QUANTIFYING IMPACTS OF ANTHROPOGENIC DISTURBANCES ON WILDLIFE

By

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ABSTRACT

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In this dissertation I examined the interconnectedness of human population growth, energy development, human-wildlife coexistence, and wildlife population ecology. In Chapter One, I reviewed literature and categorized the of effects of oil extraction on wildlife. Broadly, the effects included: i) increased poaching, ii) curtailed space-use, iii) increased harassment, iv) risk of introduction of invasive species, v) contamination, and vi) heightened severity of impacts due to synergistic effects. Overall, I found that efforts to evaluate the consequences of oil extraction, particularly in peer-reviewed form, were limited. Research should be conducted pre-, during, and post-oil extraction to increase knowledge of effects of oil extraction on wildlife to enable more effective policy decisions.

In Chapter Two, I studied human-wildlife co-existence and found that conflict was the most important factor determining local people's attitude towards poaching. Less than 20% of the local people had ever visited the park and there was limited flow of benefits for local communities from protected areas. My findings highlight the importance of providing remedies compatible with local livelihoods and could be used to improve wildlife management to address poaching.

In Chapter Three, I predicted the African lion (*Panthera leo*) carrying capacity in Murchison Falls National Park (MFNP) from existing primary prey biomass. I found that the extant African lion density was four times less than what the prey biomass inside the park could support. I compared the African lion density estimated from prey biomass to that estimated from

direct counts and found that estimating lion density from indirect methods such as prey biomass can result in overestimation of existent populations.

In Chapter Four, I described an approach for estimating the density, configuration and lethality of poacher-set snares and discussed their effects on wildlife inside MFNP. Murchison Falls National Park had the highest known density of wire snares in the world. I provide a litany of anthropogenic and environmental configurations that made snares more likely to catch an animal. The ability of snares to trap an animal were significantly predicted by snare thickness, noose width, vertical drop, wire circumference, grass height, and anchor tree diameter at breast height. Regulating the disposal of dis-used vehicle tires which provided the material for the wire snares was likely to reduce snare poaching inside the park. Additionally, providing alternative livelihoods to people involved in snare poaching would discourage the recruitment of locals in snare poaching. My method of surveying snares provides the opportunity to standardize temporal and spatial measurements of snare density and configuration as a first step to refine mitigation techniques.

I conclude my dissertation with a summary of my key findings and recommendations for future research. The results of my research are applicable to biodiverse-rich portions of the world that are at risk of human development. My methods could also be used to quantify the severity of subsistence poaching. This is relevant because subsistence poaching remains a significant conservation challenge in the 21st century.

For

Sylvester Negaga Muhwana Musimami and Florence Hamba Musimami

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"*Gloria in excelsis Deo*"

PREFACE

The four main chapters of this dissertation have been submitted to peer-reviewed journals with co-authors. The citations for these chapters are below.

Chapter 1: Mudumba, T., S. Jingo, D. B. Kramer, K. Elliott, S. Riley, E. Tans, M. W. Hayward, D. W. Macdonald, C. Astaras, and R. A. Montgomery. The quest for oil and subsequent implications for wildlife conservation. *Conservation Science and Practice*. In review.

Chapter 2: Mudumba, T., R. J. Moll, S. Jingo, S. Riley, D. W. Macdonald, C. Astaras, and R. A. Montgomery. Acceptability of wildlife poaching is predicated upon specific socio-economic characteristics. *Biological Conservation*. In review.

Chapter 3: Mudumba, T., M. W. Hayward, S. Jingo, H. Kasozi, C. Astaras, and R. A. Montgomery. Prey biomass is a poor predictor of African lion population size in the dynamic 21st century. *Ecological Applications*. In review.

Chapter 4: Mudumba, T., S. Jingo, D. Heit, and R. A. Montgomery. The landscape configuration and lethality of snare poaching. *African Journal of Ecology*. In review.

Despite the fact that I am recorded as the sole author and use the pronoun I inside this dissertation, every chapter involved several individuals and all manuscripts under peer-review produced out of this work include co-authors.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The global human population is presently estimated at 7.2 billion people and is projected to exceed 10 billion by 2100 (Gerland et al., 2014). Given this rapid growth, previously uninhabited areas are being developed and sparsely populated areas are experiencing rapid urbanization. Consequently, the footprint of the world's cities is expanding rapidly (Burdett, Sudjic, & Cavusoglu, 2011). Concurrently, the global economy continues to be dependent upon finite natural resources (Stern, Common, & Barbier, 1996). Non-renewable fossil fuels still provide the primary energy sources and every year, several million acres of wildlands are converted into farmland which has put enormous pressure on natural systems (Abas, Kalair, & Khan, 2015). The negative impacts of human population growth and the associated unsustainable use of natural resources are well studied and include global warming (Adger & Brown, 1994), accelerated habitat degradation (Tilman et al., 2001), and environmental contamination (Carlson & Adriano, 1993) among others. These challenges either individually or synergistically not only have consequences for human livelihood but also for wildlife population viability (Brook, Sodhi, & Bradshaw, 2008). The people and wildlife located in the global south are particularly vulnerable to these negative effects. For instance, due to poverty, higher dependence on natural resources, and rapid human population growth, the global south is at a higher risk of facing an energy crisis than the rest of the world (Thomas & Twyman, 2005; Bilgen, 2014).

Efforts to locate new oil reserves around the globe have intensified (Abas et al., 2015; Nyambuu & Semmler, 2014). Keen financial investors and novel technologies have enabled previously known but hard-to-reach deposits to now be economically viable to pursue (Chen & Jia, 2000; Frassy et al., 2015; Tang et al., 2012). Yet, due to their remoteness, these formerly inaccessible oil deposits tend to occur in areas with comparatively higher species richness and diversity (Finer, Jenkins, Pimm, Keane, & Ross, 2008; Ramirez & Mosley, 2015; Sovacool, 2007). In the global south, some of the areas under consideration for oil extraction overlay key biodiversity hot spots and include national parks (Butt et al., 2013; Watkins, 2010). Therefore, one of the growing concerns for wildlife conservation is the renewed interest to expand oil extraction to new sites including areas overlaying critical wildlife habitats (Butt et al., 2013). The effects of oil extraction on people (Jobin, 2003; Obi, 2010; Ogwang, Vanclay, & van den Assem, 2018) and on the environment have been widely investigated (Dowhaniuk, Hartter, Ryan, Palace, & Congalton, 2018; Esterhuyse, Redelinghuys, & Kemp, 2016). Comparatively little research has investigated the impacts on wildlife. Therefore, decisions to extract oil in biodiverse-rich regions are likely to be undermined by the lack of knowledge of the effects on wildlife.

Another anthropogenic disturbance of importance to wildlife conservation is the unsustainable utilization of wildlife in form of poaching. There are three distinct types of poaching that include trophy poaching, trafficking poaching, and subsistence poaching (Montgomery in review). However, subsistence poaching is the most widespread version and involves the illegal harvest of wildlife for the purpose of consumption (Neumann & Machlis, 1989). Subsistence poaching is strongly linked with higher levels of poverty and lack of alternative livelihoods (Roe, 2008). Subsistence poaching can bear serious consequences for local wildlife populations (Knapp, Peace, & Bechtel, 2017). For instance, in West Africa, subsistence poaching led to a decline in the local population of the African lion (*Panthera leo*) and giraffe (*Giraffa camelopardalis rothschildi*) to a level that necessitated a separate classification of these species (Henschel et al., 2010; Winter, Fennessy, & Janke, 2018).

The effects of anthropogenic perturbations on wildlife and their coping mechanisms remains a serious challenge in the 21st century. Given human population growth, there will be an increase in the number of people living in proximity with wildlife which could increase the potential for human-wildlife conflict. Human-wildlife conflict can directly lead to wildlife persecution or indirectly harm wildlife via prey depletion and loss of preferred habitat (McKee, Sciulli, Fooce, & Waite, 2004). Currently, the world is amidst what is being called the 6th mass extinction of wildlife and the first to be driven by humans (Pievani, 2014). Therefore, plans must continue to refine and broaden our knowledge of the consequences of anthropogenic disturbances on wildlife in order to devise reliable solutions that foster human-wildlife co-existence.

In my research, I have examined the current literature on impacts of oil extraction on wildlife, studied the socioeconomic conditions that give rise to subsistence poaching, researched the relationship between African lions and their prey, and defined the landscape configuration and lethality of snare poaching. In Chapter One, I conducted a literature review to identify papers assessing impacts of oil extraction on terrestrial wildlife and applied the resultant topology to a case study of Murchison Falls National Park (MFNP), Uganda. In Chapter Two, I completed household interviews in villages surrounding MFNP to gain knowledge of drivers of poaching and demographic profiles of poachers. I assessed the acceptability of tools used to poach wildlife, and the respondents' perceptions toward wildlife and park authorities. In Chapter Three, I predicted the African lion carrying capacity from prey biomass and compared it with the extant population. Then, in Chapter Four, I developed and tested a new approach to understanding the configuration and density of poacher -set snares. I conclude my dissertation with a summary of my key findings and recommendations for future research. At the end of each chapter, I discuss the implications of my research for wildlife conservation and human livelihood improvement. Thus, each chapter concludes with a set of applied management and conservation actions that are informed by my research examining the interconnectedness of human population growth, energy development, human-wildlife coexistence, and wildlife population ecology.

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CHAPTER 1: THE QUEST FOR OIL AND SUBSEQUENT IMPLICATIONS FOR WILDLIFE CONSERVATION

1.1 Abstract

Global dependence upon fossil oil persists in the 21st century. Consequently, vast deposits of oil are being exploited in highly biodiverse regions. The breadth of effects of oil extraction, however, on wildlife remain unclear. I reviewed literature on the effects of oil extraction on terrestrial wildlife to develop a typology of the effects documented. Among the 34 relevant papers that I identified, three (9%) demonstrated wildlife adaptation to certain aspects of the oil extraction process. All other papers (91%) documented negative effects. Broadly, these effects included: *i*) increased poaching, *ii*) curtailed space-use, *iii*) increased harassment, *iv*) risk of introduction of invasive species, *v*) contamination, and *vi*) heightened severity of impacts due to synergistic effects. I applied this typology of effects to Murchison Falls National Park (MFNP), Uganda, where oil extraction is ongoing. I illustrate that MFNP's immediate concern should be indirect oil effects including the potential increase in poaching and human-wildlife conflict. Clearly, extracting oil in the vicinity of wildlife biodiverse regions presents a number of threats to conservation. I provide recommendations for additional research, which if conducted pre-, during, and post-oil extraction will increase knowledge and understanding of effects on wildlife and enable more effective policy decisions.

1.2 Introduction

With <15% of global energy generated from alternative renewable sources, the world's human population continues to be dependent upon fossil fuels (Lund 2007; Arbuthnott & Dolter 2013). Crude oil remains the most sought after energy source and is predicted to remain so into the foreseeable future (Krichene 2006; Mirchi et al. 2012; Abas et al. 2015). Current predictions suggest that known oil reserves could be exhausted within the next century (Mirchi et al. 2012; Hook & Tang 2013). Consequently, efforts to locate new oil reserves around the globe have intensified (Nyambuu & Semmler 2014; Abas et al. 2015). Keen financial investors and novel technologies enabled previously known but hard-to-reach deposits to now be economically viable to pursue (Chen & Jia 2000; Tang et al. 2012; Frassy et al. 2015). Yet, due to their remoteness, these formerly inaccessible oil deposits tend to occur in areas with comparatively higher species richness and diversity (Sovacool 2007; Finer et al. 2008; Ramirez & Mosley 2015).

Given that the world is in the midst of the sixth mass extinction event and the first that is primarily driven by human actions, competing priorities relating to energy and wildlife conservation are predicted to intensify (Casetta et al. 2015; Newbold et al. 2016). The potential for conflict is particularly apparent in Africa given large oil deposits directly beneath wildlife protected areas and the lack of a prior knowledge of the effects of oil extraction on wildlife (Butt et al. 2013). Effects of oil extraction on people are generally well known (Jobin 2003; Obi 2010; Ogwang et al. 2018) and on the environment (Esterhuyse et al. 2016; Dowhaniuk et al. 2018), but not specifically on wildlife. Hence, highlighting the potential effects of oil extraction on wildlife is of critical importance to conservation practice and policy formation.

I conducted a review of peer-reviewed literature to determine the various ways in which wildlife are affected by oil extraction. In doing so, I developed a typology of effects that I applied to a case study in Murchison Falls National Park (MFNP), Uganda, the only national park in the world where active oil drilling is ongoing within its border. This national park sits in the Greater Albertine Rift Valley of East Africa, which is one of the most biodiverse areas on

Earth and also a region with vast oil deposits (Dou et al. 2004; Uganda 2008). Given the competing motivations of oil extraction and wildlife conservation, succinctly stating the possible effects of oil extraction on wildlife is a critical first step to a satisfactory solution. I discuss the implications of this research for the Greater Albertine Rift Valley and beyond and provide recommendations on how to lessen negative impacts created by oil extraction on wildlife.

1.3 Methods

I conducted a literature review (completed in June 2019) to identify papers assessing impacts of oil extraction on terrestrial wildlife. I searched the bibliographic databases of the Web of Science Core Collection, Wildlife and Ecology Studies Worldwide, and Engineering Village. I used "*oil extraction*" AND "*wildlife*" as search terms and restricted my assessment to peer-reviewed literature. Ecological Impact Assessment reports were excluded from my analysis given that they are neither peer-reviewed nor required to be published as grey literature. As my interest was to apply the resultant topology to a case study of MFNP and develop a generalized framework for terrestrial settings, I did not consider papers on marine wildlife. I also eliminated papers that were either purely lab tests or those conducted in non-biodiverse areas (e.g., oil sand mines). I recorded study area, habitat type, year of publication, and wildlife species studied in each paper. Then I categorized the effects of oil extraction on wildlife from: oil exploration, development, production, and abandonment (Davidsen et al. 1990). Here, I use abandonment to refer to the period either between exploration and production or after production when there is no detectable oil extraction activity. Categorization among these four broad categories enabled us to develop a typology of effects.

I applied the typology of effects to MFNP. Located in the northern end of the Albertine Rift Valley in Uganda (02°15′N 31°48′E; Fig. 1.1), MFNP was gazetted in 1952, more than 50 years before oil was discovered in the area.

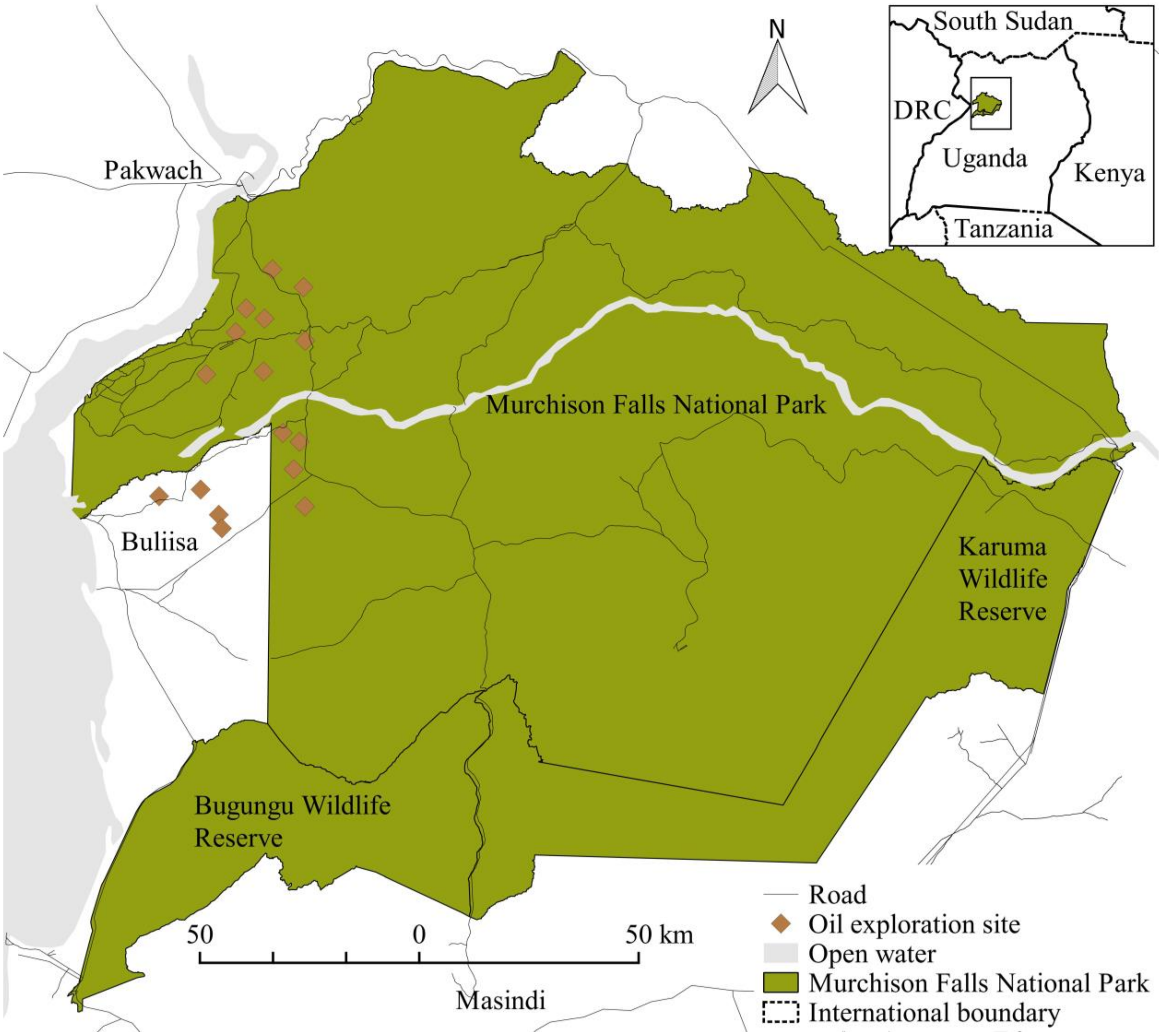

Figure 1.1. Map of Uganda showing Murchison Falls National Park with the locations of major oil exploration wells.

Three and a half billion barrels of recoverable oil in and around MFNP was confirmed in 2006 (Van Alstine et al. 2014; Polus & Tycholiz 2016). Preliminary research conducted on large mammals and birds during 2D and 3D seismic tests identified that oil extraction activities affected wildlife (Ayebare 2011; Mudumba et al. 2012; Plumptre et al. 2015). I used the *Uganda National Red list* to evaluate the number and diversity of species of conservation importance in MFNP (Wildlife Conservation Society 2016). I restricted the analysis to six taxa including birds, mammals, butterflies, dragonflies, amphibians, and reptiles.

1.4 Results

1.4.1 *Characterization of paper*

My search returned 106 papers, 34 (32%) of which met the criteria for consideration (Tables 1.1 to 1.4). The number of papers returned from my literature review demonstrated an increase in research on oil extraction and wildlife over the last twenty years (Fig. 1.2).

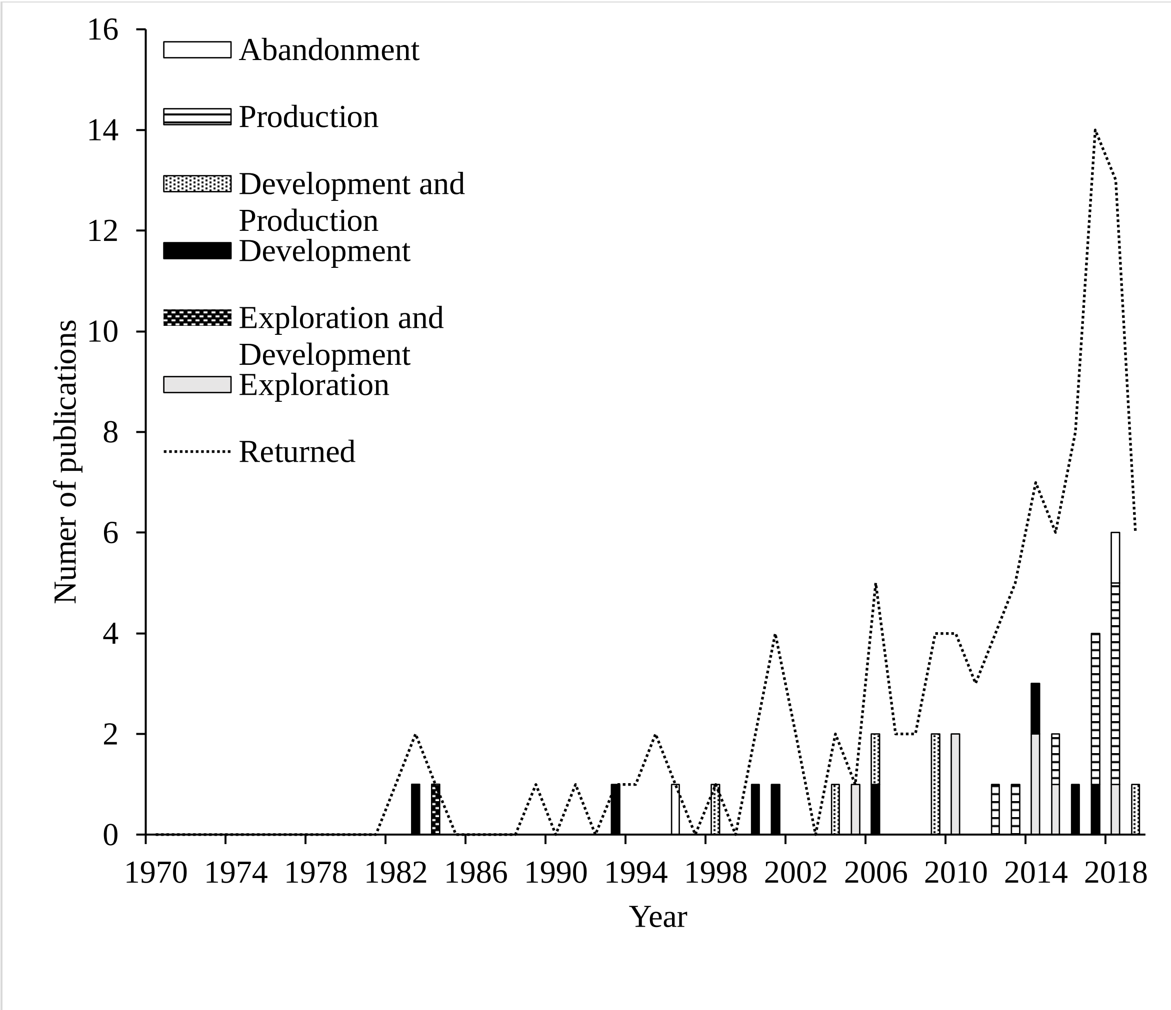

Figure 1.2. Peer-reviewed papers published between 1970 and 2019 returned from a literature search evaluating the impact of oil extraction on wildlife. The dotted line shows the number of all papers returned while the bars reflect the number of papers returned for each activity of oil extraction.

