

2023-08

Effect of retaliatory killing on African lion coalitions in Tarangire-Manyara ecosystem, Tanzania

Felix, Nancy

<https://doi.org/10.58694/20.500.12479/2212>

Provided with love from The Nelson Mandela African Institution of Science and Technology

**EFFECT OF RETALIATORY KILLING ON AFRICAN LION
COALITIONS IN TARANGIRE-MANYARA ECOSYSTEM, TANZANIA**

Nancy Felix

**A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of
Master's in Life Sciences of the Nelson Mandela African Institution
of Science and Technology**

Arusha, Tanzania

August, 2023

ABSTRACT

In landscapes where people and lions coexist, conflicts are common due to livestock predation and threats to human safety. Retaliatory lion killing by humans is often a consequence of such conflicts. In Tarangire-Manyara Ecosystem (TME) lion population are threatened by retaliatory killing, but little is known how retaliatory killing affects lion social structure, particularly male coalitions. Fourteen years dataset of lion monitoring was used to map the spatial-temporal dynamics of male coalition. Lion killing data was used to assess the effects of retaliatory lion killing on the male coalitions for ten prides. Interviews on two hundred and fourteen respondents was used to assess the attitudes and awareness of the community on effects of retaliatory killing to lions. Lion coalitions were found larger and lasted for a longer tenure period in low-risk areas of retaliatory killing, and far from active hunting blocks. Twelves lions were killed for livestock loss, while fifteen attempts of lion killing were prevented. Attitude towards lion existence and conservation was positive for young people (18-35 years) compared to older age class. People with primary or secondary level of education were more likely to have lions killed if they attack livestock compared to people with no formal education. Community attitude on retaliation effect varied widely, as people perceptions depends on benefits/losses they incurred. This study showed retaliatory killing negatively affects long-term lion coalition and population. Also, recommends implementing better education programs and participatory conservation activities to protect the declining lion populations.

DECLARATION

I, Nancy Felix, do hereby declare to the Senate of the Nelson Mandela African Institution of Science and Technology that this dissertation is my original work and that it has neither been submitted nor being concurrently submitted for a degree award in any other institution.

Nancy Felix



19/08/2023

Name of Candidate

Signature

Date

The above declaration is confirmed by:

Prof. Anna Treydte



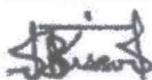
19/08/2023

Name of Supervisor 1

Signature

Date

Dr. Bernard Kissui



19/08/2023

Name of Supervisor 2

Signature

Date

Prof. Linus Munishi



19/08/2023

Name of Supervisor 3

Signature

Date

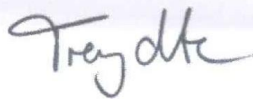
COPYRIGHT

This dissertation is copyright material protected under the Bern Convention, the Copyright Act of 1999 and other international and national enactments, in that behalf, on intellectual property. It must not be reproduced by any means, in full or in part, except for short extracts in fair dealing; for researcher private study, critical scholarly review or discourse with an acknowledgement, without written permission of the Deputy Vice Chancellor for Academic, Research and Innovation, on behalf of both the author and the Nelson Mandela African Institution of Science and Technology.

CERTIFICATION

The undersigned certify that they have read and hereby recommend for acceptance by the Nelson Mandela African Institution of Science and Technology, a dissertation titled "*Effect of Retaliatory killing on African lion coalitions in Tarangire-Manyara Ecosystem, Tanzania*" in partial fulfillment of the requirements for the degree of Master's in Life Sciences of the Nelson Mandela African Institution of Science and Technology.

Prof. Anna Treydte



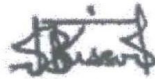
19/08/2023

Name of Supervisor 1

Signature

Date

Dr. Bernard Kissui



19/08/2023

Name of Supervisor 2

Signature

Date

Prof. Linus Munishi



19/08/2023

Name of Supervisor 3

Signature

Date

ACKNOWLEDGMENTS

A journey of a thousand miles always begins with a single step. I am delighted and honored to express my sincere gratitude to people and various organization that assisted me in one way or another to accomplish this Master's degree journey. First and foremost, I am very grateful to God, my Creator for without his grace and protection this study would not have been completed. He made the way for me where there was no way and strengthened me in times that I was heartbroken.

