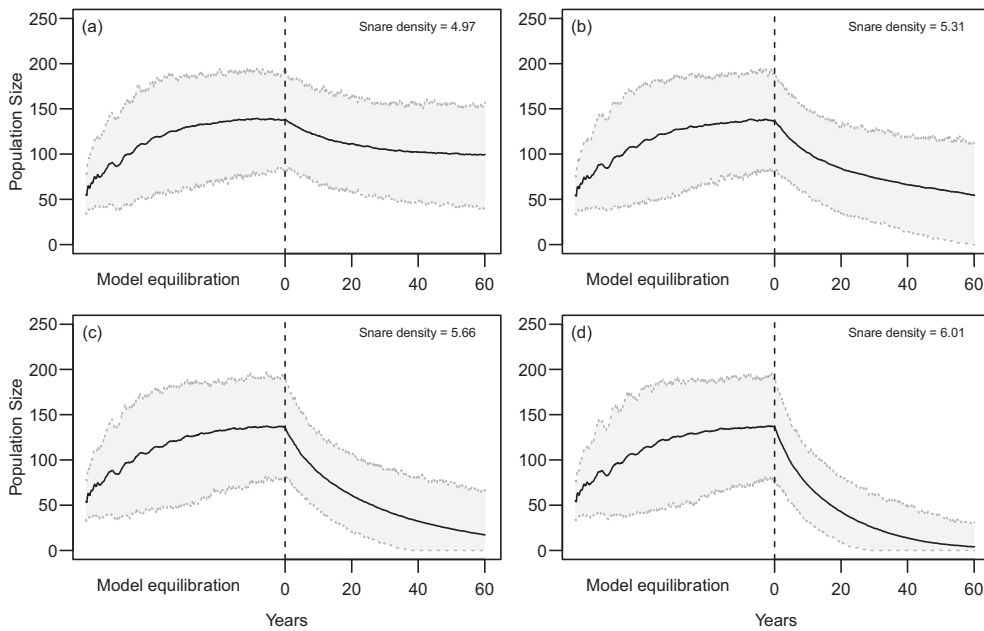
Finally, using the snare density data, we developed a univariate linear regression model to explore the relationship between the density of wire snares and the mortality rate of lions attributable to non-target subsistence poaching via wire snares. We then used this fitted linear model to predict the wire snare densities that would be associated with the simulated lion mortality rates.

## 3. Results

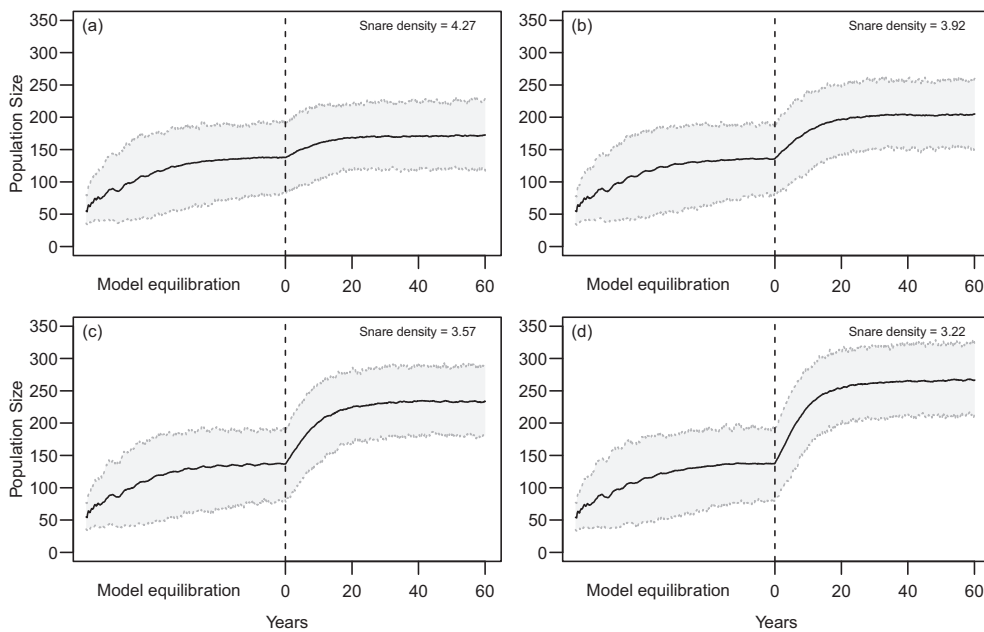
In the beginning of the simulations, the lion population steadily grew and stabilized at  $\sim 137 \pm 28$  (mean  $\pm$  SD) individuals (Figs. 2 and 3). With an annual lethal poaching pressure of 0.07, the estimate of this stable population is quantitatively similar to the minimum population estimate of 139 lions deriving from our field data collection efforts (Fig. 2). When we increased lethal poaching pressure by 25 %, the simulations showed a downward population trajectory with a mean of  $100 \pm 30$  individuals in the lion population after 60 years (Fig. 2a). With simulated increases of lethal poaching pressure by 50 %, the lion population declined to a mean of  $54 \pm 30$  lions after 60 years with 3 % of iterations predicting local population extirpation (Fig. 2b). When we increased lethal poaching pressure by 75 % the lion population was reduced to a mean of  $17 \pm 19$  individuals after 60 years with 28 % of iterations leading to extirpation (Fig. 2c). These extirpations happened within 42 years of the increase in lethal poaching pressure (Fig. 2c). Simulated increases of lethal poaching pressure by 100 % reduced the mean population to  $4 \pm 9$  individual lions with 67 % of iterations leading to local population extirpation (Fig. 2d). These extirpations happened within 32 years of the increase in lethal poaching pressure (Fig. 2d).