Most (91%) of the research of the returned papers was carried out in the Americas with research in just three papers (9%) conducted on the African continent (Fig. 1.3).

Figure 1.3. The spatial configuration of research on the impacts of oil extraction on wildlife among peer-reviewed papers published between 1970 and 2019.

Most of these papers (49%, Table 1.1) evaluated wildlife effects during oil development. Another 20% and 26% of the reviewed papers studied wildlife during the extraction phase (Table 1.2) and production (Table 1.3) respectively.

Table 1.1. List of source references with elements and major findings of peer reviewed studies on wildlife and oil extraction conducted during the oil exploration phase between 1970 and 2019.

Elements	Main findings from the study	Name / kind	Taxon	Reference
Roads	Population declined due to increased poaching due to access provided by road network.	Guanaco	*Lama guanicoe*	Radovani et al.,2014

Table 1.1 (cont'd)

Seismic survey	Increased variation in inter-patch distances in bear habitat.	Grizzly Bear	*Ursus arctos*	Linke et al., 2005
	No detectable impact on activity and population. No change in activity patterns due to oil extraction.	Ocelot	*Leopardus pardalis*	Kolowski & Alonso, 2010
	Avoided seismic activity areas	African elephant	*Loxondata africana*	Rabanal et al., 2010
	Avoided seismic activity areas on small and intermediate scales.	Chimpanzee	*Pan troglodytes*	Rabanal et al., 2010
	Affected predator-prey relationships (black bear and caribou) Potentially altered black bear ability to locate and capture ungulate prey	Black Bears	*Ursus americanus*	Tigner et al., 2014
Hydraulic fracturing	Avoided areas near energy development	River Otters	*Lontra canadensis*	Godwin et al., 2015
Various extraction perturbations	Displaced from suitable habitat, Interfered with free movement Increased harassment Attracted carnivores and scavengers to food waste areas and increased conflict	Large Mammals		Klein, 1984

Table 1.2. List of source references with elements and major findings of peer reviewed studies on wildlife and oil extraction conducted during the oil development phase between 1970 and 2019.

Elements	Main findings from the study	Name / kind	Taxon	Reference
Roads	Depleted local populations	Howler Monkey Spider Monkey	*Ateles belzebuth*, *Alouatta seniculus*	Franzen 2006
	Doubled extraction of bushmeat Increase in spatial extent of hunting area.	Various	*Various*	Espinosa et al., 2014
	No significant impact on density or activity	Ocelot	*Leopardus pardalis*	Salvador & Espinosa, 2016
	No evidence of avoidance	Caribou	*Rangifer tarandus*	Noel et al., 2004
	Increased the impacts of hunting Reduced species richness and density	White-lipped peccary, paca, woolly monkey	*Tayassu pecari*, *Cuniculus pac*, *Lagothrix poeppigii*	Suarez et al., 2009

Table 1.2 (cont'd)

Infrastructure and roads	Reduced range Shifted the calving ground	Caribou	*Rangifer tarandus*	Joly et al., 2006
	No detectable change in space use	Northern Bobwhite	*Colinus virgianus*	Dunkin et al., 2009
	Shifted calving and seasonal ranges Potentially lost suitable habitat	Woodland Caribou	*Rangifer tarandus caribou*	Dyer et al., 2001
	Used up high value habitat Avoided roads	Pronghorn	*Antilocapra americana*	Christie et al., 2017
	Minimal response to oil development, but increased development would lead to lasting negative effects	Black Bears	*Ursus americanus*	Tietje and Ruff, 1983
	Increased likelihood of disturbance of denning polar bears	Polar Bear	*Ursus maritimus*	Amstrup et al, 1993
	Destroyed the habitat Polluted by oil and noise Encouraged invasive species	Wildlife		Olive, 2018

Table 1.3. List of source references with elements and major findings of peer reviewed papers on wildlife and oil extraction conducted during the oil production phase between 1970 and 2019.

Elements	Main findings from the study	Name / kind	Taxon	Reference
Roads	Facilitated hunting, agriculture and urbanization	Wildlife		Vanthomme et al., 2013
	Increased speed in response to roads Increased movement in response to high traffic volume. Roads reduced the quality of the habitat	and	*Gulo gulo luscus*	Scrafford et al., 2018
Infrastructure and roads	Caused synergistic effects such as decreased abundance	Pronghorn	*Antilocapra americana*	Christie et al., 2015
	Increased the risk of nest failure (ecological traps)	Killdeer	*Charadrius vociferus*	Atuo et al., 2016
	Higher nest success rate because of lack of predator interaction in more developed areas but increased predation in adjacent areas	Prairie Chickens	*Tympanuchus phasianellus*	Burr et al., 2017
	Lower nest sites re-use of near high energy extraction sites thus long-term population declines could be expected	Ferruginous Hawk	*Buteo regalis*	Wiggins et al., 2017

Table 1.3 (cont'd)

Contamination	Wildlife and indigenous communities were exposed to oil polluted soils and river sediments	Wildlife		Rosell-Mele et al. 2017
	Reduced amphibian abundance in wetlands reflecting multi-decadal ecological effects.	Amphibians		Hossack et al., 2018
	Exposure to oil polluted soils and leaks at oil wells	Tapir, Paca, Red-Brocket Deer, Collared Peccary	*Tapirus Terrestris, Cuniculus paca, Mazama americana, Peccary Tajacu*	Orta-Martinez et al.,2018

Finally, 5% of the studies were carried out during the abandonment phase (Table 1.4). I found two papers (5%) that assessed wildlife during habitat restoration and one paper (2%) that was conducted in relation to hydraulic fracturing. There were no papers that simultaneously evaluated the effects of any element (i.e., roads, oil pads etc.) across all the four oil extraction phases. The impact of roads was the most (33%) investigated element, tied in second place was seismic surveys and various oil extraction perturbations (13%), effect of oil pads and contamination on wildlife each had 3 papers (8%).

Table 1.4. List of source references with elements and major findings of peer reviewed papers on wildlife and oil extraction conducted during the oil abandonment phase between 1970 and 2019.

Elements	Main findings from the study	Name / kind	Taxon	Reference
Restoration	Increased herbivore abundance at restored sites	Wildlife		Fuda et al., 2018
	Less vulnerable to site specific disturbances. Some migratory routes made the fish vulnerable	Dolly Varden Trout	*Salvelinus malma*	Underwood et al., 1996

The vast majority of these papers (70%) examined the impact of oil extraction on mammals, 9% assessed impacts on birds, and just 3% of the papers looked at impacts on freshwater fish. In 18% of the papers, the impacts of oil extraction were measured across all wildlife with no distinction on species.

1.4.2 *Typology of effects*

Oil extraction was reported to increase consumption and displacement, inhibited natural movements and space use, and concentrated human pressure on wildlife (Table 1.1 and 1.2). I found four species that were deemed to be adaptable to seismic tests, hydraulic fracturing, and oil pads (Table 1.2). Among the negative effects, secondary impacts included population decline, increased harassment, higher incidences of invasive speciation, poor waste disposal, and wildlife exposure to contamination (Table 1.2 and 1.3). In combination with other factors like climate change, oil extraction worsened synergistic effects on wildlife (Table 1.3). The positive impacts of oil extraction upon wildlife were higher nest success rates near oil pads (although adjacent areas took the hit) and increased herbivore species richness at a restored site (Table 1.4).

Out of 2,291 red list species reported for Uganda, MFNP had 172 species, 46 of which are species of conservation concern (see Table 1.5 for common and species names). Only two of these species were evaluated in the papers I reviewed. African elephants were found to avoid seismic areas at all scales, while chimpanzees avoided seismic activities at small and intermediate scales. All other species in MFNP went un-evaluated among the papers in this review.

Table 1.5. The list of IUCN taxonomic ranks for species found inside Murchison Falls National Park, Uganda, in 2014 (Wildlife Conservation Society 2016).

	Mammals	Birds	Reptiles	Amphibians	Fish	Total
Threatened						46
Critically endangered	3	4	1	0	1	9
Endangered	2	6	0	0	4	12
Vulnerable	3	18	1	1	2	25
Other categories						126
Data deficient	5	3	7	4	0	19
Near threatened	3	6	5	1	0	15
Least concern	38	7	29	16	0	90
Not applicable	0	0	1	1	0	2

1.5 Discussion

Human priorities relating to energy and wildlife conservation have, and could, conflict when deciding whether to extract oil within wildlife protected areas. The stakes are high because of the enormous economic returns from oil contrast with threatened species of wildlife deemed vulnerable to the oil extraction process (Butt et al. 2013; Northrup & Wittemyer 2013). Take, for example, the proposed oil extraction in the Arctic National Wildlife Refuge (ANWR). In ANWR, oil extraction has been predicted to affect large mammals (Cameron et al. 1992; Pelley 2001). The Deepwater Horizon oil leak and the 1989 Exxon Valdez oil spill leaked millions of liters of oil that harmed wildlife and continues to affect human health (Gill et al. 2012; Drescher et al. 2014). Therefore, extracting oil in the vicinity of wildlife biodiverse regions presents a complex challenge of how to balance conservation and economic values.

Although there is spatial variation in oil reserves and wildlife biodiversity across the world, efforts to evaluate the consequences of oil extraction, particularly in peer-reviewed form, are limited. This was evident from the small number of papers returned from my review. Furthermore, when examining the case study in MFNP, just two species of conservation concern (elephants and chimpanzees) were subjects of two papers. I acknowledge that assessments may have been done prior to oil extraction for other species both in MFNP and elsewhere that remained unpublished or inaccessible to the public. I emphasize here the need for accessible peer-reviewed evidence to provide vital information on these ecological assessments to policymakers and the public. I believe that these results speak to the research-implementation gap that may be made wider due to the lack of peer-reviewed evidence (Arts et al. 2006; Gray et al. 2019). Nonetheless, the increase in the number of search results starting in 2001 indicates a growing academic interest on this issue.

I found that the onset of oil exploration and extraction led to an increase in the number of access roads to an area (Tables 1-3). In some cases, the roads protected wildlife when they enabled antipoaching work (Linke et al. 2005; Kolowski & Alonso 2012). Nonetheless, new roads were also found to foster widespread poaching in previously inaccessible areas (Kotze 2002). Similarly, access roads often went through villages which made it easier to move hunting tools and poached game in and among the local human communities (Suárez et al. 2013; Espinosa et al. 2014). These dynamics are likely to be influential in MFNP, which experiences some of the highest rates of wildlife poaching in the world (Mudumba et al. n.d.). The impacts of roads on the conservation of biodiversity is relevant more broadly also (Kleinschroth et al. 2017). The ways in which these poaching rates connect with the oil industry have yet to be mechanistically evaluated.

Oil extraction has the potential to initiate or worsen negative human-wildlife interactions such as human-elephant conflict (Munshi-South et al. 2008; Kolowski et al. 2010). African elephants are highly sensitive to ground tremors, sounds, and chemical signals (Munshi-South et al. 2008; Lindsey et al. 2018). When subjected to stress-inducing cues in the environment, elephants have been found to increase movement rates (Jachowski et al. 2013). This can lead them through community lands with potentially negative interactions with local people (O'Connell-Rodwell et al. 2006). Additionally, although African elephants are listed as *vulnerable* internationally and *critically endangered* in Uganda, their population in MFNP is expanding (Chase et al. 2016). The oil exploration phase inside MFNP changed the movement patterns of African elephants (Plumptre et al. 2014, 2015). Given this background, I recommend that MFNP quantifies and curbs the anticipated human-elephant conflict by minimizing other human disturbances (see Munshi-South et al. 2008; Kolowski et al. 2010).

Based on my findings, I propose recommendations to mitigate the impacts of oil extraction on wildlife. Maintaining a low density of roads and oil lines constructed away from key wildlife habitats is expected to reduce poaching and negative behavioral effects of human encroachment such as habituation and food conditioning. Increased law enforcement in the form of traffic control gates and ranger posts in areas accessible by new roads may have some deterrence for poaching and wildlife trafficking. Providing environmental education training to staff and communities in the vicinity of parks may help raise awareness of conservation issues created by oil extraction. In addition, developing options for alternative livelihoods in the local communities may mitigate the economic incentive for poaching and trafficking. I suggest key wildlife ecological features and offset sites be mapped and protected for key species as insurance against oil extraction. I strongly recommend surveying wildlife species and habitats in areas affected by oil extraction to enable reintroduction and restoration once extraction is complete to quantitatively assess effects of extraction. Policies inhibiting wildlife harassment and to regulate human-wildlife interactions are likely to reduce negative behaviors of wildlife that lead to increased mortality. An active program to reduce the risk of invasive species and contamination/pollution through policy, law enforcement, and civic awareness campaigns will promote awareness of the importance of habitat conservation in maintaining native fauna. To ensure conservation of wildlife populations, high disturbance activities should be conducted with minimal intensity, frequency, and outside key wildlife ecological cycles such as breeding, calving, and migration. It will be important to establish communication pathways and training for all stakeholders to detect and appropriately respond to mishaps related to oil extraction at various levels of engagement, while also creating specialized rapid-response, environmental protection teams. Finally, I suggest that peer reviewed, scientific studies should be conducted to understand the local ecosystem functioning and connectivity. The result of these studies will determine the potential triggers of synergistic effects and make recommendations.

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CHAPTER 2: ACCEPTABILITY OF WILDLIFE POACHING IS PREDICATED UPON SPECIFIC SOCIO-ECONOMIC CHARACTERISTICS

2.1 Abstract

Subsistence poaching threatens the persistence of wildlife populations worldwide as well as the well-being of people, who participate in poaching. Despite the gravity of this issue, little is known of the local acceptability of subsistence poaching, the tools regularly used in the poaching trade, or the wildlife species targeted by poachers. I conducted interviews of 691 households in 36 villages surrounding Murchison Falls National Park, Uganda to gain knowledge of drivers of poaching and demographic profiles of poachers. I assessed the acceptability of tools (e.g., nets, wire snares, spears, wheel traps, and guns) used to poach nine species of wildlife in the national park. I also assessed respondents' perceptions toward wildlife and park authorities as well as their experience with human-wildlife conflict. Conflict with wildlife was the most important factor determining attitudes towards poaching and the tools of the trade. Fewer than 20% of the respondents living within 5 km of the park boundary indicated they ever had been inside the park for any reason. My results affirm current belief that a primary determinant for poaching acceptability among people living alongside wildlife species is the limited flow of benefits for local communities from protected areas. My results improve the capacity of local wildlife managers to address poaching and emphasizes the importance of providing remedies compatible with local livelihoods and conditions to mitigate subsistence poaching.

2.2 Introduction

Poaching is the illegal killing or maiming of wildlife in violation of governing laws and policies (Muth and Bowe, 1998; Duffy et al., 2016). Though poaching often is conflated into one macro problem, there are at least two distinct types (Eliason, 1999). The first version of poaching involves the illegal taking of animals for various products sold into the black market (Eliason, 1999). For example, species of rhinoceros, in the family *Rhinocerotidae,* are hunted for their horn which is ground into a powder and distributed as an aphrodisiac, whereas elephant (family *Elephantidae*) ivory is sold predominantly for trinkets and sculptures (Douglas-Hamilton, 1987; Leader-Williams, 1993; Martin, 1994; Duffy and St John, 2013; Montesh, 2013). Although this type of poaching receives attention throughout the world, commercial poaching has a small user community when compared to subsistence poaching (Musgrave et al., 1993; Eliason, 1999; Robinson and Bennett, 2004; Duffy et al., 2014). Subsistence poaching involves localized noncommercial illegal take of wildlife typically for meat and cultural purposes to meet basic human needs (Hitchcock, 2000; Kahler and Gore, 2012; Lindsey et al., 2013). This form of poaching is widespread globally and increasing in frequency (Robinson and Bennett, 2002; Wilkie et al., 2005; Watson et al., 2013). Subsistence poaching occurs in every habitat around the world where people consider local wildlife species palatable (Tumusiime et al., 2010; Watson et al., 2013; Fischer et al., 2014). Whereas the main driver of commercial poaching is financial gain, subsistence poaching is predicated upon cultural norms and beliefs that condone poaching (Wake and Vredenburg, 2008; Rizzolo et al., 2017), vague national park boundaries or inadequate law enforcement (MacKenzie et al., 2012), poverty (Naughton-Treves, 2008; Kühl et al., 2009; Mancini et al., 2011; Duffy et al., 2016), poor relationships between local communities and wildlife managers, and human-wildlife conflict (Michalski et al., 2006; Burgoyne and Kelso, 2014; Radovani et al., 2014).

Traditional practices of subsistence poaching typically involve tools fashioned out of locally-available, non-synthetic materials such as wooden spears and snares made from tree bark

(Gray et al., 2018). Increased urbanization and expanding road networks however, make it possible for synthetic materials (such as wires from discarded radial car tires or motorcycle brake cables) to be re-purposed to trap wildlife (Becker et al., 2013; Watson et al., 2013). Snaring is perhaps the most common method used in subsistence poaching around the world for killing terrestrial vertebrates (Lewis and Phiri, 1998; Tumusiime et al., 2010; Watson et al., 2013). By varying the diameter of the noose and the height of the set, snares target species from small rodents to elephants (Tumusiime et al., 2010; Becker et al., 2013). In the savannah and woodland areas of Africa, the most common target however, is wildlife in the infra-order *Ungulata* (Martin et al., 2013; Gray et al., 2017). Given that snares are indiscriminate in what they catch, all comparably-sized wildlife species in a given habitats can be caught as bycatch (Becker et al., 2013). The impact of such inadvertent snaring on species of conservation concern, which typically occur in low densities, as such that it constitute subsistence poaching as a major conservation threat (Rochlitz, 2010).

The illegal nature of subsistence poaching undermines conservation efforts (Duffy and St John, 2013; Lindsey et al., 2013; Watson et al., 2013). For example, unsustainable wildlife harvest due to subsistence poaching can cause local extinction of species (Becker et al., 2013; Kimanzi et al., 2015). Subsistence poaching also exacerbates numerous conservation problems, including mammal population declines, receding wildlife habitats, and can make wildlife populations less resilient due to impacts of growing human populations and the effects of climate change (Wake and Vredenburg, 2008; Bellard et al., 2012; Fischer et al., 2014; Briggs, 2017).

Negative impacts created by subsistence poaching are not exclusive to wild animal populations. Local human communities tend to suffer as a result of subsistence poaching as well. Around the world, people caught in the act of subsistence poaching are subject to fines or jail time (Balakrishnan and Ndhlovu, 1992; Duffy, 1999; Forsyth and Forsyth, 2012). Consequences can be particularly steep in the Global South where poaching can lead to a life sentence or even the death penalty (Yi-Ming et al., 2000; Yiming et al., 2003; Mogomotsi and Madigele, 2017). Rates of subsistence poaching tend to be high in poverty-stricken communities that lack sufficient sources of protein (Lewis and Phiri, 1998; Wato et al., 2006; Tumusiime et al., 2010; MacKenzie et al., 2012). Each wire snare can only catch one animal and thus several trap lines are needed to increase odds of successful catch (Noss, 2010). Thus, subsistence poaching can be thought of as a high risk-low yield activity, which lends credence to the belief that subsistence poaching is practiced mostly by people with limited alternative livelihoods (Knapp et al., 2017). Given that subsistence poaching is spatially variable and widespread, it is often more difficult to mitigate than commercial poaching (Wato et al., 2006; Harrison et al., 2015). Additionally, unmitigated subsistence poaching can lead to commercialized poaching when more people are drawn into wildlife consumption leading to creation or expansion of game markets (Baldus, 2002; Lindsey et al., 2013; Harrison et al., 2015).