I would like to express my sincere appreciation to my main supervisor Prof. Anna Treydte for her endless encouraging and supportive words that encourage me to work even harder. I am also grateful to my Co-supervisors Prof. Linus Munishi and Dr. Bernard Kissui for their endless support in shaping the work from proposal development, data collection and towards this end of my Master's program. I am particularly, thankful to the Tarangire Lion Project team especially Dr. Bernard Kissui (Principal Investigator) for his unmeasurable support, invaluable advice, valuable suggestion and also to allow me use part of the Tarangire Lion Project data set for my Maser's degree.

I would like to acknowledge the support of various institutions that made this project possible; Tanzanian National Parks, Tanzanian Wildlife Research Institute, the Tanzania Commission for Science and Technology (COSTECH), Babati and Monduli District Council for granting research permits to conduct this study. This research would not have been possible without the funding provided by the Rufford Small Grant. Support of equipment from Idea Wild Organization. I am also very grateful for the scholarship support from DAAD Exchange Program through the Nelson Mandela African Institution of Science and Technology (NM-AIST).

Finally, I wish to thank my family for all of their patience, unconditional love and support during all the study period. Also, to my schoolmate from the School of Life Sciences and Bio-engineering 2018, specialty Biodiversity and Ecosystems Management for their advice during rehearsal among ourselves.

DEDICATION

With great joy I dedicate this work to myself and my family for their unconditional love and support to me in my life and education.

TABLE OF CONTENTS

ABSTRACT.....	i
DECLARATION	ii
CERTIFICATION	iv
ACKNOWLEDGMENTS	v
DEDICATION.....	vi
TABLE OF CONTENTS.....	vii
LIST OF TABLES	ix
LIST OF FIGURES	x
LIST OF APPENDICES.....	xi
LIST OF ABBREVIATIONS.....	xii
CHAPTER ONE.....	1
INTRODUCTION	1
1.1 Background of the Problem	1
1.2 Statement of the Problem.....	4
1.3 Rationale of the Study.....	4
1.4 Research Objectives.....	5
1.4.1 General Objective	5
1.4.2 Specific Objectives	5
1.5 Hypothesis.....	5
1.6 Significance of the Study	5
1.7 Delineation of the Study	6
CHAPTER TWO	7
LITERATURE REVIEW	7
2.1 Lion Ecology, Distribution and Conservation Status	7
2.2 Lion Habitat Selection and Home Range.....	8
2.3 Male Lion Coalition and Retaliation.....	9
2.4 Human-Lion Conflict and Community Understanding on Retaliation Effects	9

CHAPTER THREE	11
MATERIALS AND METHODS.....	11
3.1 Study Area	11
3.2 Data Acquisition and Field Protocols	12
3.2.1 Mapping Male Lion Coalitions.....	13
3.2.2 Retaliation Effect on Male Lion Coalitions	13
3.2.3 Community Perceptions on the Effect of Retaliation to Lion Population	14
3.3 Data Analysis	15
CHAPTER FOUR.....	17
RESULTS AND DISCUSSION	17
4.1 Results.....	17
4.1.1 Spatio-Temporal Dynamics of Male Lion Coalition	17
4.1.2 Effect of Retaliatory Killing on Male Lion Coalition.....	19
4.1.3 Community Awareness and Attitude on the Effect of Retaliatory Killing to Lion Population	20
4.2 Discussion	25
4.2.1 Spatio-Temporal Dynamic of Male Lion Coalition.....	25
4.2.2 Effect of Retaliation and Lion Hunting on Coalition.....	25
4.2.3 Community Attitude and Awareness on the Effect of Retaliatory Killing to Lion Population	26
CHAPTER FIVE	29
CONCLUSION AND RECOMMENDATIONS	29
5.1 Conclusion	29
5.2 Recommendations.....	29
REFERENCES	31
APPENDICES	40
RESEARCH OUTPUTS.....	46

LIST OF TABLES

Table 1:	Description of variables included in the analysis of the factors influencing retaliatory killing on male coalition in TME.....	14
Table 2:	Predictor variables used in the analysis of generalized linear mixed model to understand community attitude towards the effect of retaliatory killing on lion population in TME.....	16
Table 3:	A priori generalized linear mixed models representing the effect of retaliatory killing on coalition size in TME.....	19
Table 4:	Candidate models under generalized linear mixed models for determining the effect of retaliatory killing on the tenure period of male coalitions in TME.....	20
Table 5:	Parameter estimates and 95% confidence intervals (CI) of the top-ranking model for the effect of retaliatory killing on the tenure period of male coalition in TME	20
Table 6:	A descriptive statistics of the data obtained from the interviews conducted in villages surrounding TME.....	21
Table 7:	Candidate models under generalized linear mixed models for whether lions have right to live or not in TME.....	23
Table 8:	Prior candidate models under generalize linear mixed models for whether lions should be killed due to livestock depredation in TME	24