Conversely, we also simulated the impacts of reduced lethal poaching pressure on lion population dynamics (Fig. 3). When we decreased lethal poaching pressure by 25 %, the simulations showed an upward population trajectory with a mean of  $\sim 162 \pm 29$  lions after 11 years (Fig. 3a). With simulated decreases of lethal poaching pressure by 50 %, the lion population reached a mean of  $\sim 193 \pm 29$  individuals after 17 years (Fig. 3b). When we decreased lethal poaching pressure by 75 % the lion population rose to  $\sim 221 \pm 30$  individuals within 17 years (Fig. 3c). When we removed lethal poaching pressure altogether, the lion population rose quickly reaching the carrying capacity of  $\sim 250$  individuals after 18 years (Fig. 3d).

We detected a density of wire snares across the study area of 4.58/km<sup>2</sup>, 4.21/km<sup>2</sup>, 4.35/km<sup>2</sup>, and 5.20/km<sup>2</sup> in 2018, 2019, 2020, and 2021, respectively. Across these same years, we detected a total lion mortality attributed to wire snaring of 10 lions in 2018, six in 2019, nine in 2020, and 13 in 2021 (Table 2). The minimum population count during the period from 2018 to 2021 was estimated to be 139 individuals and therefore the annual minimum lion mortality rates were calculated as 0.072, 0.043, 0.065, and 0.094 respectively (ratio of dead lions/minimum lion numbers). From these data, the univariate linear regression model predicted wire snare density as a function of lion mortality rate with an equation of  $y = 19.905x + 3.2246$  and an R<sup>2</sup> value of 0.89 (Fig. S1). We predicted wire snare density from lion mortality rate (and not the other way around) to be able to quantify the wire snare density that would be associated with each level of lethal poaching pressure simulated in our model and therefore to infer plausible decline and recovery of the lion population (see Figs. 2 and 3). An increase in wire snare density of 1.04/km<sup>2</sup> changed the downward population trajectory of lions from one that had a mean of 100 lions after 60 years (Fig. 2a) to one that was driven to local extirpation in 67 % of simulations across the same time period (Fig. 2d). In contrast, reductions in wire snare density of 2.79/km<sup>2</sup> had the lion population moving from local extirpation in 67 % of the simulations (Fig. 2d) to reaching carrying capacity within 18 years (Fig. 3d).



**Fig. 2.** Results of simulations showing the effects of increasing current snaring mortality (0.07) by 25 % (a), 50 % (b), 75 % (c), and 100 % (d) on the African lion (*Panthera leo*) population residing in the northern bank of Murchison Falls National Park, Uganda. All changes are applied at 60 years as indicated by the vertical dotted line. The solid black trend line indicates the mean population size and the grey shaded region represents the 95 % quantile range. The wire snare densities corresponding to the simulated lion mortality rates are provided in the panels.