Though subsistence poaching occurs around the world, it is most intense in the Global South and particularly influential in East Africa (Lever, 1983; Steinhart, 1994; Skonhoft and Solstad, 1996; Baldus, 2002). Uganda is a country that experiences high rates of subsistence poaching regionally (Rwetsiba et al., 2014; Harrison et al., 2015; Moreto and Lemieux, 2015). Wildlife conservation depends heavily on local perceptions of wildlife and wildlife managers (Loker et al., 1998; Decker et al., 2012). Little is known, however, of how coupled human and natural systems function with respect to subsistence poaching (Hartter et al., 2016; Kukielka et al., 2016; MacKenzie A. et al., 2017; Salerno et al., 2017). Here I assessed the context and consequences of subsistence poaching in Uganda. My research objectives were to: i) define the social demographics of subsistence poachers, ii) determine the attitude of the local communities towards wildlife managers, iii) ascertain the acceptability of using common poaching tools to hunt or kill wildlife and level of conflict, and iv) determine the influence of socio-economic factors on poaching acceptability. Understanding the drivers and demographic profiles of communities that partake in subsistence poaching will help inform any strategies to develop alternative income generating economic activities (Zapata Rios, 2001; Engel et al., 2017). Thus, I discuss the implications of this research for improving the co-existence of humans and wildlife in the Global South.

2.3 Methods

2.3.1 Study area

Murchison Falls National Park (MFNP) in northwestern Uganda (02°15’N 31°48’E; Fig. 2.1) has experienced high rates of subsistence poaching in the form of wire snaring (Oneka, 1995). First established as a game reserve in 1926 and a national park in 1952, MFNP (3,893 km^2) is flanked to the east by Karuma Wildlife Reserve (820 km^2, gazetted in 1964) and to the south by Bugungu Wildlife Reserve (473 km, gazetted in 1964). Together, these protected areas comprise the broader Murchison Falls Conservation Area (5,308 km^2). Although the exact rates of poaching are difficult to establish, it is thought that subsistence poaching occurs here at the global peak and has led to the local extinction of white rhinoceros (*Ceratotherium simum*) and the decline of numerous species of wildlife in and around MFNP (Savidge, 1961; Kato and Okumu, 2008; Mudumba and Jingo, 2015).

Between 1987 and 2006, a war in the greater MFNP landscape restricted local people to camps (Harrison et al., 2015; Dowhaniuk et al., 2017). The absence of major human activities on habitat near the park boundary led to a dramatic increase in wildlife populations (Ruddy and

Vlassenroot, 1999; Kato and Okumu, 2008;Wanyama et al., 2014). The people returned to their villages on the periphery of MFNP upon the war's conclusion in 2006 (Arieff and Ploch, 2014; Dowhaniuk et al., 2017). Upon this return, many found a lack of opportunity for gainful employment and consequently, these districts are among the poorest in Uganda.

In contrast to the war period where human activity was limited in MFNP landscape, since 2007 areas within and surrounding MFNP have been developed for oil extraction, leading to rapid increase in human activity and infrastructure in close proximity to the park (Watkins, 2010; Uganda Wildlife Authority, 2014). The extractive oil industry, with accompanying workers, equipment, and roads has been found to be a gateway for increased subsistence poaching within protected areas (Muth and Bowe, 1998). The establishment of new roads, for instance, enables people to travel further and faster in exploration of new hunting areas (Tietje and Ruff, 1983; Suárez et al., 2009; Tigner et al., 2014).

There are 76 species of mammals that inhabit MFNP (Plumptre et al., 2007) including the largest remaining population of the endangered Rothschild's giraffe (*Giraffa camelopardalis rothschildi*; Brenneman et al., 2009; Wanyama et al., 2014; Muneza et al., 2016), elephants, large populations of many species of terrestrial ungulates, and several species of large carnivores. Abundance of large carnivores in MFNP plummeted between 1999 and 2009. For example estimates of the African lion (*Panthera leo*) population indicated a >40% decline over this period (Omoya et al., 2014). Murchison Falls National Park is representative of African wildlife parks for its location in the Albertine rift which has more than 40% of the protected areas in the region, and also for the sort of human-wildlife issues that one might encounter in other places in the region and beyond. Therefore, studying subsistence poaching in MFNP will provide information that could aid the formulation of solutions to manage or mitigate subsistence poaching wherever it occurs.

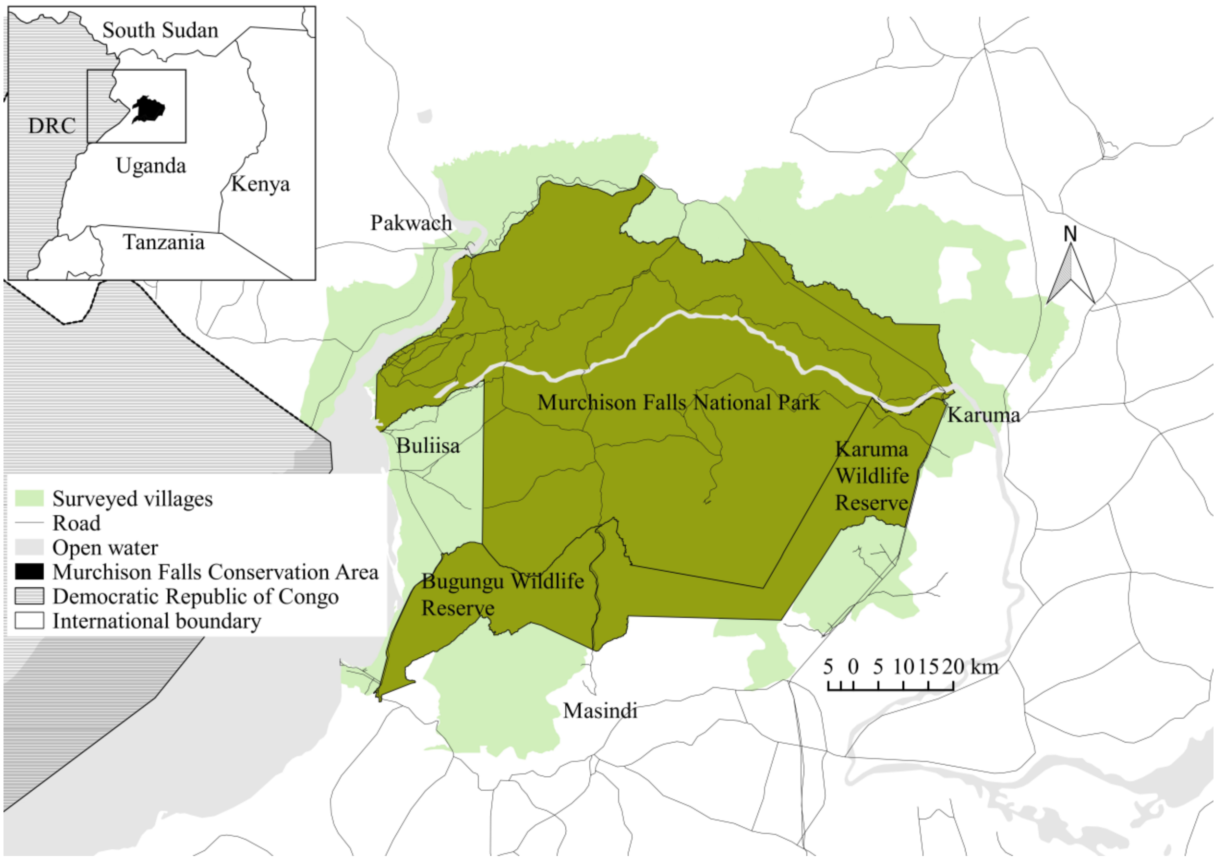

Figure 2.1. The study area for my research examining acceptability of subsistence poaching tools in Murchison Falls National Park, Uganda. The surrounding parishes in which this research was situated are also featured.

2.3.2 Data collection

I conducted semi-structured face-to-face interviews with residents of villages bordering MFNP between July and August 2017. I trained eight local residents fluent in all local languages (Swahili, Luganda, Acholi, Alur, Lugbara, Lugungu and Lunyoro) as research assistants, to administer these interviews. By conducting the interviews in the native language of each interviewee, I reduced potential bias in the selection of respondents, as well as in their responses due to differing educational level (Converse, 1976; Krosnick et al., 2001). Approvals for field use of the survey instrument was obtained from the Michigan State University Institutional Review Board (approval number x17-593e; see Figure 2.4). I also obtained clearance to conduct interviews from the local councils in the parishes (a territorial division composed of at least two villages) around MFNP. I piloted the survey on 30 households, prior to formal data collection, so as to improve the clarity of the questions. I excluded households that were part of the pilot from the main study. Interviews lasted on average 25 minutes.

In each parish, I restricted the interviews to those villages that bordered MFNP, Bugungu Wildlife Reserve, or Karuma Wildlife Reserve (Uganda Bureau of Statistics, 2012; Fig. 2.1). I randomly sampled households from a list of all village households generated by the local council leader. Once a household was selected, I randomly determined whether to interview the head-of-household or the spouse. Where there was no spouse, I interviewed the oldest household member. All participants were informed about the objectives of the study in advance, signed a consent form and were able to terminate the interview at any time. Such an informed and voluntary participation of interviewees, and the option to terminate the interview has been shown to improve the accuracy of responses (Ritchie et al., 2013).

The questionnaire had four sections including:

i) Wildlife-related activities and interactions. In this section I sought to identify the types of interactions that people had with wildlife in the area.

ii) Attitudes towards wildlife. In this section I asked questions that evaluated the respondent’s attitude towards wildlife.

iii) Wildlife interactions in the village. Here, I evaluated the types of interactions between people and wildlife at the village-level as well as questions regarding local people's attitudes specific to nine common species of wildlife around MFNP (Ayebare, 2011; Omoya et al., 2014; Wanyama et al., 2014). and

iv) Benefits and respondent demographics. In this section I assessed respondent demographic information and inquired as to potential benefits deriving from oil and oil infrastructure on the respondent's land.

2.3.3 Data analysis

Respondents were asked to classify their interactions with nine common species either as observed, seen tracks, threatened, crops / livestock destroyed, person injured / killed or other. I counted the number of responses for each species and also report number of responses for each kind of interaction. The 691 respondents each scoring in a nine by six grid provided 6,679 responses to this question.

To assess the acceptability of tools to poach wildlife, I scored the respondents' attitudes towards five instruments (nets, wire snares, spears, wheel traps, and guns). These are the five most commonly used tools to poach nine common wildlife species in MFNP. For each species and each poaching instrument, I scored answers of *Not acceptable* as a 0 and answers of *Somewhat acceptable*, *Acceptable*, and *Very acceptable* as a 1, 2, and 3, respectively. I excluded from analysis responses of *No opinion as* indicative of either lack of knowledge or lack of willingness to answer. I then calculated an acceptability to use poaching tool index for each respondent based upon these answers. This index ranged from 0 (all poaching instruments unacceptable for all species) to 135 (all poaching instruments very acceptable for all species). Hereafter I refer to this variable as "poaching acceptability".

I examined the distribution of poaching acceptability by inspecting the central tendency, dispersion, and form to guide secondary data analysis (Vaske et al., 2006). I analyzed poaching acceptability using a hurdle model, which is specifically designed to analyze count response data that are zero-inflated (Militino, 2010). Hurdle models consist of two sub-models. The first sub-model assumes data arise from a binomial distribution and estimates the probability of a given outcome occurring (i.e., a binary response). The second sub-model assumes data arise from a count distribution and evaluates the value of an outcome, given that it occurred (i.e., a count response; Militino, 2010). Here, the binomial sub-model assessed whether a respondent expressed beliefs that poaching was unacceptable (i.e., a value of zero) or at least partly acceptable (i.e., a poaching acceptability > zero). The count sub-model assessed the degree to which a respondent reported poaching as acceptable, given that poaching was at least partly acceptable. Due to the dispersion in my data, I used a negative binomial distribution for the count sub-model (Greene, 2008).

Socio-economic dynamics (Dickman, 2010; Rizzolo et al., 2017), the presence of extractive industries such as oil (Suárez et al., 2009), and the nature of human-wildlife interaction (Loker et al., 1998; Engel et al., 2017) influence the intensity and valence of attitudes towards wildlife. Therefore, I used the hurdle model to evaluate respondents' poaching acceptability as a function of nine explanatory variables that encompassed respondent's socio-economic status, demographics, benefits from the park and oil industry, and interactions with wildlife (Table 2.1). These variables were calculated from survey responses (see Appendix 2.1 for survey questions) and are described in detail in Table 2.1. Demographic and socio-economic variables included the duration the respondent lived in a village (Duration_Village), the annual household income (Income), and whether or not the household owned livestock

(Own_Livestock). Variables related to the oil industry included whether a household member was employed by the oil company (Employed_Oil) and whether oil infrastructure existed on a household's land (Oil_Land). Wildlife and park-related variables included the degree of conflict a household member had experienced with wildlife (Conflict_Wildlife), whether any household income comes from MFNP (Benefit_Park), and the respondent's attitude towards MFNP park authority (Attitude). Conflict with wildlife primarily referred to depredation of goats by large carnivores. Many of the goats were originally donated by the Uganda Wildlife Authority (UWA; the agency in charge of wildlife in the country) to local residents as an alternative source of protein to wild game (Mertzlufft, 2014). Others were raised by locals inspired by the experience of raising those first donated goats. Anecdotal reports indicated goats around MFNP were subject to depredation by large carnivores. Consequently, the provision of these goats actually exacerbated human-wildlife conflict.

All the above variables could influence overall acceptability of poaching (i.e., unacceptable or partly acceptable, a binomial response) and the degree to which poaching was acceptable (i.e., a count response, given a respondent was at least partly accepting of poaching). Therefore, I included all variables in both sub-models of the hurdle model. Prior to modeling, I checked for collinearity among explanatory variables using variance inflation factors, which were all well below threshold levels (i.e., < 2.0; Zuur et al., 2010). My interviews were spatially clustered around villages; I checked for spatial autocorrelation in model residuals using a spline correlogram (Rhodes et al., 2009). I interpreted model results using a cutoff of $P < 0.05$ for statistical significance. All analyses were conducted using the R environment (Version 3.4.1) in RStudio (RStudio Team 2015; R Core Team 2017) and the packages *car* (Fox and Weisberg, 2017), and *pscl* (Jackman et al., 2017).

2.4 Results

2.4.1 Demographic and socio-economic characteristics

I completed 691 interviews (42.7% female respondents) in 36 parishes (mean = 19.4 per parish, standard deviation [SD] = 9.2, range = 2 - 38). Respondents reported having lived in their village for an average of 25.1 years (SD = 16.5) and in their current residence for an average of 10.6 years (SD = 10.3; Table 2.1). Respondents lived with an average of 3.7 other members above the age of 18 in their household and 4.4 residents below 18 years of age (Table 2.1). Nearly half of the respondents (48.1%, *n* = 332) reported household income greater than 936,000 Ugandan shillings, with 35.3% reporting incomes 275,000 – 936,000 shillings, and 16.6% reporting incomes <270,000 shillings (Table 2.1; in 2017, 3800 shillings ≈ $1USD). Greater than half (74.0%, *n* = 471) of respondents indicated they owned livestock, 87.8% which were goats (*n* = 397 of all respondents who owned livestock; Table 2.1). A majority of respondents (71.3%, *n* = 478) maintained a peasant livelihood. The second-most common occupation reported was related to business (8.7%, *n* = 58). Few respondents (13.0%, *n* = 89) were formally employed by the oil industry and even fewer (5.8%, *n* = 40) reported having oil infrastructure positioned on household land (Table 2.1). Direct income from MFNP was received by 8.0% (*n* = 54; Table 2.1) of the respondents. A small proportion of respondents' household members (11.4%, *n* = 659) had visited MFNP either legally or illegally (Table 2.1). For those individuals who had been inside MFNP, park visits had occurred on average 37.1 months prior to the study (SD = 83.4, range: 1 - 480).

2.4.2 Park and wildlife related responses

Olive baboon (*Papio anubis*), African buffalo (*Syncerus caffer*), African elephant, and Ugandan kob (*Kobus kob thomasi*) were species most frequently reported observed by respondents from the point at which they moved into their village (Table 2.2). Slightly greater than 13% (*n* = 886) of interactions with wildlife were reported as threatening. Elephants were the most frequently reported threatening species (27.7%, *n* = 245) whereas waterbuck (*Kobus ellipsiprymnus*) were the least (1.5%, *n* = 13). Baboons and lions were the two species reported to most often injure or kill people. Livestock and crop destruction occurred 18.0% (*n* = 1200) of the time when wildlife moved onto community land. Baboons (29.1%, *n* = 349), elephants (22.5%, *n* = 270), and buffalo (19.0%, *n* = 227) were disproportionately mentioned as species involved in crop raiding (Fig. 2.2).

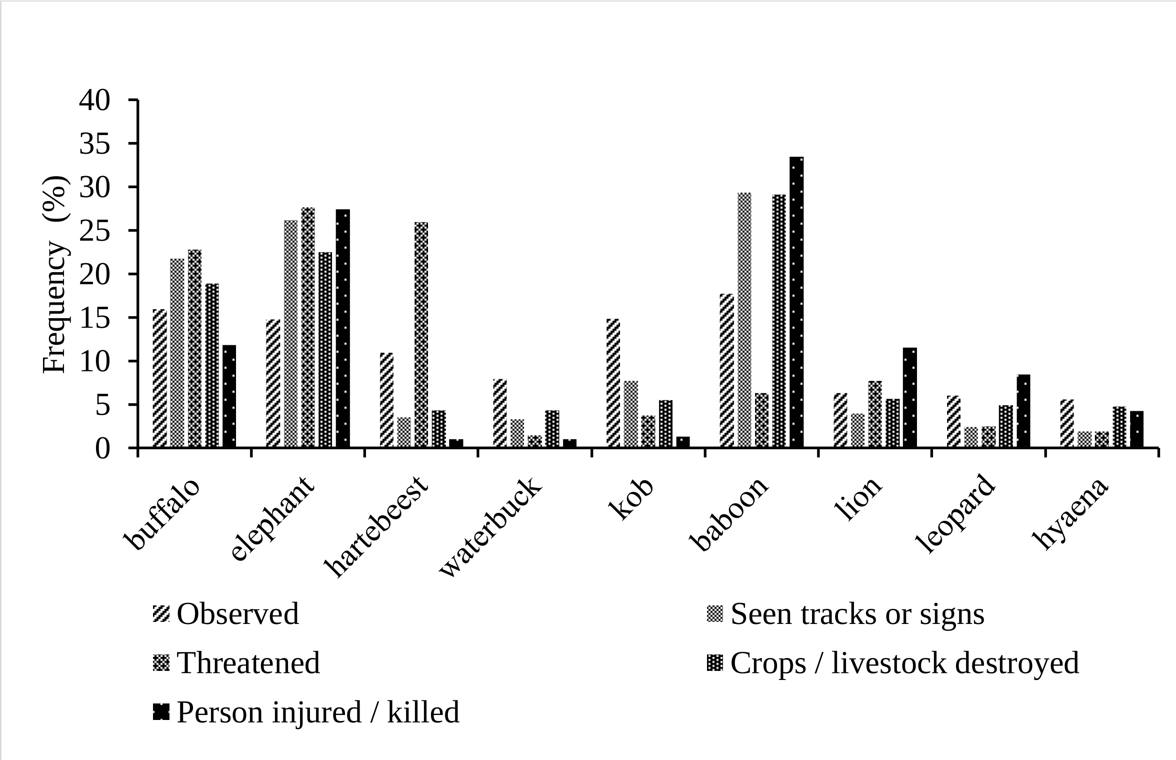

Figure 2.2 The nature of interactions that respondents had with nine common species of wildlife since they moved into their village adjacent to Murchison Falls National Park, Uganda. The height of the bar (Frequency) is the number of times each species was reported by respondents of the study.

2.4.3 Attitudes towards use of poaching tools

Of the 691 interviews, 42.0% (*n* = 290) included complete answers for the 15 survey questions that were used to model poaching acceptability. No spatial autocorrelation was evident in the model residuals (Figure 2.3), suggesting spatial dependence was adequately captured by the model's explanatory variables. The data were zero-inflated, with 86.2% (*n* = 250 of 290) of respondents indicating that all poaching instruments were unacceptable (i.e., a poaching acceptability of zero). The non-zero poaching acceptability data were widely dispersed (mean = 37.6, sd = 16.8, range 6-135). In the binomial sub-model, three variables had a statistically significant ($P < 0.05$) relationship with poaching acceptability (Table 2.3). The probability that a respondent condoned poaching was positively related to increased experience of wildlife conflict and duration of having lived at the village, whereas it was lower among respondents owning livestock (Table 2.3). In the count sub-model, two variables had a statistically significant association with poaching acceptability (Table 2.3). Poaching acceptability decreased as respondents' attitude toward MFNP became more positive and increased when a respondent owned livestock (Table 2.3).