LIST OF FIGURES

Figure 1:	Map of the Tarangire-Manyara Ecosystem with the surveyed villages, hunting blocks and villages with high and low retaliation risk based on retaliatory killing data collected over the years 2004 to 2018 by TLP.....	12
Figure 2:	Interviewing villagers from March to May 2019 in Tarangire-Manyara Ecosystem	15
Figure 3:	Maps showing spatial distribution of male lion coalitions and village surrounding the protected areas of the study site in TME based on data collected from 2004 to 2018	18
Figure 4:	Percentage of the respondents with positive attitude and negative attitude towards lion presence in TME.....	22

LIST OF APPENDICES

Appendix 1:	Matrix Plot of Spearman Correlation Coefficient for predictor Variables	40
Appendix 2:	Male Lion Coalition Found in Tarangire-Manyara Ecosystem	41
Appendix 3:	Data of Retaliatory Lion Killing in Tarangire-Manyara Ecosystem.....	43
Appendix 4:	Questionnaire to Communities Found in Tarangire-Manyara Ecosystem.....	44
Appendix 5:	Poster Presentation.....	47

LIST OF ABBREVIATIONS

AICc	Akaike's Information Criterion corrected
COSTECH	The Tanzania Commission for Science and Technology
GCA	Game Controlled Areas
GLMM	Generalized linear mixed model
GPS	Global Positioning System
GR	Game Reserve
LMNP	Lake Manyara National Park
m.a.s.l	Metres above sea level
NGO	Non-Governmental Organization
NM-AIST	The Nelson Mandela African Institution of Science and Technology
PA	Protected area
TLP	Tarangire Lion Project
TME	Tarangire- Manyara Ecosystem
TNP	Tarangire National Park
VHF	Very high Frequency
WMA	Wildlife Management Area

CHAPTER ONE

INTRODUCTION

1.1 Background of the Problem

The global increase in human population has led to over-exploitation of natural resources, both fauna, and flora (Karant & Chellam, 2009). Conversions of natural habitats into cultivation fields, developing urban areas, extraction of resources through logging and activities such as poaching has had serious impacts, particularly on large carnivore populations and has triggered human-carnivore conflicts (Loveridge *et al.*, 2010). Human-carnivore conflict represents a universal problem that is negatively impacting lion (*Panthera leo*) populations and local livelihoods (Constant *et al.*, 2015; Morrison *et al.*, 2007; Ripple *et al.*, 2014). Currently, in sub-Saharan Africa, the African lion (*Panthera leo*) occupies a range of about 2.5 million km², which is only about 13% of their historical range (IUCN SSC Cat Specialist Group, 2018). This is lower than what was reported to be approximately 3 million km² for the year 2013 (Riggio *et al.*, 2013). Over the past 21 years, the population of African lions has declined by 43% to a number that lies between 20 000 and 30 000 individuals (IUCN SSC Cat Specialist Group, 2018). As a result of increasing land exploitation for economic purposes causing habitat destruction and fragmentation, overhunting of natural prey, spread of disease, illegal trade and unsustainable levels of trophy hunting (IUCN, 2006).

Recent increases in the human rural population have triggered the conversion of open areas into agricultural fields and settlements, thus, restricting wildlife movements and threatening their persistence (Nyahongo, 2007). In Eastern and Southern Africa, lions exist both in protected areas and in surrounding unprotected habitats, where the decrease in their population is particularly significant (Ray *et al.*, 2005). In most sub-Saharan Africa, the pastoral community lives in close proximity to the protected areas (Okello *et al.*, 2014), which accelerates the interaction of human and wildlife and frequently leads to conflicts. The emerging conflict often includes livestock depredation and human injuries/attack (Loveridge *et al.*, 2010; Dickman *et al.*, 2014). Such losses of property, that are linked to a reduction in family wealth, cause people to retaliate by killing lions or other carnivores that may have caused the loss (Packer *et al.*, 2005; Woodroffe & Frank, 2005; Kissui, 2008). These retaliatory killings have been shown to threaten the persistence of carnivore populations (Woodroffe & Frank, 2005; Ikanda & Packer, 2008). Yet, little is known about the extent to which retaliation

affects carnivore populations, particularly in the long-term. Some studies in Kenya and Tanzania reported that the number of carnivores killed may be proportional to the number of livestock killed by carnivores (Holmern *et al.*, 2007; Kissui, 2008; Ikanda & Packer, 2008; Muriuki *et al.*, 2017), but nothing has been studied about the impact of retaliatory killing on social grouping and losses within lion populations.