**Fig. 3.** Results of simulations showing the effects of decreasing current snaring mortality (0.07) by 25 % (a), 50 % (b), 75 % (c), and 100 % (d) on the African lion (*Panthera leo*) population residing in the northern bank of Murchison Falls National Park, Uganda. All changes are applied at 60 years as indicated by the vertical dotted line. The solid black trend line indicates the mean population size and the grey shaded region represents the 95 % quantile range. The wire snare densities corresponding to the simulated lion mortality rates are provided in the panels.

**Table 2**

African lion (*Panthera leo*) mortality from non-target subsistence poaching via wire snares recorded between 2018 and 2021 in the project study area in Murchison Falls National Park, Uganda.

Year	Lion mortality		Total
	Adult male	Adult female	
2018	6	4	10
2019	3	3	6
2020	6	3	9
2021	7	6	13

**4. Discussion**

Via a combination of empirical field data collection and simulation modelling we predicted the population-level consequences of subsistence poaching on a non-target species. We found that the persistence of the lion population in Murchison Falls National Park, Uganda was highly vulnerable to subsistence poaching pressure via wire snares where several species of sympatric antelope are the intended target. Iterations of the simulated model began to predict population extirpation following an increase in lethal poaching pressure of 50 %, equivalent to a rise of just 4.85 lions killed annually above the observed. When that lethal poaching pressure doubled, the lion population was predicted to be extirpated in 70 % of the iterations. Furthermore, these extirpations were typically predicted within 32 years of the increase in lethal poaching pressure. Given that lions in the wild can live up to ~15 years

(Barthold et al., 2016), these extirpations occurred across approximately two lion generations. In contrast, when lethal poaching pressure was reduced, the simulations predicted swift population recovery. This was evidenced by reductions in lethal poaching pressure of 50 % leading to the lion population expanding to approximately 200 individuals (e.g., ~45 % increase) in less than 20 years. When lethal poaching pressure was removed altogether, meaning a transition from 9.7 lions dying annually to 0 dying annually, the lion population was predicted to almost double and reach the population carrying capacity of ~250 individuals in just 18 years. These results demonstrate the ways in which subsistence poaching, or lack thereof, can affect the persistence of a non-target species of conservation concern.

We acknowledge that our model did not account for possible variation in snaring risk across different age and sex classes nor spatial variation in snaring pressure across the study area. These would present opportunities to further parameterise the *pop.lion* model in future. It is important to note that removal of adults, particularly reproductively mature females, can have more detrimental impacts on a population than the loss of individuals in other age and sex cohorts (Chapron et al., 2008; Gerber and White, 2014). In the event that adult females are more vulnerable to snaring, we would expect even steeper declines in the population trend in the simulations in which lethal snaring pressure increased and slower population recoveries in the simulations in which snaring was decreased. Furthermore, we recommend that future research efforts seek to determine the reproductive consequences of lions living with a snaring injury. We do not yet know, for instance, whether snaring injuries decrease the reproductive success of affected lions, as has been found in other species (see Benhaïem et al., 2022). Thus, our model output should be interpreted as conservative estimates of lion population dynamics.

Lions have experienced dramatic population loss in the last century with 43 % population reductions in the last two decades alone and presently occur across just 8 % of their former range (Bauer et al., 2016; Loveridge et al., 2022). While habitat loss, range fragmentation, and prey depletion have been discussed as causal mechanisms associated with these declines (Bauer et al., 2022), the impact of non-target subsistence poaching on lion survival has not been widely studied. The threat of poaching using wire snares has, within the last ten years, been highlighted as an underappreciated conservation threat globally (Becker et al., 2013; Watson et al., 2013; Gray et al., 2018) and we have illustrated the ways in which it can drive even the populations of non-target species to extirpation. Snares, whether they be made from wire or rope, are perhaps the most common and widely-used tool of consumptive poachers globally (Rochlitz, 2010). We note, however, that our models assumed interannual consistency in lethal poaching pressure. In reality, these pressures should be expected to exhibit temporal dynamism as a function of various characteristics of the coupled human and natural system (e.g., community agricultural productivity, law enforcement regime, political influence, trapping success). Within our simulations, we also assumed stasis in other conditions such as the availability of habitat and prey abundance, which should also be expected to vary temporally. Thereby, we once again caution that these population persistence estimates should be viewed as conservative in relation to estimates that might derive from more complex modelling approaches. Furthermore, there may be other methods (e.g., individual-based models or stage-structured approaches) that could add further resolution to predictions of the consequences of subsistence poaching on non-target animal populations. We encourage continued progression in the modelling techniques used within this context.