2.5 Discussion

My results affirm that perceptions of human-wildlife conflict was the most statistically significant determinant of acceptability to poaching. I found that the majority (88.6%, $n = 659$) of the respondents had never visited nor received any direct income from the national park. More than half of respondents owned livestock, with goats being the predominant livestock type. Elephants were disproportionately reported by respondents to destroy crops, and injure or kill people, even though they accounted for just 28% ($n = 179$) of reported human-wildlife interaction. Survey respondents' poaching acceptability was higher when they had experienced a negative interaction with wildlife, owned livestock and had lived longer in the village. For those respondents who found poaching acceptable, the degree to which poaching was acceptable increased with negative interactions with wildlife and when they owned livestock but decreased when the respondents had a positive attitude towards national park management.

Conflict with wildlife increased acceptability of poaching around MFNP. In this way, my results are congruent with assessments of people who perceived wildlife as a threat to their wellbeing typically have negativistic attitudes towards wildlife (Treves and Naughton-Treves, 1999). I found that human-wildlife conflict around MFNP is largely provoked by elephants and baboons, and much less by predators. Baboons are considered to be vermin in Uganda and problem animals are regularly managed by a certified Vermin Control Officer (The Republic of Uganda, 1996). On the contrary, elephants are a protected species. Murchison Falls National Park is the only national park in Uganda, and one of the few across Africa, with increasing populations of elephants and ungulates following the dramatic, continent-wide large mammal declines in the 1970s (Craigie et al., 2010; Rwetsiba and Nuwamanya, 2010; Chase et al., 2016). Therefore, human-wildlife conflict involving elephants could increase if left unmitigated.

Positive relationships between local people and park managers is considered important for the co-existence of people and wildlife (Frank et al., 2015; Samia et al., 2015). I found that when the people living around MFNP found poaching acceptable, the magnitude of acceptability declined when they reported having a good relationship with the national park management. However, local people's attitudes toward national park managers had little impact on whether one found poaching acceptable or not. This could mean the measures of national park authorities to engage with local communities are biased towards a group that is already inclined to poach. Thus, managers should not exclusively focus on working with people popularly known as "reformed poachers" at the expense of interacting with other locals who could still be recruited into poaching (Kato and Okumu, 2008).

An emergent and additional source of direct potential benefit from the park involves the oil industry. Revenues from the extractive industry are capable of minimizing the local community's dependence on the park's natural resources occurred with palm oil in southeast Asia (Koh and Wilcove, 2007). I found no relationship between the benefits from the oil industry (presence of oil infrastructure on one's land and employment in oil industry) and poaching acceptability. This disparity could arise because the oil industry had offered few opportunities for the local populace given its infancy, and thus I could not detect its impacts in this study. I found few (13% of respondents) people were directly employed in the oil industry and even fewer (5.8%) leased land to oil companies to put infrastructure. The oil industry is a highly specialized industry with unskilled workers relegated to casual jobs (Figgis and Standen, 2005). Therefore, for citizens to benefit from proximity to industrial developments, they need to be trained in the basic requisite skills in the oil industry. At the time of my study, there was no evidence that proceeds from the oil industry were changing local people's attitudes wildlife.

Ownership of livestock is a major predictor of local people's attitude towards wildlife (Mir et al., 2015; Schieltz and Rubenstein, 2016). I found that goats were the most-commonly owned livestock type in my study. Contrary to other studies of conflict between livestock owners and wildlife, individuals who owned livestock had lower probability of accepting poaching than those who did not own livestock. My results add evidence that benefits perceived to result from wildlife influence attitudes towards wildlife (Browne-Nuñez, 2010; Nyhus, 2016). I also show that even modest benefits can be influential. I found less than ten percent of the households interviewed received direct benefits from the national park and I was able to detect the link between positive attitudes towards wildlife resulting from benefiting from the national park. The lack of direct benefits associated with living alongside wildlife has been previously thought to undermine willingness of people to tolerate wildlife (Karanth et al., 2013; Decker and Chase, 2016). For respondents who found poaching acceptable, even by a small margin, the level of poaching acceptability increased when they owned livestock. This negativity cannot be explained solely by loss of livestock to carnivores, as the depredation of goats around MFNP was estimated to be low, with less than ten cases had been confirmed by UWA in the period between 2009 - 2017 (Mudumba and Jingo, 2015). The more likely reason owning livestock made the degree of poaching acceptability higher is the perceived risk of potential losses, which is known to result in resentment for wildlife (Naughton-Treves and Treves, 2005; Nsonsi et al., 2018).

There is growing evidence that limiting the interaction of people and wildlife exacerbates human-wildlife conflict (Weladji and Tchamba, 2003; Woodroffe et al., 2005). I found that most people living in the neighborhood of MFNP had never been inside of the national park. Those respondents who had been inside the park had been there more than three years before my study, during the time of oil exploration inside the park when many casual laborers were hired for seasonal jobs (Mudumba and Jingo, 2015; Plumptre et al., 2015). Outreach to local communities can generate improved conservation practice (Steinmetz et al., 2014). Active participation of local people in conservation decision-making can foster positive attitudes for wildlife by the community (Kato and Okumu, 2008; Danielsen et al., 2009) and better working relationship with park management (Loker et al., 1998; Riley and Decker, 2000; Carter et al., 2014), but can result in improved livelihoods due to increased access to ecotourism opportunities in the area and thus reduced direct subsistence dependence on natural resources (Archabald and Naughton-treves, 2001; Romanach et al., 2007).

In conclusion, my study adds to the evidence that human-wildlife conflict is a key predictor of attitudes towards wildlife, yet perceived benefits from wildlife can improve positive attitudes towards wildlife. Effectiveness of wildlife conservation fundamentally is affected by perceived benefits and costs of living with wildlife by those people living most closely to the situation (Decker et al., 2012). The importance of providing remedies to human-wildlife conflict that are compatible with local livelihoods avoid worsening the problem. My results are representative of many situations elsewhere with similar conditions. For example, modifying the nature of interaction between humans and carnivore was found to be a good management strategy where humans lived in close proximity with predators in central India (Treves and Karanth, 2003). I recommend providing opportunities for positive reinforcement of communities living with wildlife as well as specific interventions compatible with the cultural heritage and livelihoods of local people. Additionally, engaging local people as early as possible, based on the fact that positive beliefs for wildlife are developed through time, should lead to greater tolerance of living with wildlife (Inskip et al., 2016). These types of measures will be necessary to conserve wildlife in perpetuity.

2.6 Acknowledgements

I am grateful to P. Luhonda and W. Tumusiime who participated in data collection for this study. H. Kasozi, E. Sande, and R. Kityo provided comments on an earlier draft of this manuscript. This study was supported by Wildlife Conservation Network [Pat J. Miller Fellowship], World Wide Fund for Nature [grant number SZ42], The Rufford Foundation [grant number 23564-1] and African Wildlife Foundation [grant number AWF-001 (Mudumba)]. RJM was supported by an NSF Graduate Research Fellowship.

APPENDIX

APPENDIX

Table 2.1. Names, descriptions, and value summaries of explanatory variables used in models predicting poaching acceptability in Murchison Falls National Park, Uganda. These data were collected via 691 face-to-face interviews with local people inhabiting villages adjacent to the park in July and August of 2017

Variable	Description	Value Type and Summary
Attitude	Respondent's attitude towards MFNP park authority including how they managed wildlife and responded to wildlife conflict	*Likert scale* (3) Strongly disagree (A): *N* = 284, 41.1% Agree (B) : *N* = 107, 15.5% Strongly agree (C): *N* = 288, 41.7%) No response (NR): *N* = 12, 1.7%
Duration_Village	Number of years respondent has lived in the current village	*Numerical* Mean = 25.1, SD = 16.1, Range = 1-86
Occupation	The income-generating activity that the respondent spent the most time on	*Categorical* Business: *N* = 60, 8.7% Fisherman: *N* = 50, 7.2% Pastoralist: *N* = 25, 3.6% Peasant: *N* = 493, 71.3% Other: *N* = 34, 4.9% NR (*N* = 29, 4.2%
Income	Annual household income	*Categorical* <270,000*: *N* = 109,15.8% 275,000-936,000: *N* = 236, 34.2% > 936,000: *N* = 314, 45.4% NR: *N* = 32, 4.6%
Own_Livestock	Whether a respondent's household owned livestock	*Binary* No: *N* = 229, 32.1% Yes: *N* = 449, 65.0% NR: *N* = 20, 2.9%
Benefit_Park	Whether any household income comes from MFNP	*Binary* No: *N* = 612, 88.6% Yes: *N* = 55, 8.0% NR: *N* = 24, 3.5%
Conflict_Wildlife	Whether a household member had been threatened, lost crops or livestock, or been injured or killed by wildlife	*Numerical* Mean = 4.0, SD = 3.7, Range = 0-27

Table 2.1 (cont'd)

Employed_Oil	Whether the household member was formally employed by the oil company	*Binary* No: *N* = 591, 85.5% Yes: *N* = 90, 13.0%, NR: *N* = 10, 1.4%
Oil_Land	Whether there was oil infrastructure on household-owned land	*Binary* No: *N* = 651, 94.2% Yes: *N* = 40, 5.8% NR: *N* = 0, 0%

*Income in Ugandan shillings (3800 shillings ≈ $1USD)

Table 2.2. The experiences that the respondents had with wildlife since they moved into their village. %spp is the ratio of experience such as observed the species over the total number of experiences for that species given by the respondent. %all spp is the ratio of the species experience over the total for that experience over all other species.

	Baboon		Buffalo		Elephant		Hartebeest	
	%spp	% all spp	%spp	% all spp	%spp	% all spp	%spp	% all spp
Observed	40.9	17.7	44.2	16.0	35.3	14.88	53.2	11.0
Seen tracks or signs	13.3	29.3	12.0	22.0	12.3	26.2	3.3	3.5
Threatened	4.0	6.3	17.3	23.0	18.1	27.7	34.5	26.0
Crops / livestock destroyed	24.9	29.1	19.4	19.9	19.9	22.5	7.8	4.3
Person injured / killed	17.0	33.4	7.2	11.8	14.4	27.4	1.1	1.0

	Hyaena		Kob		Leopard		Lion		Waterbuck
	%spp	% all spp	%spp	% all spp	%spp	% all spp	%spp	% all spp	%spp
Observed	60.5	5.5	75.1	14.8	43.3	6.0	45.5	6.3	73.2
Seen tracks or signs	4.1	1.9	7.7	7.7	3.4	2.4	5.6	3.9	6.0

Table 2.2 (cont'd)

Threatened	5.7	1.9	5.2	3.7	4.9	2.8	15.2	7. 7	3.7
Crops / livestock destroyed	19.3	4.8	10.3	5.5	13.2	4.9	15.8	5.7	14.8
Person injured / killed	10.4	4.2	1.4	1.3	13.4	8.4	18.3	11.5	2.0

Table 2.3 Model parameter estimates, standard errors, and statistical significance from a hurdle model predicting poaching acceptability. The model was fit to data from 290 surveys administered in Murchison Falls National Park, Uganda in July and August 2017. See Table A.1 for variable descriptions. P-values: *< 0.05 **< 0.01 ***< 0.001

	Binomial sub-model		**Count sub-model**	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**
Intercept	-3.12***	0.69	3.07***	0.39
Conflict_Wildlife	0.10*	0.04	0.04*	0.02
Duration_Village	0.03**	0.01	0.00	0.01
Annual_Income_M[A]	1.15	0.62	0.11	0.37
Annual_Income_H[A]	0.80	0.61	0.64	0.36
Benefit_Park[Y]	-0.90	0.84	-0.49	0.71
Attitude_Pos[B]	-0.98	0.62	-0.84*	0.35
Attitude_V_Pos[B]	-0.27	0.39	-0.80***	0.23
Visit_Park[Y]	0.93	0.59	0.24	0.44
Own_Livestock[Y]	-0.97*	0.39	0.45*	0.22
Oil_Land[Y]	0.54	0.65	-0.11	0.43
Employed_Oil[Y]	-0.80	0.63	0.16	0.52

[A]The reference category for Annual_Income was Low; thus, model parameters represent the effect of Medium and High income compared to Low income (Table A.1). [B]The reference category for Attitude_Park was Negative; thus, model parameters represent the effect of Positive and Very Positive compared to a Negative attitude (Table A.1). [Y]The reference category was No for all Yes/No variables, thus model parameters represent the effect of answering Yes compared to No

Figure 2.3. Spline correlogram showing spatial autocorrelation among model residuals as a function of distance in kilometers. My research examining acceptability of using poaching tools in Murchison Falls National Park, Uganda was clustered around villages and so I checked for spatial autocorrelation in model residuals. The 95% confidence envelope consistently overlaps zero, indicating a lack of spatial autocorrelation among model residuals.

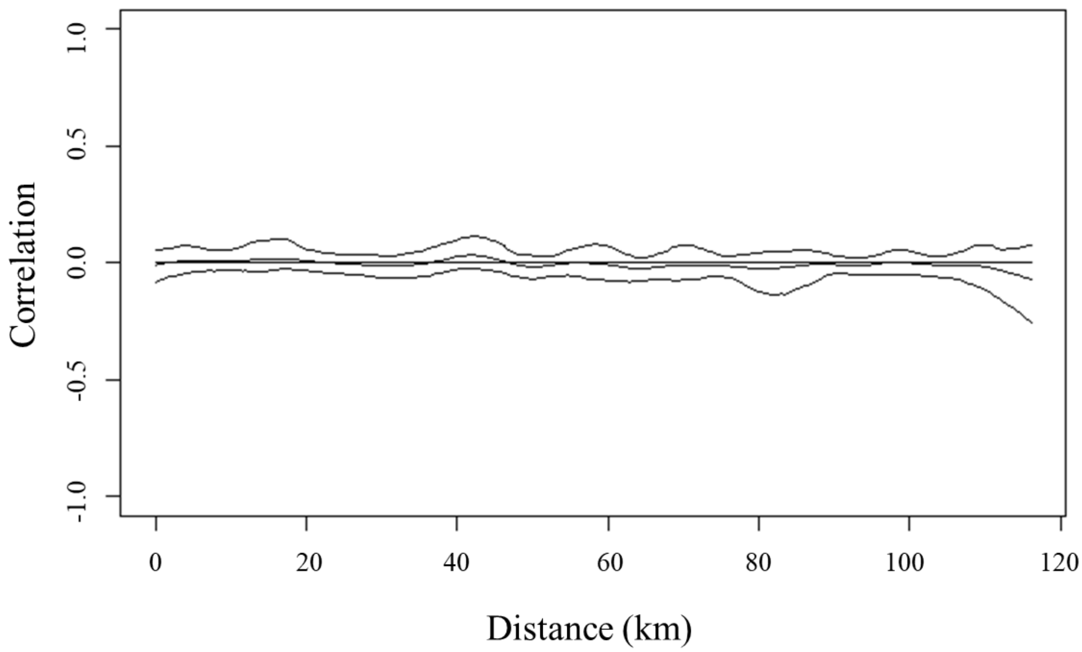

Figure 2.4. Questionnaire used to interview respondents during the research examining acceptability of using poaching tools in Murchison Falls National Park, Uganda.

MICHIGAN STATE UNIVERSITY

2017.

Sheet No. ....
GPS Position (UTM) E……………………….. N………………………
Interviewer……………………...........
Date (D/M/Y)…..…/………/……… Time (24Hr)………....
Figure 2.4. (cont'd)

Figure 2.4. (cont'd)

Village………….......................... Parish…………………………….……

WILDLIFE-RELATED ACTIVITIES AND INTERACTIONS IN YOUR VILLAGE

1. Please indicate which, if any, of the following types of interactions with wildlife you or a member of your household have experienced? *(Choose ALL that apply)*

		Yourself	Member of Household
a.	Observed wildlife in the wild	[ ]	[ ]
b.	Heard about other people being threatened or killed by wildlife	[ ]	[ ]
c.	Know a friend or neighbour threatened or killed by wildlife	[ ]	[ ]
d.	Hunted wildlife	[ ]	[ ]
e.	Heard of wildlife being killed by park management	[ ]	[ ]
f.	Heard about livestock threatened or killed by wildlife	[ ]	[ ]
g.	My livestock was threatened or killed by wildlife	[ ]	[ ]
h.	Have been personally threatened by wildlife	[ ]	[ ]

i. Other types of experiences: ....

2. Since you moved into the village, have you experienced any of the following?

Species	Observed	Seen tracks or signs	Threatened	Crops / livestock destroyed	Person injured / killed	Other
Kob						
Hartebeest						
Waterbuck						
Baboon						
Hyena						
Buffalo						
Leopard						
Lion						
Elephant						
All wildlife in general						

GENERAL ATTITUDES TOWARDS WILDLIFE INYOUR VILLAGE

Figure 2.4. (cont'd)

3. How has the population (numbers of animals) of the following wildlife species in your village changed during the past five years?*(Choose only ONE option for each species)*

Species	Decreased greatly	Decreased somewhat	Remained about the same	Increased somewhat	Increased greatly	Don't know
Buffalo						
Giraffe						
Kob						
Hyena						
Lion						
Elephant						
Leopard						
Hartebeest						
Waterbuck						
All wildlife in general						

4. What is your first reaction when the following wild animals' species attacks or threatens your livestock?

Species responsible	Nothing		Report to local leader		Report to park / police authorities		Mobilize locals to chase it away		Mobilize locals to kill animal	
	Threaten	*Attack*	*Threaten*	*Attack*	*Threaten*	*Attack*	*Threaten*	*Attack*	*Threaten*	***Attack***
Kob										
Hartebeest										
Waterbuck										
Giraffe										
Baboon										
Hyena										
Buffalo										
Leopard										
Lion										
Elephant										
All wildlife in general										

5. What is your first reaction when the following wild animals' attack or threaten people?

Figure 2.4. (cont'd)

Species responsible	Nothing		Report to local leader		Report to park / police authorities		Mobilize locals to chase it away		Mobilize locals to kill animal	
	Threaten	*Attack*	*Threaten*	*Attack*	*Threaten*	*Attack*	*Threaten*	*Attack*	*Threaten*	***Attack***
Kob										
Hartebeest										
Waterbuck										
Giraffe										
Baboon										
Hyena										
Buffalo										
Leopard										
Lion										
Elephant										
All wildlife in general										

6. There are epizootic diseases as a result of wildlife in my village that can be transmitted to human and livestock. *(Tick all that Apply except 5(a) and 5(f) that are stand-alone)*

5(a) [ ] No, I do not agree

5(b) [ ] I have heard about wildlife diseases in my village

5(c) [ ] I have lost livestock to wildlife diseases

5(d) [ ] People have fallen sick due to wildlife diseases in my village

5(e) [ ] People have been killed by wildlife diseases

5(f) [ ] No Opinion

RELATED INTERACTIONS IN YOUR VILLAGE

Reponses are coded as (-2) strongly disagree, (-1) disagree, (0) Neither Agree or Disagree, (+1) agree, and (+2) strongly agree for analysis.

7. Interactions between wildlife and people is something new and novel in my village?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

8. Member(s) of my household are at risk from wildlife in the villages that I live, work, or recreate?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

9. All the risks associated with living with wildlife are well understood by the wildlife managers and experts?

Figure 2.4. (cont'd)

Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

10. My community can live with crop or livestock damage associated with wildlife over time?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

11. My community can live with the risk of being threatened or injured associated with wildlife over time?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

12. My community can live with the risk to health or death associated with wildlife with over time?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

13. My community has got a good working relationship with the park authorities?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

14. The people who benefit from wildlife in the park are the same people who are exposed to the potential risks of living with wildlife?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

15. We would like to know whether you want the following wildlife populations in your village to increase, decrease or remain at its current level over the next five years. *(please choose ONLY ONE option for each species)*

Species	Decrease greatly	Decrease somewhat	Remain at its current level	Increase somewhat	Increase greatly	No Opinion
Kob						
Hartebeest						
Waterbuck						

Figure 2.4. (cont'd)

Giraffe						
Baboon						
Hyena						
Buffalo						
Leopard						
Lion						
Elephant						
All wildlife in general						

16. How important is it to you personally that the wildlife population trend match your response to the question 17 above?

16(a) [ ] Very Unimportant
16(b) [ ] Somewhat Unimportant
16(c) [ ] Neither Important nor Unimportant
16(d) [ ] Somewhat Important
16(e) [ ] Very Important

16(f) [ ] No Opinion

17. What tools/methods are used for hunting animals in the village? *Please tick all those that you know*

Species	Nets	Wire snare	Spear	Wheel traps	Guns	Other
Kob						
Hartebeest						
Waterbuck						
Baboon						
Hyena						
Buffalo						
Leopard						
Lion						
Elephant						
All wildlife in general						

18. What is your attitude towards the use of the following tools or methods for hunting the species below?
Fill up all gaps in this table. For each species and tool, answer can be: (NA) Not acceptable, (SA) Some-what acceptable, (NO) No opinion, (A) Acceptable, (VA) Very acceptable.