Coalition refers to a cooperative group formed with a number of individuals for reproductive advantage and defending other resources (Bygott *et al.*, 1979). Coalitions are formed by male lions, cheetah, striped hyenas, chimpanzees, baboons and feral horses for resource protection, territory defense and reproduction enhancement (Mosser & Packer, 2009; Borrego *et al.*, 2018). Often, coalitions are formed by species living in communal structure having social groups (Mosser & Packer, 2009; Chakrabarti & Jhala, 2017). Male lions form a coalition from the age of three years and above after leaving their natal pride. These coalitions are formed by brothers, cousins or even non-relative males (Packer & Pusey, 1982). These males roam around until they attain sexual maturity and being capable of fighting males from another pride and driving them away, this is also termed as pride takeover (Mosser & Packer, 2009). During pride takeover, a new coalition will kill any cubs less than 2 years old and expels sub adults of the evicted coalition to speed up female return into estrus for reproduction (Bygott *et al.*, 1979). Male coalitions are, therefore, important as they protect and support females in rearing their cubs to independent age and patrolling their territory (Packer & Pusey, 1982). Thus, the loss of any individual that can form a coalition or frequent replacement of resident males increases the vulnerability of the entire pride and offspring, also it severely depress cubs recruitment leading to overall population decline (Whitman *et al.*, 2004; Loveridge *et al.*, 2007). The size of a coalition group is a component in ensuring cubs, female and pride survival at large and can be a good indicator for population fitness (Bygott *et al.*, 1979). Further, the longer time a coalition group with three or more individuals can last in different prides, the more they ensure survival of their offspring (Bygott *et al.*, 1979). Thus, the tenure period of a coalition is also a good proxy for understanding population fitness, and both coalition size and tenure might strongly be compromised through retaliatory killing. Up to now, few studies have investigated how killing of male lions affect their social structure, particularly male coalition groups. Furthermore, no study has quantified the impact of retaliation incidences of male lions and compared them with tenure period and environmental aspects.

Therefore, expectation of the study where indiscriminate killing through retaliation will decrease size of male lion coalitions. And, coalitions that are closer to village areas with high risk of retaliatory lion killings will be smaller than in village areas with low risk. Also, the tenure period will be short for small male coalition (two individuals) and for coalitions close to villages with high retaliatory killing. Further, the closeness to anthropogenic disturbances might influence pride size as was shown by Woodroffe and Frank (2005). Hunting activities that are not properly managed have been reported to pose adverse impact on lion prides, particularly male lion coalitions, as they are hunted for trophies (Whitman *et al.*, 2004; Packer *et al.*, 2010; Creel *et al.*, 2016). Thus, male coalition found in active hunting blocks will have small size and short tenure period than male coalitions further away from hunting blocks.

Positive attitude of people towards carnivore conservation has been reported to be dependent on the benefits such as revenue, and employment opportunity (Dickman *et al.*, 2011; Ontiri *et al.*, 2019). While, negative attitudes are often linked with livestock loss and human injuries/death (Dickman, 2008; Maddox, 2003; Roskaft *et al.*, 2007; Romañach *et al.*, 2007). In addition, socio-economic factors i.e., demography, age and gender (Dickman *et al.*, 2014; Kellert & Berry, 1987) as well as education and social factors (Dickman, 2008; Dickman, 2010) have also been reported to influence people's attitudes towards carnivores. Thus, the study aimed to understand communities' attitudes and awareness on the impact of retaliatory killing to lion population. Expectation were people living in villages with high levels of livestock predation and with low level of education would be least tolerant towards livestock losses by lions and most likely to support retaliatory lion killing. Moreover, other hypotheses include: business owners, agro-pastoralist, employees perceive lions with less threat than pure pastoralist as they strongly depend on livestock only. Also, young men i.e., Maasai warriors had a higher chance of engaging in retaliation compared to older men and women due to traditional activities in the Tanzanian Maasai pastoralist culture.