Snare removal remains an important activity for the conservation of lions and various other species vulnerable to poaching pressure. The removal of snares can be an effective way to mitigate the harmful effects to wildlife, and the process can be optimized via spatial prediction of areas with a higher snaring likelihood (Watson et al., 2013; Mudumba et al., 2020). Even with these technological and quantitative advancements however, snare removal remains a highly intensive and time-

consuming activity (Ibbett et al., 2020). Further research and innovation into the mechanisms of snare detection, removal, and the creation of novel anti-snare technologies are needed. However, despite our best efforts, snaring is a threat that learns and adapts. Most subsistence poaching via wire snares in Murchison Falls is due to poverty and a lack of alternative means of support (Mudumba et al., 2020). Snaring will continue to pose a threat so long as the surrounding community has a need for the resources provided by snaring. Therefore, empowering the local community to end poaching and providing substantive methods of survival may be a more effective tool for snare elimination.

Encouragingly, while subsistence poaching is a large and multifaceted problem, interventions positioned in local communities can present solutions. To access these solutions however, it is necessary to address the root cause of subsistence poaching which is human poverty and a lack of alternative livelihood options (Montgomery, 2020; Montgomery et al., 2022b). Thus, the simulation modelling that we implemented herein can be useful in predicting the consequences of poaching, to both target and non-target species, and prioritizing interventions. Importantly, these interventions cannot be solely based on protecting the species of conservation concern but must also seek to uplift local human communities in conservation (see Montgomery et al., 2020b). We have found that 88.6 % of local people ( $n = 659$  respondents) living around Murchison Falls have never been inside of the national park and only 8.0 % derived any financial benefits, all of them very modest, from the park (Mudumba et al., 2022). Without benefits, there are few incentives for people to support the implementation of conservation policies and practices. For these reasons, authors of this paper created the Snares to Wares Initiative (Mudumba et al., 2020; Montgomery et al., 2022b).

The Snares to Wares Initiative is a human heritage-centred conservation (HHCC; Montgomery et al., 2020b) initiative which seeks to empower local people in the communities bordering Murchison Falls National Park. In collaboration with Uganda Wildlife Authority, the initiative conducts wire snare sweeps inside the national park, repurposes the metal wires as raw materials, and provides artistic training to local people (many of which are reformed poachers) to convert the wire into sculptures of wildlife vulnerable to poaching. The Snares to Wares Initiative then creates local and international markets for the sale of these sculptures with proceeds that generate employment for local people, uplift their livelihoods and those of their families in conservation, and provide a productive alternative to subsistence poaching inside the national park. Solutions such as the Snares to Wares Initiative, are needed at scale to decrease consumptive and subsistence poaching globally. Consistent with the HHCC framework, the solutions applied globally will be highly variable in that they must be complementary to the cultural heritage of the local human communities. Thus, while snare wire art is consistent with the heritage of the communities around Murchison Falls National Park, alternative solutions may better fit in other parts of the world. Nevertheless, as our modelling has shown, even modest reductions in wire snare density could lead to dramatic increases in lion population size. Our paper emphasizes the importance of interdisciplinary collaborations between conservation scientists and host-country wildlife agencies to strengthen conservation policies as well as optimized practices to remove wire snares and engage local communities to provide alternatives to subsistence poaching. These are scalable principles that can aid in the recovery of lion populations vulnerable to subsistence poaching across their range.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110147>.

#### Declaration of competing interest

The authors have no conflicts of interest to declare.

## Data availability

Data will be made available on request.

## Acknowledgements

S. Jingo, P. Ariyo, P. Luhonda, W. Tumusiime, I., A.O. Zakayo, B. Olowo, H. Kasozi, and UWA staff participated in data collection for this study. E. Sande, and R. Kityo provided comments on an earlier draft of this manuscript. This study was supported by National Geographical Society [grant number NGS-86536C-21] and with the financial support of the European Union through IUCN Save Our Species [grant number 2020A-163].