Figure 2.4. (cont'd)

Species	Nets	Wire snare	Spear	Wheel traps	Guns	Other
Kob						
Hartebeest						
Waterbuck						
Baboon						
Hyena						
Buffalo						
Leopard						
Lion						
Elephant						
All wildlife in general						

OIL EXTRACTION IN YOUR VILLAGE

19. Is there oil infrastructure on your land?
Yes [ ] No [ ]
20. How far is the nearest oil infrastructure from your house? …………………..metres
21. Are you/have you or any member of your household been employed by the oil companies?
Yes [ ] No [ ]
21(a). If Yes, what was the duration of the employment? ……………Months
21(b). What was the average monthly salary or wage? ……….........../=
22. What are the major concerns, if any, you have about oil exploration and extraction in your village?

…………………………………………………………………………………………………

22(a). How might the concerns above (Qn. 22) be addressed?

…………………………………………………………………………………………………

23. The oil exploration and extraction in my village will increase the frequency of human-wildlife interaction?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*
24. The effects of oil exploration and extraction in my village to wildlife largely have been positive?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

25. Oil exploration and extraction in my village has improved the human welfare of my village?
Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*
26.

Figure 2.4. (cont'd)

27. The oil exploration and extraction in my village will have a positive effect on the current human-wildlife interaction in the future?

Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

28. Overall, the long-term impacts of oil exploration and extraction to the human population in my village will be beneficial?

Strongly disagree *Neither Agree or Disagree* *Strongly agree*

-2 *1* *0* *+1* *+2*

DEMOGRAPHICS

29. Gender of respondent?
- ☐ Female
- ☐ Male
- ☐ No answer

30. In what year where you born? 19__ __

31. How many people currently live in your household?

Adults (Over18yrs) ____

Children (Under18yrs) ____

32. Do you currently own any livestock? Yes ( ) No ( )

31(a) if Yes, Predominant type ……………………………

33. Have you ever owned livestock in this village? Yes ( ) No ( )

34. Literacy: < P6 ☐ P7 – S4 ☐ Other …………………......................

35. How many years have you lived in this village? ....Years

36. How many years have you lived at current residence? ....Years

37. Occupation..................................

38. Have you or a member of your household ever been inside the national park?

No ( ) Yes ( )

40(a). How long ago? .... months

39. Do you own the land on which your house is built?

Yes ( ) 38 (a). What is the estimated value ……………… /=

Rent ( ) 38(b). What is the estimate annual rental fees ……………………. /=,

No ( ) 38(c). Neither of the options above

40. Do you use more land in addition to your own?

Yes ( ) No ( )

39(a). If YES, for what purpose? ……………………………….……….......

39(b). What is the estimated size? ……….. Acres

39(c). What is the estimated annual rental fees ……………………. /=

Figure 2.4. (cont'd)

41. What proportion of your house hold income is gotten directly or indirectly from the park?
a) None ( )

b) Little ( )

c) Half ( )

d) Most of it ( )

e) All of it ( )

42. How much non-monetary income does your house-hold?
Annual crop or fish / farm harvest (List):

Item	**Quantity**	**Estimated market price**

43. What is your approximate household annual income?

a) < 270,000/= ( ) **b)** 275,000/= to 936,000/= ( ) **c)** > 936,000/= ( )

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CHAPTER 3: PREY BIOMASS IS A POOR PREDICTOR OF AFRICAN LION POPULATION SIZE IN THE DYNAMIC 21ST CENTURY

3.1 Abstract

The majority of remaining African lion (*Panthera leo*) populations are distributed among comparatively small and isolated protected areas. The exact number of lions within these populations, however, is coarsely estimated with large confidence limits on the estimates. Beyond having accurate population estimates, knowing the number of lions that can be supported by such protected areas is critical for guiding lion population management to reduce population isolation and inbreeding depression. Preferred prey biomass is a key determinant of lion population size. Murchison Falls National Park (MFNP) is the largest protected area supporting lions in Uganda. Although lion surveys have been conducted in MFNP, there have been no attempts to determine the population size of lions that can be supported by prevailing prey biomass. Between June 2016 and August 2017, using vehicle-based surveys and photogrammetry techniques I obtained a total count of all lions > one-year-old in my study area in MFNP. Concurrently, I estimated common ungulate prey densities using transect surveys. I compared lion density estimates from an indirect (i.e. prey biomass regression model) and direct (i.e. total counts) method. The lion density estimates calculated from the prey biomass data was approximately four times higher than the total count. Considering that there has been no recent disease epidemic afflicting lions in MFNP and that populations of sympatric and competitive carnivores (i.e., hyaena *Crocuta crocuta* and leopard *Panthera pardus*) are comparatively low, incidental snaring by subsistence poachers remains the most likely factor restricting the park's lion population from reaching these potential population levels. While indirect methods, such as prey biomass, may overestimate potential lion populations, the inherent rarity of apex carnivores

means that any population decline must be urgently remedied in isolated populations before too much genetic diversity is lost. Methods that enable managers to monitor the impact of poaching pressure on large carnivores are critical tools for conservation management of this important ecological guild. My study adds credence to the hypothesis that estimating lion density from indirect methods such as prey biomass can result in overestimation of existent populations in the dynamic 21st century.

3.2 Introduction

The persistence of large carnivores in the dynamic 21st century is dependent upon developing an improved understanding of the factors that cause their populations to decline. Addressing the key threats faced by isolated carnivore populations is especially urgent, if apex carnivores are to persist in the long run. A key determinant of a healthy carnivore habitat is high prey abundance (Shackell, Frank, Fisher, Petrie, & Leggett, 2009; Lindsey et al., 2013; Simcharoen et al., 2014), as prey availability dictates to a large extent the number of carnivores that the area can support without undermining environmental integrity of the area (Orsdol, Hanby, & Bygott, 1985; Karanth, Nichols, Kumar, Link, & Hines, 2004; Hayward, O'Brien, & Kerley, 2007). Therefore, accurate monitoring of preferred prey biomass is important for assessing the conservation status of carnivores by comparing observed population trends against potential population that available prey can support (Sergio, Newton, & Marchesi, 2005; Hayward et al., 2007). Indeed, this has become accepted as the primary management tool in South Africa (Ferreira & Hofmeyr, 2014).

Where there are few natural prey available, carnivores may switch to hunting domesticated livestock (K. K. Karanth, Naughton-Treves, Defries, & Gopalaswamy, 2013; Michalski, Boulhosa, Faria, & Peres, 2006; Treves et al., 2004). This action can have negative impacts on large carnivore survival when affected livestock-owners retaliate in discriminant or indiscriminate ways (Bencin, Kioko, & Kiffner, 2016; Rosenblatt et al., 2014; Tufa, Girma, & Mengesha, 2018). Therefore, monitoring the population size of large carnivores that is supported by prevailing prey biomass can also help anticipate the urgency of human-carnivore conflict mitigation strategies (Riley et al., 2002).

There are less than 25,000 African lions (*Panthera leo*) left in the wild, with the majority found in East Africa (Riggio et al., 2013). The International Union for Conservation of Nature (IUCN) lists the species as vulnerable - Appendix II (Bauer, Nowell, Sillero-Zubiri, & Macdonald, 2018). A significant portion of the remaining lion populations are located in isolated protected areas with limited or no natural dispersal opportunities (Riggio et al., 2013). Small and fragmented habitats typically support a lower population size of lions because of low prey biomass relative to their size due to high edge effects exhibited as reduced suitable habitat for individual species (Woodroffe & Ginsberg, 2008). Which means that even in protected areas, because of source-sink dynamics, large carnivore populations are still jeopardized by human action. In such instances, the impact of prey biomass on carnivore populations is more magnified than relatively larger areas (Mills & Shenk, 1992; Hayward et al., 2007; Owen-Smith & Mills, 2008). This is partly due to the fact that small fragmented wildlife populations have equally lower numbers of natural prey, which makes them susceptible to local extinction especially in absence of human interventions (Lawton, 1994; Turner, 1996; Fahrig, 2001).

Murchison Falls National Park (MFNP) in northwestern Uganda provides the largest contiguous habitat for lions and other large mammals in the country. Consequently, the park supports large ungulate populations and contains one of the largest population of lions in Uganda (Rwetsiba & Nuwamanya, 2010; Omoya, Mudumba, Buckland, Mulondo, & Plumptre, 2014;

Mudumba & Jingo, 2015). However, there has been little research on lion population estimates in the park. Theory would suggest that large carnivore populations can be predicted as a function of vital rates and preferred prey abundance (Hayward et al., 2007). So, the test here is whether that is the case in a dynamic 21st century where environmental change and human action might decrease potential population size (Bouley, Poulos, Branco, & Carter, 2018; Cushman, Elliot, Macdonald, & Loveridge, 2016). While that is likely the case, the interest is to determine how much lower lion populations are in comparison to their prediction. Here, I predict the population size of lions that can be supported by prevailing prey biomass from an indirect (prey-biomass regression model) and compare this to total counts of known groups of lions in MFNP. My study provides baseline information on lions and their prey at a time when MFNP is threatened with oil mining on the north bank of the River Nile, inside the park. Understanding the number of lions that can be supported by the current prey populations is critical for the continued conservation of lions in Uganda and the broader region. My findings may be expanded to areas where prey-based estimates of top carnivores are used to estimate lion populations in Africa. A secondary benefit of the study is to inform the debate about lion conservation efforts amidst competing interests inside MFNP.

3.3 Methods

3.3.1 Study area

Murchison Falls National Park is subdivided into a north and south bank by the Victoria Nile river. I positioned the study area in the north bank where most of the lion population in MFNP occurs and is bordered to the north by community land and to the south and west by the Victoria Nile and Albertine Nile Rivers (Driciru, 2005; Omoya et al., 2014; Mudumba & Jingo, 2015). This is a 1,096 km^2 study area featuring grassland, bushland, and mixed woodland habitat types

(Fig 3.1). To the east of MFNP is Karuma Wildlife Reserve and to the south is Bugungu Wildlife Reserve. The national park and surrounding reserves are located within the greater Albertine rift which is the most biodiverse region in the world (Plumptre et al., 2007). Although physically possible, there is no evidence of lion or prey movement between the north and south bank of the River Nile and so it is likely MFNP supports at least two distinct and isolated lion populations (Mudumba & Jingo, 2015).

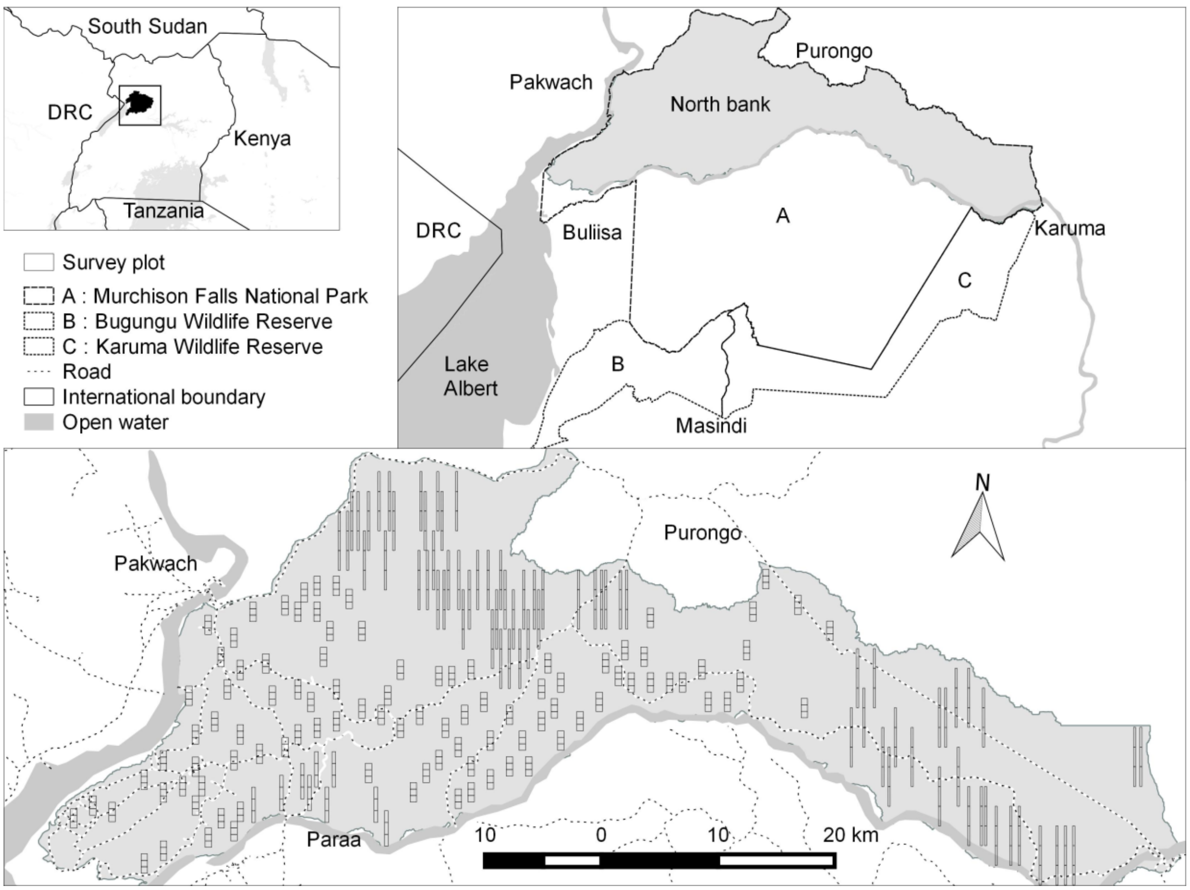

Figure 3.1. Map of the study area in the north bank of Murchison Falls National Park, Uganda where I assessed African lion (*Panthera leo*) population ecology. Survey plots are represented as rectangular boxes with the width determined by the mean maximum distance of sighted oribi (Ourebia ourebi) within each vegetation type (grassland, bushland, and woodland)

There is ongoing oil mining within MFNP's north bank sector, centered on the area with the highest lion density (Kityo, 2011; Uganda Wildlife Authority, 2014; Mudumba & Jingo, 2015). There are three main habitat types in MFNP. These include open grasslands (55.2%), bushland (40.0%), and woodland (4.8%). The MFNP has a rainy season from April to June and a dry season from December to February. Temperatures in the MFNP region can reach up to 40^{o}C and average 31^{o}C with annual rainfall between 1,000 and 1,250 mm. There is limited anthropogenic use permitted inside the wildlife reserves adjacent to MFNP, such as firewood and thatch collection, while no harvest is permitted inside the park (The Republic of Uganda, 1996). Furthermore, lion hunting is prohibited in MFNP. While a permit may technically be purchased to hunt a lion in the reserves or community land surrounding the national park, no such lion hunt has ever taken place.

Of the 76 mammal species occurring in MFNP, Cape buffalo (*Syncerus caffer caffer*), waterbuck (*Kobus ellipsiprymnus*), and Rothschild's giraffe (*Giraffa camelopardalis rothschildi*) are lion preferred prey (Hayward & Kerley, 2005). The accessible prey species include: Ugandan kob (*Kobus kob thomasi*), warthog (*Phacochoerus africanus*), Lelwel hartebeest (*Alcelaphus buselaphus lelwel*), oribi (*Ourebia ourebi*), and Bohor reedbuck (*Redunca redunca;* Mudumba & Jingo, 2015). This population of Rothschild's giraffe on the north bank is the largest of the endangered species in the world (Rwetsiba & Nuwamanya, 2010). Beyond lions, the carnivore community consists of an unknown number of leopards (*Panthera pardus*), a small population of spotted hyenas (*Crocuta crocuta*; last estimated in 2008 to be ~30), as well as meso-carnivores such as servals (*Leptailurus serval*), black-backed jackals (*Canis mesomelas*) and side-striped jackals (*Canis adustus*; Plumptre et al., 2007).

In 2010, the lion population in Uganda had declined by >40% in a period of 10 years and was fragmented in three populations of about 100 individuals each (Omoya et al., 2014). Murchison Falls National Park, the largest protected area in Uganda, had the largest lion population decline in this period, from >300 to <130 (Omoya et al., 2014). This troubling lion population trend is thought to have been driven by high levels of lion mortality due to subsistence poaching and primarily as by-catch in wire snares set to catch antelope (Mudumba, unpublished data). In addition to the importance for lions, the Uganda Wildlife Authority lists MFNP as an irreplaceable conservation area for the high number of locally and internationally threatened species (Wildlife Conservation Society, 2016; Plumptre et al., 2017).

3.3.2 Data collection

I conducted a total count of lions on the north bank of MFNP. The prides have been a subject of long-term studies and therefore I was able to count all individuals (Mudumba & Jingo, 2015). To do this, I identified individuals either directly from the whisker spot and other lion features or from photographs of the right side of their faces as per (*sensu* Bertram, 1975). I estimated lion prey densities using line transect sampling technique as per Buckland & Turnock (1992), and calculated the study area’s population size of lions that can be supported by prevailing prey abundance from biomass of preferred and accessible prey (Hayward et al., 2007). I then compared the lion estimates calculated from available prey biomass to the actual lion total count. My survey techniques have previously resulted in reliable estimates for large mammal including lions (Caro, 1999; Wilson & Delahay, 2001).

Prey abundance

To estimate lion prey abundance, I conducted vehicle-based surveys between June and August 2017. I developed a network of transects plotted randomly and positioned in a north-south direction in each vegetation type in the study area (Buckland & Turnock, 1992). Elevation change throughout the study area (mean 800 m) is moderate and so I was not concerned about positioning transects perpendicular to the contours. I conducted a pilot survey in each vegetation type to estimate survey effort required to give reliable abundance estimates for all key lion prey species (Marques et al., 2001; Thomas et al., 2010).

To account for the variation in detection, I tested the sighting distance in each vegetation type by estimating the mean of ten randomly distributed locations in each vegetation type. I navigated to each location with the aid of a hand-held GPS receiver and using a rangefinder measured the distance to the farthest away oribi. I used the oribi as my detection species for two reasons: 1) oribi were common and present at each of my randomly sampled locations of all habitat types, and 2) oribi is the smallest lion prey species I considered in my study and it occurs in MFNP mostly as solitary individuals or small herds , which permitted us to assume that the sighting distance of larger prey species would be at least as high as that for oribi (Mudumba & Jingo, 2015). I used the mean maximum distance of sighted oribis for each vegetation type as the radial viewshed for the transects in these habitats. This way, I had sufficient empirical knowledge to estimate the effective strip width for each vegetation type without having to use a detection function (Marshall, Lovett, & White, 2008).

I then developed a network of grid cells at a resolution calculated via this radial distance, given that I positioned observers on either side of the vehicle. Each observer was responsible for detecting and counting kob, oribi, buffalo, hartebeest, warthog, giraffe, waterbuck, bushbuck, and reedbuck looking out their side of the vehicle. For example, if the radial sighting distance was 100 m, then the resultant grid cell would be 200 m by 200 m.

I surveyed multiple grid cells along a transect with each grid cell being an individual part of the whole transect. I randomly selected the transect end from which to start the counts and then used a compass to determine the direction in which the observers drove. I drove as straight routes as practical along the predetermined transect line counting the individuals of each lion prey species detected within that grid cell. Each observer kept detailed notes on the counts of prey observed on their side of the vehicle. At the end of each grid cell survey, the observers compared counts and tallied the total count for the grid cell. I assumed that during the repeat counts of lion prey surveys along a given transect, the prey distribution was constant and not affected by my presence and that all individuals where counted just once during each survey effort.

Lion density

To determine the density of lions, I used the total count of all lions I encountered during a systematic search conducted over a one-year period between June 2016 and August 2017. To do so, I searched the north bank of MFNP looking for lions and their signs between 5 am and 7 pm. To extend my reach, I relied on environmental cues such as vulture parties, Uganda Wildlife Authority rangers who notified us whenever they found lions on the north bank and prey behavior such as alarm calls and forward vigilance (Creel, Schuette, & Christianson, 2014). When lions were found, individuals in the group had the right hand side of their face photographed and identified from whisker spot patterns and other body marks (Bertram, 1975). I grouped lions by age as inferred from known life history parameters (i.e., when my long term records identified date of birth) or from inspection of their body condition (Bertram, 1975), body size (Smuts, Robinson, & Whyte, 1980) and nose color (Whitman, Starfield, Quadling, & Packer, 2007). I compiled a cumulative list of known lions (Appendix Fig 3.2). I continued with the search until no more new lions were added to the list. To measure my effort during the lion survey, I recorded the GPS track log of every field day spent looking for lions.

Concurrently, I opportunistically recorded locations of all carcasses I found either near lions or could identify to have been killed by lions with the lion survey. For every carcass I found, I recorded the species, estimated age of the carcasses, and sex of species killed. Every carcass was recorded once and ignored on subsequent trips.

3.3.3 Data analysis

Estimating prey abundance

To estimate lion prey biomass in my study area, I first calculated the mean number of individuals recorded for each species per transect visit. Then, I summed the average transect count for each species to obtain an overall estimate of the number of animals in my surveyed area and extrapolated my finding for the entire north bank sector of MFNP. I calculated the vegetation type density estimates by extrapolating from the density of the surveyed area. Therefore, the density of each species for the north bank was given as the sum of that species' counts for the north bank divided by the area of north bank.

I calculated the available lion prey biomass by multiplying the weight of each species (¾ female body weight; see Schaller 1972) by the total population of the species in the study area. Following Hayward et al (2007) and Clements et al (2014), I calculated three different available lion prey biomasses indices: a) of the lion's preferred prey, b) of prey within preferred weight range and c) of accessible prey, i.e. other prey species determined from lion kill sites.

Calculating lion density

Lion density was calculated based on the direct count of lions > one-year-old in August 2018. I plotted the cumulative count of lions on the north bank against the survey effort (km) and assumed the horizontal asymptote marked the total number of individuals on the north bank (as per Caughley, 1977). To get an indirect estimate of lion density on the north bank of MFNP, I used regression equations of the relationship between prey biomass and lion density for: preferred prey given as lion density = -2.158 + 0.377 [log preferred prey] and preferred prey weight given as lion density = -1.363 + 0.152 [log preferred prey weight range] (Hayward et al., 2007). Additionally, using the same equation but limited to count data of only prey species whose carcasses had been observed at lion kill sites, I calculated biomass of preferred prey and preferred prey weight range which I then used to estimate the lion density. I used paired t-test to test for significant difference among the lion density estimates of the three different methods.

3.4 Results

I surveyed 120 transects (40 per vegetation type - bushland, woodland and grassland) covering 3.5% of the total area of the north bank of MFNP. I repeated surveys on average 2.7 times (Range = 1 to 5) per transect. The most abundant species in the surveyed area was the Ugandan kob with a density of 245.9 km^{-2} (Table 3.1). Because of the low encounter rates during the survey, I could not get a reliable biomass density estimate for bushbucks and reedbucks.

Table 3.1. The abundance and density of the preferred and accessible prey species on the north bank of Murchison Falls National Park, Uganda. Acronyms used in this table include NB = North bank; SA = Surveyed area; SE = standard error. The * identifies species for which the estimates are not considered reliable given very low detections.

Common name	Abundance NB	Abundance SA (±SE)	Grassland (±SE)	Bushland (±SE)	Woodland (±SE)	Density SA (km^{-2})
Kob	94,890	9,426 (±17)	7,524 (±40)	3 (±0)	1,899 (±6)	245.9
Oribi	13,665	1,357 (±2)	1,172 (±3)	149 (±4)	36 (±0)	35.4
Buffalo	12,013	1,193 (±2)	923 (±4)	108 (±6)	162 (±1)	31.1
Hartebeest	12,067	1,199 (±1)	794 (±2)	326 (±6)	79 (±1)	31.3
Warthog	7,766	3,749 (±1)	591 (±2)	105 (±2)	76 (±0)	97.8
Giraffe	3,652	363 (±1)	203 (±1)	20 (±1)	140 (±1)	9.5
Waterbuck	3,312	329 (±1)	159 (±1)	129 (±4)	42 (±0)	8.6
Bushbuck*	128	13 (±0)	11 (±0)	2 (±0)	0 (±0)	0.3
Reedbuck*	147	15 (±0)	13 (±0)	2 (±0)	0 (±0)	0.4

Buffalo and giraffe were the only species inside MFNP that meet Hayward and Kerley, 2005 definition of lion preferred prey and together had a combined biomass density of 6,568 kg km^{-2}. Most (86%; 4,735 kg km^{-2}) of this biomass consisted of preferred prey-buffalo. Buffalo, giraffe, and waterbuck were the species on the north bank of MFNP that had a weight within the lion preferred prey weight range, and these had a combined biomass density of 7,135 kg km^2. I detected 179 lion-killed carcasses of kob, oribi, buffalo, hartebeest, warthog, waterbuck, bushbuck, and reedbuck. However, my detections of bushbuck and reedbuck were too few to estimate their abundance. Therefore, I calculated the biomass from prey counts of six prey species. The estimated biomass density from count data of just these species was 10,844 kg / km^{-2}.

During the lion survey, I covered more than 7,500 km on the north bank and recorded 116 unique lions > one–year-old (0.02 lion km^{-1}; Fig. 3.2). Applying the Hayward et al (2007) equations on all the available biomass of species within the preferred prey weight of lions, the lion population on MFNP's north bank was estimated at 709 individuals (>1-year-old) – a density of 0.65 lions km^{-2} (Table 3.2). The estimate decreases to 652 if only the biomass of preferred prey is used instead and increases to 1,199 lions if I use the biomass of all species of which carcasses were observed at lion kill sites in MFNP. Since no carcasses of giraffes were observed at the kill sites, I reran the same equations but excluded the giraffe biomass, leading to a potential population estimate of 182 lions from either technique (a reduction of 25.7% and 27.9% respectively; Table 3.2). I compared whether the difference of preferred prey/preferred prey weight changed with and without giraffes. Excluding giraffe from prey species used to calculate prey biomass estimate did not significantly alter the lion density estimate either from preferred prey or preferred prey weight range (t-value = 0.37, p = 0.36).

Table 3.2. Estimates of African lion (Panthera leo) density in the study area in the north bank of Murchison Falls National Park (MFNP), Uganda. I calculated the abundance and density of lions on the north bank of MFNP via three models: 1) preferred prey (species included; buffalo, giraffe) from techniques adapted from Hayward (2007), 2) preferred prey weight range (species included; buffalo, giraffe and waterbuck), and 3) kill site data (species included; kob, oribi, buffalo, hartebeest, warthog, and waterbuck). The total counts represent cumulative counts of all lions > one-year-old detected between June 2016 and August 2017. The lower and upper confidence intervals of each estimate are featured in the parentheses.

	Preferred prey		Preferred prey weight range	
	Abundance	Density / km^2	Abundance	Density
Hayward (2007)	652 (650-654)	0.595 (0.594-0.596)	709 (707-710)	0.647 (0.645-0.648
With no Giraffe	470 (470-471)	0.428 (0.428-0.429)	527 (526-528)	0.481 (0.480-0.482)
Prey carcasses	1,199 (1,198-1,199)	1.094 (1.093-1.094)		
Total counts	116	0.11		

3.5 Discussion

For MFNP, this is the first comparison of the indirect/direct estimates and hence a comparison of actual population and potential population of lions based on prey biomass. The lion density of the north bank of MFNP from the total count was lower than what was predicted from indirect methods, but is in line with the population records of 2010 and 2015 (Omoya et al., 2014; Mudumba & Jingo, 2015). My study has found a remarkable difference between observed and potential lion population in my study area across all prey biomass availability models considered. Even the most conservative biomass availability model suggests that the north bank of MFNP could support four times the current population of lions. Thus, prevailing prey biomass does not seem to be the limiting factor explaining the flat population growth of lions in the area for the past 20 years.

Lion population growth can be limited by competition from hyaenas and leopards (Hayward & Kerley, 2008). The population of hyaenas in MFNP exists at comparatively low levels with only about 40 animals estimated in 2010 across the entire park (Omoya et al., 2014). During the study, I observed two incidents of lions killing hyaenas. The first involved a hyaena cub at a den and the other an adult male hyaena killed at a carcass site. This suggests that lions may be competitively excluding hyaenas in MFNP, rather than the other way around. I do not have information on leopard numbers in the park, but they are estimated to be low (Wildlife Conservation Society, 2016). Furthermore, although lions in MFNP do suffer from disease, including canine distemper, examination of a small sample of 14 lions in 2005 concluded that disease had only minor impairment on individuals with no population level effects (Driciru, 2005). The only known lion population in Uganda to suffer significant population decline due to disease is at the Kidepo Valley National Park where lions are reported to have TB like symptoms (S. Ludwig, pers. communication). A recent survey found MFNP to be a hotspot for giraffe skin disease (Muneza et al., 2016). However, there has been no evidence suggesting that this disease can be transmitted to large carnivores nor is it clear whether the disease is lethal. Moreover, neither this nor previous studies or ranger reports have reported MFNP lions preying on giraffes

(Driciru, 2005; Mudumba & Jingo, 2015). Given the above, giraffe skin disease is not a likely factor limiting the population of lions in MFNP.

My estimate of the density of Ugandan kob on the north bank of MFNP is one of the highest in the world. Although kob are not among lion preferred prey or preferred prey weight range species (Hayward & Kerley, 2005), lions routinely prey on kob in MFNP but not in proportion to their availability (Mudumba & Jingo, 2015). To a large extent, it is this Ugandan kob biomass present – but not fully utilized by lions –that accounts for the significantly higher lion population (1,199) estimate based on the biomass of all species whose carcasses were observed at lion kill sites. I warn that the use of all species identified as lion prey from carcasses is likely to overestimate lion densities in similar studies, compared to estimates based on preferred species or preferred range weight species. However, diets of large carnivores including lions have been observed to change as large prey are selectively removed from prey populations (Bouley et al., 2018; Creel et al., 2018). Uganda, as a satellite – rather than stronghold – population might provide a good example of this premise. In this regard, Uganda kob could be a significant lion prey species determining the population of lions in MFNP.

The key anthropogenic pressures on the lions of MFNP include oil mining inside the national park and subsistence poaching primarily in the form of wire snaring (Mudumba & Jingo, 2015). A recent study examining the impact of subsistence poaching on MFNP's wildlife showed that wire snares are the leading cause of lion mortality inside the park, with about 40% of adult lions displaying snare injuries (Mudumba, unpublished data). Kiffner et al. (2009) suggested that where there is anthropogenic killing of lions – especially inside national parks, prey-biomass regression models over-estimate lion densities. I suggest that wire snaring is the primary cause of the observed difference between actual and potential lion population size in the MFNP.

I am confident in my findings because; (a) my survey techniques have previously resulted in reliable estimates for large mammal including lions (Caro, 1999; Wilson & Delahay, 2001), (b) I surveyed only during daylight under good visibility aided by the fact that most of the north bank was burnt, and (c) my study area meets the assumption of a closed habitat/lion population. For instance, the north bank has got very hard ecological boundaries that include a fast-flowing river to the south and to the west as well as community settlements close to the northern border. There was no evidence that lions disperse and survive outside of MFNP. In August 2016, one adult male was reported on community land to the north east of the north bank and was subsequently immobilized by a Uganda Wildlife Authority veterinarian and released back in the park.

My overall conclusion is that the lion density on the MFNP's north bank is likely below what the prey biomass could support. Given that the north bank has historically had most of MFNP lions, the lion population of MFNP could be below what the prey biomass could support. This low number of lions given the existent prey population is likely due to undocumented subsistence poaching. The prey biomass inside MFNP has been increasing making MFNP potentially the largest lion habitat in Uganda if subsistence poaching is controlled. However, I would like to acknowledge that only an exhaustive study of key threats to lion survival inside MFNP could authoritatively determine the most prominent external factors affecting lion population trends in the area. Specifically, there is need to expand the lion prey and lion survey to the south bank of MFNP and include an assessment of impacts of anthropogenic disturbances that include subsistence poaching and oil mining on lion survival (Green, Johnson-Ulrich, Couraud, & Holekamp, 2018). My study also adds credence to the hypothesis that estimating lion density from indirect methods such as prey biomass can result into overestimation of existent populations (Kiffner et al., 2009). I highlight the value of prey biomass regression models as a tool for determining the population size of lions that can be supported by prevailing prey biomass. While estimating lion density from indirect methods, such as prey biomass, may overestimate the potential population size, the inherent rarity of apex carnivores means any reduction in potential population size must be remedied urgently in isolated populations before too much genetic diversity is lost. Methods to identify unseen poaching pressure (i.e., when populations are existing below those that can be supported by prevailing prey biomass) are critical tools for conservation management of large carnivores.

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APPENDIX

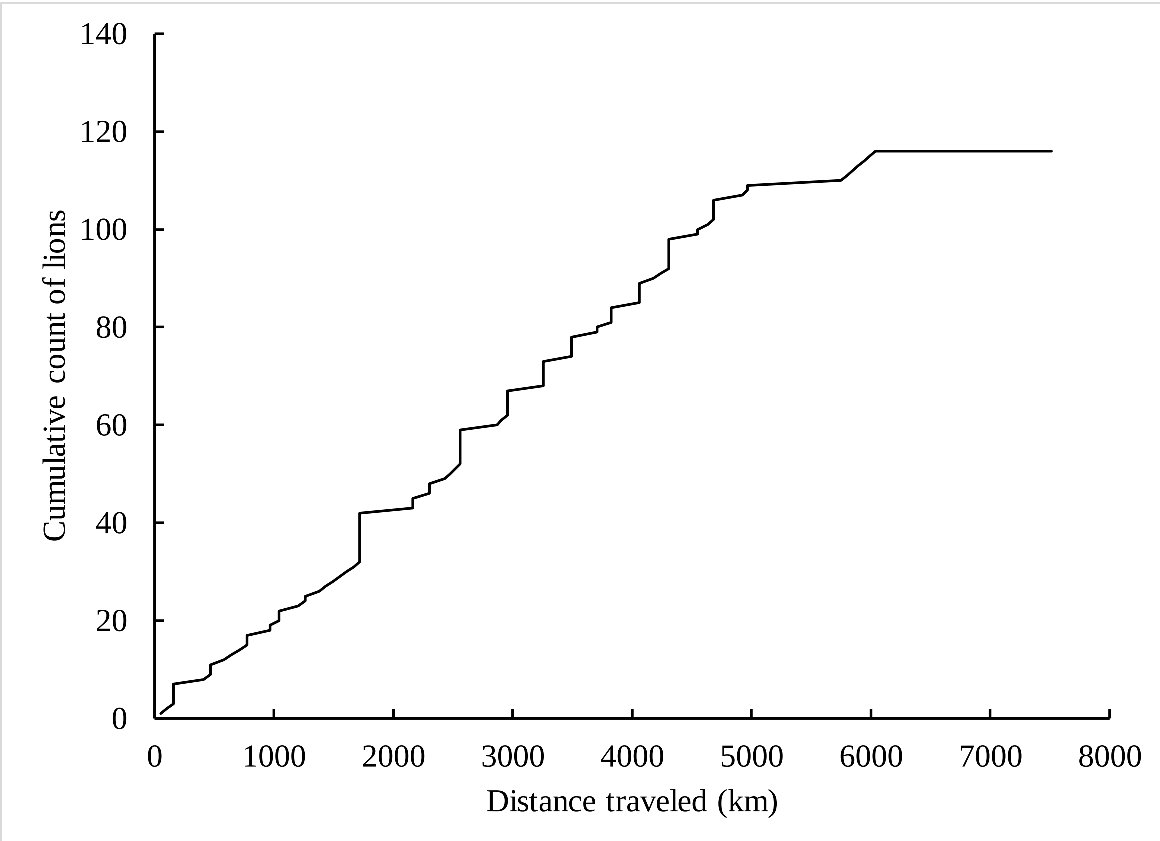

Figure 3.2. Cumulative count curve of lion encounters on the north bank of Murchison Falls National Park, Uganda. I conducted total count surveys of lions between June 2016 and August 2017 in which 116 lions > one-year-old were recorded

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CHAPTER 4: THE LANDSCAPE CONFIGURATION AND LETHALITY OF SNARE POACHING

4.1 Abstract

Poaching of wildlife presents one of the biggest conservation challenges in the 21st century. The most common form of poaching is subsistence-based where snaring is one of the primary means of capturing target animals. To prioritize interventions intending to reduce snaring, information on the density, configuration, and lethality of poacher-set snares is needed. Here I describe an approach for quantifying the configuration and lethality of snares. I positioned my study in Murchison Falls National Park, Uganda, which experiences some of the highest rates of snaring globally. I conducted wire snare transect surveys to predict the density, distribution, and lethality of snares as a function of environmental and anthropogenic parameters using logistic regression models. All of the snares that I recovered were made of wire with the majority (81.0%, $n = 546$ of 674) deriving from vehicle tire wire. The density of snares ranged from 0.08 to 4.58 snares /km^2, the highest known density in sub-Saharan Africa. I also found various snare characteristics (snare thickness, noose width, vertical drop, wire circumference, grass height, and anchor tree diameter at breast height) that significantly predicted lethality. Access to disused vehicle tires which provide material for wire snares need to be regulated in ways which provide alternative livelihood to poachers. My method illustrates the opportunity to standardize temporal and spatial measurements of snare density and configuration as a first step to refine mitigation techniques and thereby stop illegal wildlife poaching.

4.2 Introduction

Illegal subsistence hunting, commonly referred to as poaching, is a large contributor to the global decline of wildlife populations (Fitzgibbon, Mogaka, & Fanshawe, 1995; Lindsey et al., 2013; Rentsch & Damon, 2013). Overharvest of large herbivores, which are among the primary targets of poachers, is the leading cause of their population declines globally (Milner-Gulland & Bennett, 2003; van Velden, Wilson, & Biggs, 2018; Ripple et al., 2019). Over the next decade, dependence on wildlife is projected to positively correlate with increasing human populations (Jones et al., 2018). Inadequate law enforcement and policies, disenfranchisement, and local culture have rendered many regions of Global South unable to effectively control poaching (Pratt et al., 2004; Duffy et al., 2016; Knapp et al., 2017).

There are three distinct types of poaching including trophy poaching, trafficking poaching, and subsistence poaching (Montgomery in review). While the perpetrators of trophy and trafficking poaching are motivated by financial gains, subsistence poaching is predicated by individuals with important livelihood needs (Musgrave, Parker, & Wolok, 1993; Eliason, 1999; Milner-Gulland, 2018; Ripple et al., 2019). Additionally, trophy and trafficking poaching are very structured activities that require significant investments (e.g., expensive tools and knowledge of markets and middlemen) that are beyond the reach of most local people (Hariohay, Ranke, Fyumagwa, Kideghesho, & Røskaft, 2019). In contrast, subsistence poaching is carried out using locally-available materials such as spears, spiked wheel-trap, and pitfall traps. However, the tool most commonly used to poach wildlife in the Global South is the snare (Lewis & Phiri, 1998; Noss, 2008; Gray et al., 2018).

Snares can be made from sisal ropes, nylon, or wire (Becker et al., 2013; Critchlow et al., 2015; Moreto & Lemieux, 2015; Knapp et al., 2017). Though typically set to catch herbivores such as species from the infra-order Ungulata, snares are indiscriminate and other species (including large carnivores) can be trapped and maimed or killed (Noss, 2008; Tumusiime, Eilu, Tweheyo, & Babweteera, 2010; Becker et al., 2013). Studies have shown that snares disproportionally affect populations of large carnivores compared to ungulates (Fitzgibbon et al., 1995; Becker et al., 2013). With respect to large carnivores, poaching exerts both direct and indirect effects. Directly, large carnivores can be killed as either the intended or unintended targets of poachers (Becker et al., 2013; Bouley, Poulos, Branco, & Carter, 2018; Courchamp et al., 2018). Indirectly, the unsustainable harvest of large herbivores, which are often the primary targets of poachers, can affect large carnivores via prey depletion (Wolf & Ripple, 2016). The combination of the direct and indirect effects of subsistence poaching have follow-along impacts with implications for human-carnivore co-existence and ecosystem function (Ripple et al., 2014; Wolf & Ripple, 2016; Soofi et al., 2019). Subsequent dynamics can exert negative consequences on local human communities (Gandiwa, Heitkönig, Lokhorst, Prins, & Leeuwis, 2013).

The spatial distribution of snares is difficult to quantify given that; *i*) poaching is an illegal activity and *ii*) snares are typically distributed over large areas. Consequently, interview responses from poachers are often fraught with misleading information resulting from the fear of prosecution (Knapp et al., 2017). Additionally, detecting snares via anti-poaching patrols can be challenging given variable levels of investment and support necessary for local management authorities to conduct the work (Watson, Becker, McRobb, & Kanyembo, 2013). Furthermore, wildlife snaring is difficult to prosecute given that when an animal gets caught in the snare, the poacher is typically not present, problematizing efforts to associate the illegal act with the perpetrator (Moreto & Lemieux, 2015). Concurrently, wildlife snaring has not yet been widely studied and so the ways in which individuals might intervene to develop sustainable solutions are presently unclear.

In Uganda, snaring is the most common form of subsistence poaching (Critchlow et al., 2015; Harrison et al., 2015; Moreto & Lemieux, 2015). Snaring of wildlife is widespread in the country's protected areas and is reported to occur at a global peak (Critchlow et al., 2015; Tumusiime et al., 2010). From anecdotal reports and the number of snares recovered per year, wildlife snare poaching is particularly high in Murchison Falls National Park (MFNP) which is Uganda's largest savanna park (Critchlow et al., 2015; Mudumba & Jingo, 2015). Previous attempts to quantify wildlife snares inside MFNP have relied exclusively on ranger patrol data (Plumptre, 2019). Unfortunately, ranger patrols are unreliable for predicting the distribution of snares but also comparing estimates across time and space because the data are often spatially and temporally biased (Becker et al., 2013).