## References

- Barthold, J.A., Loveridge, A.J., Macdonald, D.W., Packer, C., Colchero, F., 2016. Bayesian estimates of male and female African lion mortality for future use in population management. *J. Appl. Ecol.* 53, 295–304.
- Bauer, H., Packer, C., Funston, P.F., Henschel, P., Nowell, K., 2016. *Panthera leo* (errata version published in 2017). In: The IUCN Red List of Threatened Species 2016: e.T15951A115130419.
- 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, 108–115.
- Becker, M., McRobb, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J., Kakumbi, C., 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biol. Conserv.* 158, 26–36.
- Benhaiem, S., Kaidatzi, S., Hofer, H., East, M.L., 2022. Long-term reproductive costs of snare injuries in a keystone terrestrial by-catch species. In: *Animal Conservation*.
- Bertram, B.C.B., 1975. Social factors influencing reproduction in wild lions. *J. Zool.* 177, 463–482.
- Bouley, P., Poulos, M., Branco, R., Carter, N.H., 2018. Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biol. Conserv.* 227, 233–242.
- Buckland, S.T., Turnock, B.J., 1992. A robust line transect method. *Biometrics* 48, 901–909.
- Challender, D.W., MacMillan, D.C., 2014. Poaching is more than an enforcement problem. *Cons. Lett.* 7, 484–494.
- Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S., Clobert, J., 2008. The impact on tigers of poaching versus prey depletion. *J. Appl. Ecol.* 45 (6), 1667–1674.
- Chiyo, P.I., Obanda, V., Korir, D.K., 2015. Illegal tusk harvest and the decline of tusk size in the African elephant. *Ecol. Evol.* 5, 5216–5229.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., Festa-Bianchet, M., 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426, 655–658.
- Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. *Science* 80 (349), 858–860.
- Duffy, J.E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6, 680–687.
- Everatt, K.T., Kokes, R., Lopez Pereira, C., 2019. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodivers. Conserv.* 28, 4099–4114.
- Frid, A., Dill, L., 2002. Human-Caused Disturbance Stimuli as a Form of Predation Risk. *Conserv. Ecol.* p. 6.
- Gerber, L.R., White, E.R., 2014. Two-sex matrix models in assessing population viability: when do male dynamics matter? *J. Appl. Ecol.* 51 (1), 270–278.
- Gosselin, J., Zedrosser, A., Swenson, J.E., Pelletier, F., 2014. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proc. R. Soc. B Biol. Sci.* 282.
- Gray, T.N.E., Hughes, A.C., Laurance, W.F., Long, B., Lynam, A.J., O'Kelly, H., Ripple, W. J., Seng, T., Scotson, L., Wilkinson, N.M., 2018. The wildlife snaring crisis: an insidious and pervasive threat to biodiversity in Southeast Asia. *Biodivers. Conserv.* 27, 1031–1037.
- Harris, R.B., Wall, W.A., Allendorf, F.W., 2002. Genetic consequences of hunting: what do we know and what should we do? *Wildl. Soc. Bull.* 30, 634–643.
- Hayward, M.W., O'Brien, J., Kerley, G.I.H., 2007. Carrying capacity of large African predators: predictions and tests. *Biol. Conserv.* 139, 219–229.
- Ibbett, H., Milner-Gulland, E.J., Beale, C., Dobson, A.D.M., Griffin, O., O'Kelly, H., Keane, A., 2020. Experimentally assessing the effect of search effort on snare detectability. *Biol. Conserv.* 247, 108581.
- Kenny, J.S., Smith, J.L.D., Starfield, A.M., McDougal, C.W., 1995. The long-term effects of tiger poaching on population viability. *Conserv. Biol.* 9, 1127–1133.
- Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H., Chaudhary, A., De Palma, A., DeClerck, F.A., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature* 585, 551–556.
- Loveridge, A.J., Sousa, L.L., Seymour-Smith, J., Hunt, J., Coals, P., O'Donnell, H., Lindsey, P.A., Mandisodza-Chikerema, R., Macdonald, D.W., 2020. Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biol. Conserv.* 244, 108504.
- Loveridge, A.J., Sousa, L.L., Cushman, S., Kaszta, Z., Macdonald, D.W., 2022. Where have all the lions gone? Establishing realistic baselines to assess decline and recovery of African lions. *Divers. Distrib.* 28, 2388–2402.
- Loveridge, A.J., Wijers, M., Mandisodza-Chikerema, R., Macdonald, D.W., Chapron, G., 2023. Anthropogenic edge effects and aging errors by hunters can affect the sustainability of lion trophy hunting. *Sci. Rep.* 13 (1), 1–10.