Here I describe an approach for estimating both the distribution of snares and their lethality on sympatric guilds of large carnivores and ungulates. I describe the configuration, calculate the detection probability, and estimate the density of snares inside MFNP. Additionally, I discuss the implications of this research for wildlife conservation and provide recommendations how to mitigate snare poaching.

4.3 Methods

4.3.1 Study area

I situated the study in MFNP which is located in northwestern Uganda (02°15'N 31°48'E; Fig. 4.1). The Karuma and Bugungu Wildlife Reserves border the park to the south and southeast. Together, the national park and reserves make up the 5,308 km^2 Murchison Falls Conservation Area.

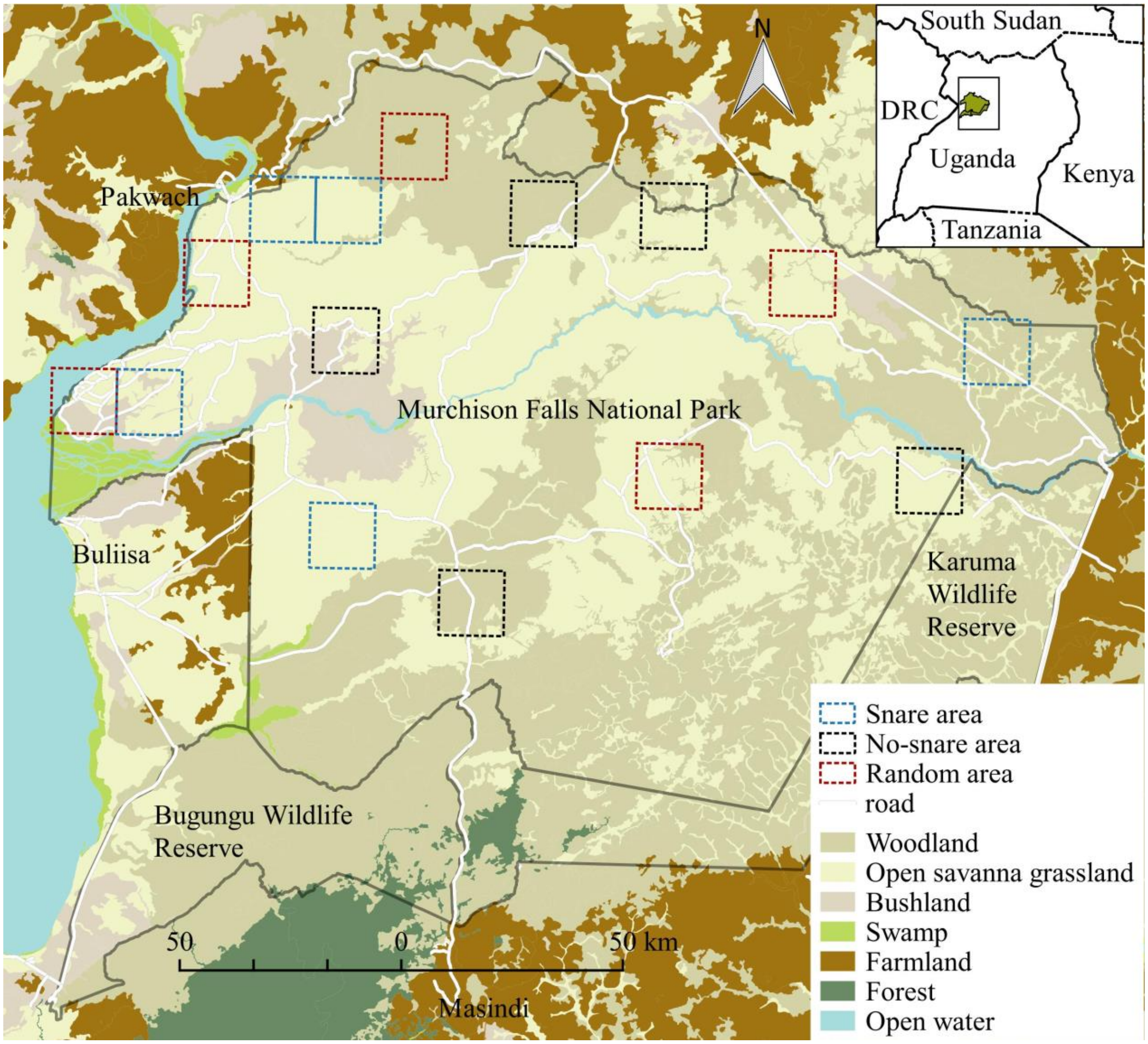


Figure 4.1. Study area showing the three predominate habitat types (open savanna grassland, bushland, and closed woodland) inside Murchison Falls National Park, Uganda. Each of the dotted squares indicates the randomly selected grid cells that were surveyed to quantify snare density in the snare areas, no-snare areas, random area. The area of each dotted square is 36 km2.

The area has a moist rain forest in the southwestern sector, bushland in the east and northwest, and undulating open savanna grassland dominated with *Acacia sieberiana* and *Borassus aethiopum* in the north and northwest. There are three predominate habitat types in my study area including open savanna grassland, bushland, and closed woodland (Nangendo, Stein, ter Steege, & Bongers, 2005). Seventy six mammal species inhabit MFNP, including the largest remaining sub-population of the endangered Rothschild's giraffe (*Giraffa camelopardalis rothschildi*), an expanding population of African elephants (*Loxodonta africana*), large populations of many species of terrestrial ungulates, and several species of large carnivores (Brenneman et al., 2009; Muneza et al., 2016; Wildlife Conservation Society, 2016).

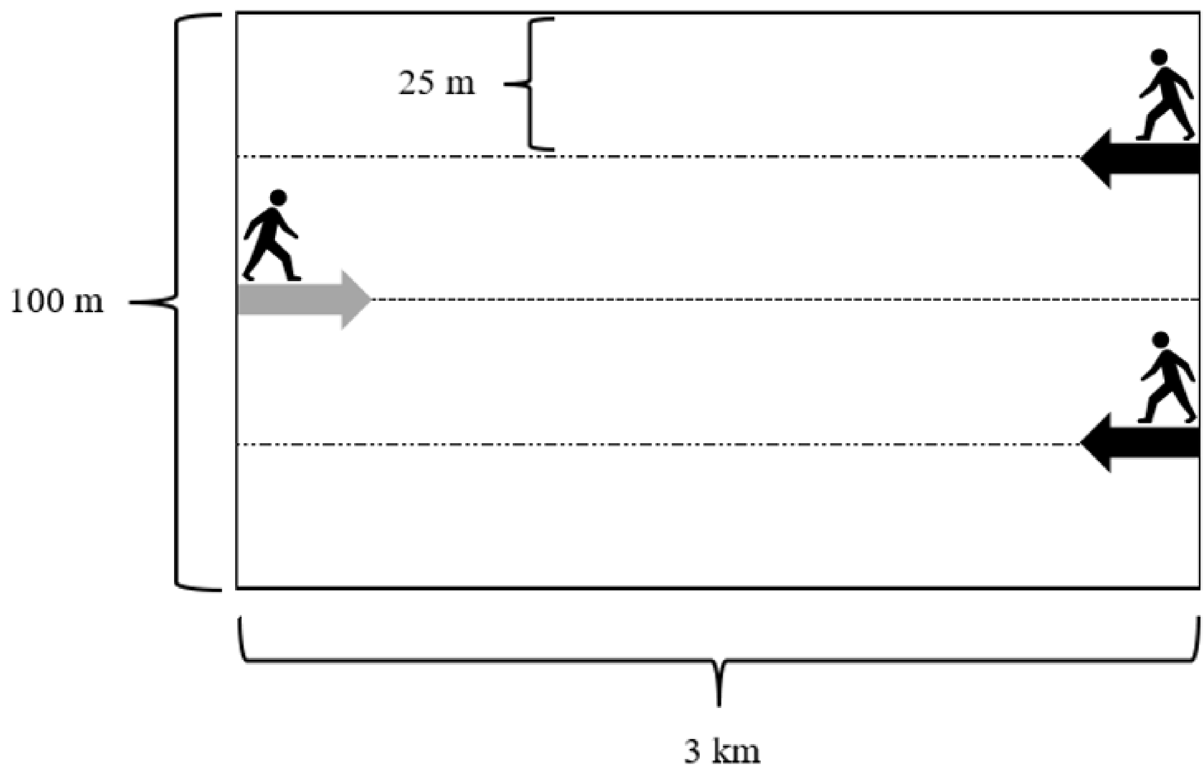
4.3.2 Data collection

I implemented separate surveys to assess the; *i*) detection probability, *ii*) density, and *iii*) lethality of snares in MFNP. I developed a geographic information system (GIS) database to create the experimental designs necessary to assess each of these snare metrics.

Detection probability

To quantify the detection probability of snares in MFNP, I developed a transect protocol involving three observers searching an area 100 m wide by 3 km long (Fig. 4.2). To randomize the areas over which I positioned these detection probability surveys, I first selected areas within MFNP that had contiguous habitat patches of grassland, bushland, and woodland > 10 km^2. With these areas, I then randomly selected eighteen patches, six for each habitat type. Then I overlaid these eighteen areas with my transect design (Fig. 4.2). Previous Uganda Wildlife Authority (UWA) ranger patrols in the area searched for snares in averagely 100 m wide by 6 km long transects and so I wanted to maintain the transect width. I positioned one experienced observer at each central point of the short end of the transect so that they were 100 m apart (Fig. 4.2). The observers walked 3 km purposely looking for a snare (Fig. 4.2; grey arrow). Once a snare was found, the observers searched all nearby trees and bushes until no other snares could be found before continuing the survey. I recorded all snares as '*count one*.' I doubled the number of observers in each transect to reduce the search area per person to 25 m wide and 3 km long and repeated the survey on the same day (Fig. 4.2; black arrows).

Figure 4.2. Sampling protocol used for determining snare detection probability in Murchison Falls National Park, Uganda. The grey arrow indicates one observer searching for snares in a transect of 100 m wide by 3 km long. The black arrows show two observers repeating the search by halving the transect size to 50 m wide by 3 km long.



At the same time, I intensified the search by checking around every tree with diameter at breast height (DBH) > 10 cm. I focused on trees > 10 cm DBH because these are stout enough to hold a large mammal once it is caught in a snare. I recorded all snares collected after the second search in the transect as *'count two'*.

Density survey

To conduct my snare density surveys, I overlaid a 6 X 6 km grid (resolution = 3600 ha) across my entire study area. Thus, this resolution grid cell could be surveyed in a single day. I used UWA ranger patrol data collected between June 2017 and May 2018 and my independent fieldwork in MFNP conducted between June 2016 and May 2018 to delineate grid cells where snares had been recovered (hence forth *snare-areas*) and those where no snares (*no-snare areas*) had been recovered in the previous five months of anti-snare patrol effort.

I randomly selected five grid cells in the *snare-areas* and five in the *no-snare areas* without replacing (Fig. 1; blue and black dotted squares). I then randomly selected five of the remaining grid cells regardless of the snare data I had at hand (Fig. 1; red dotted squares). I excluded from selection grid cells which overlay areas in which I had conducted the survey to estimate habitat detection probability. This was because I removed all the snares I encountered and including these areas could affect the density estimate. For logistical purposes, I did not consider grid cells that were > 20 km from the nearest road. I refer to these three areas (i.e. *snare area, no-snare area, random*) collectively as '*zones'*. Then, I subdivided each of the 6 X 6 km grid cells into ten 600 m wide and 6 km long transects with one side of the short length towards the park border (see Wato et al., 2006). This was to enable us to model the effect of distance from villages on snare density and lethality. I randomly selected and surveyed three transects equal to 10.8 km^2 (30.0% of grid cell area). From June 2018 until September 2018, I surveyed these transects between 7 am and 7 pm. I summed up all the snares I found per transect. The survey to estimate snare density was conducted by three groups composed of six observers each with prior experience searching for snares in the area. Every six observers in a group was assigned to a transect such that every observer searched for snares only in a 100 m wide and 6 km long strip. Each group had three data collectors who were called by whistle. Uganda Wildlife Authority rangers were called to intervene and release all the living animals I found in snares. I sampled 45 transects, 15 in each of the three *zones*.

Lethality of wire snares

Finally, I measured the lethality of snares. For every snare found, I recorded environmental and anthropogenic parameters to determine which correlated with the various animals that I found dead in the snares. The environmental parameters included average grass height, anchor tree species and DBH, the proportion of open area within 25 m radius of the snare, average diameter of thickets within 25 m radius of the snare, and elevation above sea level, and the nearest distance to ranger post, road, and village. The anthropogenic parameters recorded included UTM coordinates, thickness (number of wires bound in the snare), noose (diameter of the snare loop), and how high off the ground the snare was anchored on the tree (tree drop), vertical drop (nearest distance between snare and the ground), species captured (i.e. found in the snare) including its age and sex, and if the snare had a charm, (i.e. a talisman tied to snare that the local populace believe brings luck in capturing wildlife). I also recorded the snare as '*escaped*' whenever there were signs that the snare had been triggered but ineffectual. I identified all anchor tree species using the *Field guide to common trees and shrubs of East Africa* (Dharani, 2011).

4.3.3 Data analysis

I assumed that no additional snare (s) were set during the survey period. Likewise, every observer, given their experience finding snares in MFNP, was assumed to have equal ability to detect snares (O'Kelly, Rowcliffe, Durant, & Milner-Gulland, 2017). I calculated the nearest distance of each snare from ranger posts, villages, roads, and rivers in QGIS (version 2.12.1). I analyzed all snare encounter data in R version 2.14.0 (Team, 2013).

To estimate detection probability, I assumed that I collected all the snares in the transect during the second search. Therefore, I summed up the snares collected during the first search (*count one*) and divided by the total number of snares (*count one + count two*) collected in the transect to give detection probability per transect. Then, I averaged transect detection probabilities by the number of transects per habitat type to get a habitat detection probability estimate. I ran a *Kruskal-Wallis* test to analyze the variation of snare detection probability between habitat types (Kruskal & Wallis, 1952).

I estimated snare density by analyzing snare count data excluding those collected during the snare detection probability survey. To do so, I summed the number of snares per transect and divided by the average habitat snare detection probability. Then I summed the estimated number of snares per transects and divided by the total area of the transects per zone and per habitat type.

I examined the descriptive statistics of the anthropogenic and environmental parameters to describe the lethality of snares. I used *Jenks natural breaks optimization* based on two categories to pool the snare noose width data into small and large snares (Jenks, 1967). I measured the relationship between thickness (number of wires in the snare) and noose width using *Spearman rank correlation* (Gould, Ryan, & Wong, 2016). This was based upon the assumption that the wider the noose, the higher the number of wires. I conducted a *chi-square* test to examine the relationship between snare thickness and ability to capture (i.e. either animal found in snare or signs of animal escape) (Pearson, 1894).

I used *logistic regression* models composed of anthropogenic and environmental parameters to predict the probability that a wire snare would capture an animal. To do so, I pooled all snare data into a binary response variable (hereafter termed '*lethality*') based on whether a snare had *captured* an animal (1) or not (0; i.e., if a snare had no visual signs of animal disturbance). The independent anthropogenic parameters that I used to predict *lethality* included snare thickness, vertical drop, anchor height above ground, noose width, presence of charms, and nearest distance to village and road. The independent environmental parameters included; nearest distance to river, percentage of un-thicketed area, thicket diameter, and grass height. The distribution of *lethality* was highly skewed due to do the high number of zeroes.

4. 4 Results

Via the snare detection probability surveys, I recovered 488 snares (Table 4.1). There was no statistically significant difference at the $\alpha < 0.05$ level between number of snares detected in each habitat type (Kruskal-Wallis test; H = 3.34, p-value = 0.19, N = 18). The detection probability of wire snares was 0.82 for the study area.

Table 4.1. Number and types of snares found in closed woodland, bushland, and open savanna grassland and the associated detection probabilities in Murchison Falls National Park, Uganda. The snares were found by first searching a 0.1 km wide and 3 km long transect to get 'count 1' snares and then repeating the search by halving the size of the transect to 0.05 X 3 km to get 'count 2.

Habitat	Transect ID	Count one	Count two	Sum	Detection Probability	
					Transect	Habitat type
Closed woodland	1	48	12	60	0.80	
Closed woodland	2	5	0	5	1.00	
Closed woodland	3	30	13	43	0.70	0.81
Closed woodland	4	18	2	20	0.90	
Closed woodland	5	5	3	8	0.63	
Closed woodland	6	81	14	95	0.85	
Bushland	7	47	8	55	0.85	
Bushland	8	24	3	27	0.89	
Bushland	9	26	0	26	1.00	0.86
Bushland	10	31	0	31	1.00	
Bushland	11	20	14	34	0.59	
Bushland	12	8	2	10	0.80	
Open savanna grassland	13	9	1	10	0.90	0.79

Table 4.1. (cont'd)

Open savanna grassland	14	37	2	39	0.95
Open savanna grassland	15	2	0	2	1.00
Open savanna grassland	16	0	0	0	0.00
Open savanna grassland	17	12	0	12	1.00
Open savanna grassland	18	10	1	11	0.91

During the snare density survey, I detected and removed 674 snares. A plot of change in the lethality of snares with distance showed that they were more lethal nearer villages, roads, and river (Fig. 4.3). The snares were found mostly (91.6%) in the open savanna grassland habitats, 6.8% in bushland, and 1.8% in closed woodland (Table 4.2). I recovered 90.3% of these snares from *snare-areas*, 1.7% from *no-snare areas*, and 8.0% from the *randomly* generated areas. The results of the descriptive statistics of plausible parameters are presented in the Table 4.3 in the Appendix.

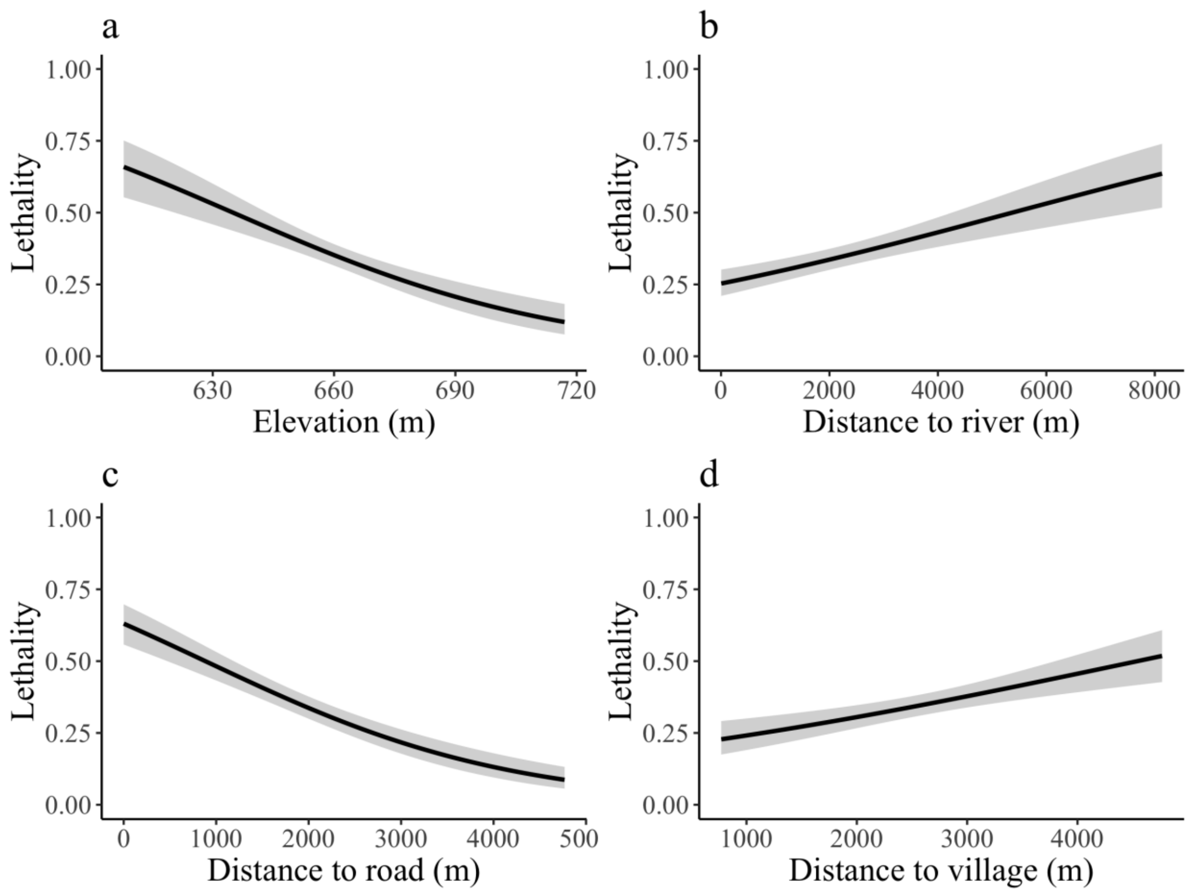


Figure 4.3. All effects graphs of individual logistic regression models for lethality including; elevation above sea level (panel a), distance to river (panel b), distance to road (panel c), and distance to village (panel d). The data were collected during snare surveys conducted in Murchison Falls National Park, Uganda between June and September 2018.

Most (65.3%) of the snares I recovered had no visible signs of animal disturbance, 21.5% had animal carcasses, 8.8% had caught wildlife that were still alive, and 4.4% had been visibly triggered by wildlife. There were no snares made of any material apart from wire. Most (81.0%) of the snares were made of wire harvested from vehicle tires, 16.0% from motor brake cables, 2.0% from vehicle tow cables, and 1.0% from electrical wire. I found 544 snares that had charms with a significant relationship between presence of a charm and noose width, X^2 (1, N = 4) =

199.70, $p < 0.05$. Small snares (noose width < 100.10 cm) were more likely than large snares (noose width > 100.10 cm) to have charms.

Table 4.2. Snare densities in the three *zones* calculated from 162 km^2 for each zone in Murchison Falls National Park, Uganda. I calculated snare type per proportion of habitat sampled in open savanna grassland (210. 24 km^2), bushland (203. 86 km^2), and closed woodland (72.90 km^2)

	Tire wire			Motor brake cable		
Zone / habitat	Estimated	Expected	No./ km2	Estimated	Expected	No. / km2
Snare area	612	597.42	3.79	104	118.58	0.64
No-snare area	52	50.90	0.32	9	10.10	0.05
Random area	1	16.69	0.01	19	3.31	0.12
Open savanna grassland	449	424.80	2.13	60	84.20	0.28
Bushland	55	70.11	0.27	29	13.89	0.14
Closed woodland	162	171.09	2.22	43	33.91	1.59

The density of snares was highest (4.58 /km^2) in the *snare-area.* The open savanna grassland habitat had the highest (4.82 /km^2) snare density among the habitat types (Table 4.4). Snare density by type of material was significantly different between *zones*, X^2 (1, N = 4) = 91.34, $p < 0.001$, and between habitat types, X^2 (1, N = 4) = 30.93, $p < 0.001$. Most (63.4%) of the carcasses I found in the snares were visibly decomposed from the smell or maggots and 36.4% looked fresh with no stiffening of the animal's muscle fibers. I identified 58.6% of the species that were captured or escaped.

Table 4.4. The density of snares per square kilometer in the surveyed zone and habitat type in Murchison Falls National Park, Uganda.

Zone / habitat	Detection probability	Estimated number	Density/km^2
Snare area	0.82	743	4.58
No-snare area	0.82	13	0.08
Random area	0.82	66	0.41
Open savanna grassland	0.79	781	4.82
Bushland	0.86	14	0.09
Closed woodland	0.81	56	0.34

Hartebeest (*Alcelaphus buselaphus*) were the most common wildlife species to be killed or captured in snares (Table 4.5). I found that the proportion of snares that had captured or in which an animal had escaped significantly differed by thickness, X^2 $(1, N = 4) = 28.90$, $p < 0.001$. The fewer the number of wires used in the snare, the more likely it was to capture wildlife.

Table 4.5. Percentage of wildlife kind captured and escaped out of poacher-set snares in Murchison Falls National Park, Uganda. The numbers are percentages of the category. There were 180 identifiable animals from the survey.

Common name	Species	Captured (% total)	Vulnerability
Hartebeest	*Alcelaphus buselaphus*	49.86	63%
Ugandan kob	*Kobus kob thomasi*	89.01	100%

Table 4.5. (cont'd)

Lion	*Panthera leo*	9.27	19%
Hyena	*Crocuta crocuta*	7.87	21%
Giraffe	*Giraffa camelopardalis rothschildi*	11.81	100%
Warthog	*Phacochoerus africanus*	26.66	100%
African buffalo	*Syncerus caffer*	5.51	63%

The majority (66.4%) of the snares were anchored on *Borassus aethiopum*, 10.5% on *Acacia sieberiana,* 9.9% were tied to *Crateva adansonii,* 6.2% on *Balanites aegyptiaca* and finally, 4.3% and 2.8% tied on *Combretum binderianum* and *Albizia coriaria* trees respectively. With the exception of *Albizia coriaria, lethality* data were homogenous across *zones* (X^2 = 388.41, $p = 0.05$). There was a significant relationship between trees species and *lethality*, X^2 (1, N = 4) = 138.85, $p < 0.001$. Snares anchored on four tree species significantly 'captured' or 'escaped' more wildlife than would be expected (*Acacia sieberiana,* $X^2 = 32.25$, $p < 0.05$; *Crateva adansonii,* $X^2 = 1.05$, $p < 0.05$; *Balanites aegyptiaca*, $X^2 = 23.31$, $p < 0.05$; *Combretum binderianum,* $X^2 = 16.73$, $p < 0.05$). Snares anchored on *Borassus aethiopum* significantly 'captured' or 'escaped' less wildlife than would be expected ($X^2 = 26.72$, $p < 0.05$). I found significant evidence that I observed less than expected undisturbed (i.e., *lethality* = 0) snares anchored on all tree species except *Borassus aethiopum* ($X^2 = 10.36$, $p < 0.05$). I found evidence that snares anchored on; *Acacia sieberiana* ($X^2 = 12.50$, $p < 0.05$), *Crateva adansonii* ($X^2 = 0.41$, $p < 0.05$), *Balanites aegyptiaca* ($X^2 = 9.04$, $p < 0.05$), and *Combretum binderianum* ($X^2 = 6.49$, $p < 0.05$) had significantly fewer observations of undisturbed snare traps than expected. It was evident from my analysis that 12 parameters (8 environmental and 4 anthropogenic) were significant predictors of *lethality* (Table 4.6).

Table 4.6. Logistic regression model output of significant predictors of the lethality of wire snares on sympatric guilds of carnivores and ungulates in Murchison Falls National Park, Uganda.

Parameter	F-statistic	p-value	Estimate	S.E	t value	DF
Thickness (number of wires)	19.86 on 1	<0.01	-0.07	0.02	-4.46	672.00
Vertical drop (cm)	2.041 on 1	<0.01	0.26	0.06	4.14	672.00
Anchor height above ground (cm)	53.99 on 1	<0.01	0.00	0.00	7.35	672.00
Tree DBH (cm)	30.65 on 1	<0.01	0.00	0.00	-5.54	672.00
Presence of charms	5.36 on 1	0.02	-0.12	0.05	-2.32	542.00
% Un-thicketed area	21.49 on 1	<0.01	0.01	0.00	4.64	672.00
Thicket diameter (m)	15.33 on 1	<0.01	0.00	0.00	-3.92	672.00
Grass height (cm)	21.18 on 1	<0.01	0.00	0.00	4.60	672.00
Elevation (m.asl)	38.76 on 1	<0.01	-0.01	0.00	-6.23	672.00
Distance to river (m)	27.57 on 1	<0.01	0.00	0.00	5.25	672.00
Distance to road (m)	85.32 on 1	<2e-16	0.00	0.00	-9.24	672.00
Distance to village (m)	17.54 on 1	<0.01	0.16	0.05	3.45	672.00

4. 5 Discussion

My study highlights the configurations of snares as a hunting tool and their effect on wildlife. I present a practical method for estimating the density of snares. I discovered that MFNP has one of the highest (4.58 /km^2) density of illegal snares in the world. I could find only one other study area, the Dzanga-Ndoki National Park in Central African Republic, that had a comparable density of 4.2 snare /km^2 (Noss, 1995). I found that even in areas where snares had not been recovered despite consistent effort in the last five months, the density of wires was at least 0.08 /km^2. Among the habitat types, grassland habitat had the highest density of snares (4.82 /km^2). This is expected because snares are set purposely to catch animals. In MFNP, the target species are densely populated in the open savanna grassland habitat (Rwetsiba & Nuwamanya, 2010). I found that snares set in areas which had more open spaces, or few small thickets, or with trees with smaller DBH, or with grass height of about 30 cm were most lethal. Furthermore, snares that were set further away from the riverbanks or low elevation were more successful than those set close to the riverbank or high ground for the same reason given above (Figure 3). The habitat of MFNP is such that areas near the rivers are mostly thicketed which keeps out animals compared to the rest of the park (Rwetsiba & Nuwamanya, 2010). I infer that poachers are setting the snares in areas of high wildlife concentration to increase the success rate of the snare.

I found that most (63.4%) of the animals that got caught were never recovered. This can be attributed to the risk involved in setting a snare and long lag time before it captures an animal. To reduce the risk, some poachers might go out of the national park to avoid arrest. Poachers rely on memory to find snares with a likelihood that not all are recovered. Snares that are unrecovered continue. Snares may have been unrecovered because the locations were forgotten by the poachers, or because UWA rangers or the observers got there before the poachers could. However, given that the carcasses were mostly rotten, it is probably more likely that the snares had been forgotten by the poachers. Therefore, snaring is abnormally wasteful relative to other forms of hunting such as spearing or shooting. Noss (2008) found a 27.0% loss to scavengers and decomposers from hunting with snares in the Central African Republic. Additionally, the majority (65.0%) of snares I found during the study were undisturbed (i.e. had no sign that an animal had triggered it and were still functional) but would remain functional for at least two years (Noss, 2008). Therefore, snaring in an area is akin to a creating a ‘mine field’ for animals that remains a threat until they are removed.

Murchison Falls National Park has more than 200 km of a tarmacked section of Africa’s great north road encircling its eastern and northern borders (Fig. 4.1). Several towns along this road are unmarked stop points for truckers who discarded their worn off tires. I found that 81% of the wire snares were comprised of metal from radial vehicle tires. Thus, it is from this constant supply of disused tires that snares are predominantly made. I also found that vehicle tire wire snares were more lethal compared to other kinds of materials making them an effective tool for trapping animals. Additionally, the community around MFNP is one of the poorest in Uganda which lends credence to the idea that the widespread snare hunting evidenced from my study is being driven by poverty and a lack of alternative livelihoods (Okidi & McKay, 2012).

Human infrastructure including roads and distance to village were related with the density of snares and significantly predicted lethality. Areas closer to villages and roads had more snares. This same pattern was observed in Zambia and is indicative of the convenience and allocation of effort needed to set up a snare (Watson et al., 2013). Wire snare poaching is an activity that occurs on foot. Closer is more convenient and less costly in terms of effort but also less risky for the poacher. Snares provide poachers the ability to minimize the risk associated with the act of killing the animal and the chances of being caught in the illegal act (Moreto & Lemieux, 2015). However, I found that snares were more lethal when they were further away from villages and closer to the roads. This could mean that animals perceived villages as risky places and were more risk averse leading to fewer captures and escapes.

During the study, I witnessed a Ugandan kob (*Kobus kob thomasi*) walking along a game trail in an open savanna grassland and as it approached a snare with noose vertical drop near its eye level, the Ugandan kob paused right in front of the snare then jumped over it before running off the game trail into the open field (Mudumba field notes, 2018). I made a similar observation with a hartebeest in the bushland habitat type. I found that snare thickness, noose width, vertical drop, wire circumference, grass height, and anchor tree diameter at breast height significantly predicted lethality. Snares tied higher on the anchor tree, and those with the noose higher off the ground were more successful than those set closer to the ground (i.e., lethality increased with height above the ground). It is reasonable that in areas with high snare densities, animals could be able to associate snares with danger and avoid them especially if the snare is set in a configuration that is easily noticeable. If animals actively avoided snares, then snares created a landscape of fear similar to natural predator cues and impacted target species beyond maiming and killing (see Moll et al., 2017). Evidence of trap avoidance has been observed in several species including; beavers (*Castor canadensis*; McNew, Nielson, Bloomquist, & McNew Jr, 2007), the little brown bat (*myotis lucifugus*; Kunz & Anthony, 1977), kinkajou (*potos flavus*; Schipper, 2007). However, because of limited empirical evidence on this phenomena specifically describing animal-snare interaction, I recommend that this possibility be examined in future studies similar to those of their natural predators (Laundré, Hernández, & Altendorf, 2001; Lone et al., 2014; Gaynor, Brown, Middleton, Power, & Brashares, 2019).

Most (66.4%) of the snares were anchored on *Borassus aethiopum* trees. There was significant evidence that snares tied to *Acacia sieberiana, Crateva adansonii*, *Balanites aegyptiaca, Combretum binderianum* were comparatively more successful than expected. These species either provide shade or fruit which attract animals. The *Balanites aegyptiaca* tree has branches that form a shade but also dangle and can conceal a wire snare (Fig. 4.4). This could be the reason snares anchored under its canopy were considerably more successful than those set in other trees such as *Borassus aethiopum.*

Although poachers significantly tied charms on snares to increase the chance capturing an animal, I could detect no clear pattern in these snares being more successful. In fact, I found moderate evidence that snares with charms were less successful in catching animals than those that did not have charms. However, I did find that the fewer the number of wires used in the snare (thickness), the more lethal the snare (Table 4.6). I suspect that this has to do with how easily collapsible a snare is given its thickness. Generally, wire snares with more than two wires (thicker) take more effort to collapse and hold in place compared to those with fewer wires (thinner). This attribute can permit an animal to escape. Moreover, thinner snares could be easier to conceal as opposed to thicker snares. My evidence supports the possibility that thinner snares are more effective because they easily collapse around the animal and are more difficult for the animal to see.

Panel a) Panel b)

Figure 4.4. A hartebeest (*Alcelaphus buselaphus*) under a *Balanites aegyptiaca* tree shade directly adjacent to a wire snare (panel a) and another hartebeest with a wire snare around its neck after having broken the wire snare from its anchor (panel b) in Murchison Falls National Park, Uganda.

Wildlife snaring can have drastic effects on several species of conservation concern. In West Africa, subsistence poaching led to a decline in the local population of the African lion and giraffe to a level that necessitated a separate classification of these species (Henschel et al., 2010; Winter, Fennessy, & Janke, 2018). I identified seven wildlife species caught in snares during my study including the African lion and giraffe. The hartebeest was the species that was captured most often (49.9%). Compared to other large bodied mammals in the area such as African buffalo (*Syncerus caffer*) or giraffe, the hartebeest, weighing 110 kg on average, should make for a relatively easy field-butcher by a few experienced poachers who can carry all the carcass away quickly. However, it remains an area of future research if there is poacher preference (through the snare configuration) or species behavior that led to more capture of hartebeest in comparison to the other locally edible species including the Ugandan kob, warthog (*Phacochoerus africanus*), giraffe and African buffalo. However, it is more likely that lion and hyaena (*Crocuta crocuta*) are by-catch. This is because African lions and hyaenas occur at a low density inside MFNP (Omoya, Mudumba, Buckland, Mulondo, & Plumptre, 2014; Mudumba et al. In review). Moreover, hyaena, like the lion and leopard have local taboo that forbid their consumption making their carcasses less desirable (Pakwach village chief, per. comm). Therefore, it would be illogical to hunt African lions, hyaena, and leopards using wire snares. However, this is also an area that needs to be addressed more conclusively in future studies.

In conclusion, my methodology might be underestimating the number of species that get caught in snares. Rather, my results are representative of species that can be anchored once caught in a snare. For instance, I observed > 20 elephants with injuries (i.e., missing portion of a trunk) but did not find any elephant captured or escaped during the survey. Therefore, species such as elephant and hippopotamus (*Hippopotamus amphibious*), that are larger than an African buffalo, may not be detected because of their ability to break free once caught in a wire snare (Oneka, 1995; Mudumba & Jingo, 2015). I also suggest that there is a need for longitudinal comparative studies of variously snared individuals to determine the energy cost of a snare injury to animals. Finally, an area of need involves the interviewing of poachers to determine other parameters I could not measure such poacher effort and harvest rates.

Murchison Falls National Park is > 3000 km^2 which necessitates a high cost of law enforcement for wildlife protection and ecotourism (Moreto, 2016; Plumptre, 2019). Disused vehicle tires provide an effective free material to make wire snares to a desperate populace living in the vicinity of the park. Given the scale and disconnect between the snare and the poacher, solely engaging in confrontational law enforcement or fortress conservation in MFNP is likely to fail as a strategy against wildlife snaring. Rather, efforts should be made to find alternative uses of the raw material so that they are not capable of being used as snares. Concurrently, I recommend that urgent efforts should be made to search and remove wires snares from protected areas so as to decrease the negative effects of snares on wildlife.

4.6 Acknowledgements

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CONCLUSION

My research examined several topics relevant for wildlife conservation in the 21st century. Particularly, I examined the interconnectedness of human population growth, energy development, human-wildlife coexistence, and wildlife population ecology. My dissertation was motivated by the current global trends including projected human population growth and how it might impact wildlife conservation. The results of my research are applicable to biodiverse-rich portions of the world that are at risk of human development. My methods could also be used to quantify the severity of subsistence poaching in other sites. This is relevant because subsistence poaching remains a significant conservation challenge in the 21st century.

In summary of the main findings, in Chapter One, I reviewed literature and categorized the of effects of oil extraction on wildlife. Broadly, the effects included: i) increased poaching, ii) curtailed space-use, iii) increased harassment, iv) risk of introduction of invasive species, v) contamination, and vi) heightened severity of impacts due to synergistic effects. Overall, I found that efforts to evaluate the consequences of oil extraction, particularly in peer-reviewed form, were limited. Research should be conducted pre-, during, and post-oil extraction to increase knowledge of effects of oil extraction on wildlife to enable more effective policy decisions. In Chapter Two, I studied human-wildlife co-existence and found that conflict was the most important factor determining local people's attitude towards poaching. Less than 20% of the local people had ever visited the park and there was limited flow of benefits for local communities from protected areas. My findings highlight the importance of providing remedies compatible with local livelihoods and conditions and could be used to improve wildlife management to address poaching. In Chapter Three, I predicted the African lion (Panthera leo) carrying capacity in Murchison Falls National Park (MFNP) from existing primary prey biomass.

I found that the extant African lion density was four times less than what the prey biomass inside the park could support. I compared the African lion density estimated from prey biomass to that estimated from direct counts and found that estimating lion density from indirect methods such as prey biomass can result in overestimation of existent populations. In Chapter Four, I described an approach for estimating the density, configuration and lethality of poacher-set snares and discussed their effects on wildlife inside MFNP. Murchison Falls National Park had the highest known density of wire snares in the world. I provide a litany of anthropogenic and environmental configurations that made snares more likely to catch an animal. The ability of snares to trap an animal were significantly predicted by snare thickness, noose width, vertical drop, wire circumference, grass height, and anchor tree diameter at breast height. Regulating the disposal of dis-used vehicle tires which provided the material for the wire snares was likely to reduce snare poaching inside the park. Additionally, providing alternative livelihoods to people involved in snare poaching would discourage the recruitment of locals in snare poaching. My method of surveying snares provides the opportunity to standardize temporal and spatial measurements of snare density and configuration as a first step to refine mitigation techniques.

Generally, my dissertation has explored a scope of challenges faced by wildlife from both small and large anthropogenic activities. I identified research gaps on effects of oil extraction on wildlife. For instance, there is a general lack of information about how large mammals are affected by oil extraction. This is particularly important because the world will depend on fossil fuels into the foreseeable future. Therefore, many biodiverse rich areas of the world remain vulnerable to exploration. My research was situated in a coupled human and natural system and adds to the growing body of knowledge that promotes human-wildlife co-existence. This is critical because the world is getting more densely populated and urbanized bringing more people in proximity with wildlife. My comparative study estimating African lion population from direct and indirect methods highlights the shortfall of predicting predator densities from their prey biomass. Finally, my survey design for estimating snare density can be applied to conduct longitudinal studies to assess the performance of interventionist strategies within MFNP and in other regions of sub-Saharan Africa.

APPENDIX

APPENDIX

Table 4.3. The minimum, median mean, and maximum measurements of parameters associated with all the snares encountered and removed from Murchison Falls National Park, Uganda. I present these measurements in centimeter (cm), meter (m), and meters above sea level (m.asl).

Measurement	Min	Median	Mean	Max
Thickness (number of wires)	1	4	3.44	8
Noose width (cm)	40.00	100.10	102.90	150.00
Vertical drop (cm)	0.00	41.41	42.08	96.00
Wire circumference (cm)	10.00	50.00	55.67	154.00
Grass height (cm)	0.00	30.00	32.02	120.00
Tree DBH (cm)	5.00	40.00	51.13	150.00
Anchor height above ground (cm)	0.00	36.50	52.33	191.00
% Un-thicketed area	20.00	93.00	87.38	98.00
Elevation (m.asl)	191.00	657.00	661.40	717.00
Thicket diameter (m)	0.00	5.00	16.90	200.00
Distance to river (m)	4.12	1755.00	2193.23	8134.72
Distance to village (m)	478.90	2400.00	2498.12	5263.64
Distance to road (m)	0.40	1643.47	2109.24	4767.94
Distance to ranger post (m)	76.72	2958.81	3400.34	7762.46

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