- Macdonald, D.W., 2016. Animal behaviour and its role in carnivore conservation: examples of seven deadly threats. *Anim. Behav.* 12, 197–209.
- Marques, F.F.C., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A., Peace, A.J., 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *J. Appl. Ecol.* 38, 349–363.
- Montgomery, R.A., 2020. Poaching is not one big thing. *Trends Ecol. Evol.* 35, 472–475.
- Montgomery, R.A., Macdonald, D.W., Hayward, M.W., 2020a. The inducible defences of large mammals to human lethality. *Funct. Ecol.* 34, 2426–2441.
- Montgomery, R.A., Borona, K., Kasozi, H., Mudumba, T., Ogada, M., 2020b. Positioning human heritage at the center of conservation practice. *Conserv. Biol.* 34, 1122–1130.
- Montgomery, R.A., Raupp, J., Miller, S.A., Lisowsky, R., Comar, A., Wijers, M., Bugir, C. K., Hayward, M.W., 2022a. The hunting modes of human predation and potential nonconsumptive effects on animal populations. *Biological* 265, 109398 (Conservation).
- Montgomery, R.A., Pointer, A.M., Jingo, S., Kasozi, H., Ogada, M., Mudumba, T., 2022b. Integrating social justice into higher education conservation science. *BioScience*.
- Mudumba, T., 2011. Perceptions and Solutions to Human-Wildlife Conflict in and Around Murchison Falls National Park. Technical Report, Wildlife Conservation Society, Uganda.
- Mudumba, T., Jingo, S., 2015. Murchison Falls National Park Lions: Population Structure, Ranging and Key Threats to their Survival. Technical Report, Wildlife Conservation Society.
- Mudumba, T., Jingo, S., Heit, D., Montgomery, R.A., 2020. The landscape configuration and lethality of snare poaching of sympatric guilds of large carnivores and ungulates. *Afr. J. Ecol.* 59, 51–62.
- Mudumba, T., Moll, R.J., Jingo, S., Riley, S., Macdonald, D.W., Astaras, C., Montgomery, R.A., 2022. Influence of social status and industrial development on poaching acceptability. *Glob. Ecol. Cons.* 38, e02271.
- Mudumba, T., M.W. Hayward, E. Sande, S. Jingo<sup>1</sup>, H. Kasozi<sup>1</sup>, C. Astaras, and R.A. Montgomery. Prey biomass may be a poor predictor of African lion density in small isolated populations. *Front. Ecol. Evol.* In review.
- Nangendo, G., Stein, A., ter Steege, H., Bongers, F., 2005. Changes in woody plant composition of three vegetation types exposed to a similar fire regime for over 46 years. *For. Ecol. Manag.* 217, 351–364.
- Pennycuik, C.J., Rudnai, J., 1970. A method for identifying individual lions panthera-*leo* with an analysis of reliability of identification. *J. Zool.* 160, 497–498.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 80 (344), 1–10.
- R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>. URL.
- Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., Vira, B., 2010. Biodiversity conservation: challenges beyond 2010. *Science* 80 (329), 1298–1303.
- Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., Newsome, T.M., Peres, C.A., Wallach, A.D., Wolf, C., 2016. Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* 3, 1–16.
- Rochlitz, I., 2010. The Impact of Snares on Animal Welfare. Cambridge.
- le Roex, N., Ferreira, S.M., 2020. Age structure changes indicate direct and indirect population impacts in illegally harvested black rhino. *PLoS One* 15, 1–13.
- Tilker, A., Abrams, J.F., Mohamed, A., Nguyen, A., Wong, S.T., Sollmann, R., Wilting, 2019. Habitat degradation and indiscriminate hunting differentially impact faunal communities in the Southeast Asian tropical biodiversity hotspot. *Commun. Biol.* 2, 396.
- Vinks, M.A., Creel, S., Schuette, P., Becker, M.S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., Chifunte, C., 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.
- Wood, K.A., Stillman, R.A., Goss-Custard, J.D., 2015. Co-creation of individual-based models by practitioners and modellers to inform environmental decision-making. *J. Appl. Ecol.* 52, 810–815.
- Woodroffe, R., Redpath, S.M., 2015. When the hunter becomes the hunted. *J. Cell Sci.* 348, 1312–1314.
- Yackulic, C.B., Sanderson, E.W., Uriarte, M., 2011. Anthropogenic and environmental drivers of modern range loss in large mammals. *PNAS* 108, 4024–4029.