Therefore, this study has provided information on the effect of retaliation to the social group of lions, particularly male coalitions. Using long-term lion monitoring data from 2004 to 2018 from which coalition size and tenure period were extracted. Also, knowledge of community attitude towards the effect of retaliation to lion population through interviews conducted in selected villages surrounding Tarangire National Park where retaliatory lion killings had been frequently reported. Moreover, knowing community background and perceptions in areas surrounding the National Parks conflict hotspots were identified and communication

shortcomings for promoting sustainable conservation of the lion population in the Tarangire-Manyara Ecosystem.

1.2 Statement of the Problem

Recently, conflicts between humans and lions have escalated, resulting into loss of livestock or injury to humans and consecutive retaliation of lions, which adversely affects the lion population (Ikanda & Packer, 2008; Kissui, 2008). Tanzania harbors a large number of lions in Africa (Bauer & Merwe, 2004), with the TME hosting the fourth largest lion population in Tanzania (IUCN, 2006). However, lions in TME are threatened by retaliatory killing from pastoralists due to livestock predation as it has been reported by Mponzi *et al.* (2014) and Kissui *et al.* (2019). While Kissui (2008) in TME showed that loss of a livestock due to predation is correlated to retaliatory killing on predators especially lions. Therefore, as retaliatory killing can affect male lions that might be in a coalition, it can drastically weaken male coalitions and increase the turnover rate of the males within prides leading to increased incidences of infanticide in pride (Bygott *et al.*, 1979). Retaliatory killing can affect lions of all ages including male lions, but still little is known on how retaliatory killing affect the lions' social structures. Therefore, this study examined the effect of retaliatory killing on male lion coalitions as well as assess the overall effects to the lion population and its implication to lion conservation in the TME.

1.3 Rationale of the Study

Ongoing decline of lion population has long been reported in TME, thus this study aimed to show the effect of retaliatory killing on male lion coalitions and lion population in the ecosystem. Through examining the spatial-temporal dynamics of male coalition, coalition size and tenure period whether they are located in protected areas or outside where threats of retaliation are inevitable.

1.4 Research Objectives

1.4.1 General Objective

To assess the effects of retaliatory killings on male lion coalitions, attitudes and community awareness on the effect of retaliatory killing to lion population in the Tarangire-Manyara Ecosystem.

1.4.2 Specific Objectives

The study aimed to achieve the following specific objectives:

- (i) To assess the spatio-temporal dynamics of lion coalitions in the lion population of Tarangire-Manyara Ecosystem.
- (ii) To assess the effect of retaliatory killing on lion coalitions (coalition size and tenure period) at the midst and periphery of the Tarangire National Park.
- (iii) To assess community awareness and attitude on the effect of retaliatory lion killings in the Tarangire-Manyara Ecosystem.

1.5 Hypothesis

The study aimed to achieve the following hypothesis:

- (i) Male coalitions at the periphery of the protected area are more negatively affected (smaller in size, more frequent turnover rate) by retaliatory killing compared to coalitions found in the midst of a protected area.
- (ii) There are fewer coalitions close to villages that shows high retaliatory killing incidents than in villages with low retaliatory killing.
- (iii) The community has little awareness of the effect of retaliatory killing on the lion population.

1.6 Significance of the Study

Lions are keystone species because they regulate prey populations in the ecosystem. As top predators/apex predators they feed on ungulates zebra, wildebeest and gazelles to control their

population and allow balance in the ecosystem (Karant & Chellam, 2009). In addition, they function as umbrella species, i.e., their protection will support protection of other carnivore species with similar home range requirements (Kerley *et al.*, 2003). Economically, they provide foreign currency through trophy hunting and eco-tourism as important tourist attractions in many countries (Lindsey *et al.*, 2007). Despite their importance lions' population has continued to decline due to trophy hunting, poaching, habitat loss and retaliatory killing (Ray *et al.*, 2005). Retaliatory killing is the major threat of lion population in TME, where it is linked with seasonality as lions migrate to communal areas in wet seasons following prey migrations (Kissui, 2011; Koziarski *et al.*, 2016).

Therefore, this study examined the effect of retaliatory killing on the coalitions of male lions and their effect on the lion population. Moreover, the study provided baseline data on the distribution of the coalitions, in the prides their turnover rate after residing in a pride (tenure period). Furthermore, community assessment provided information on the awareness and attitude of the local community within TME on the effect of retaliation to lion population. In addition, the study has also provided information that will help protected area management to improve their strategies for lion conservation in the landscape.

1.7 Delineation of the Study

This study has provided the spatial distribution of male lion coalitions in TME and examined the effect of retaliation on coalition size and tenure period. Also, community attitude towards retaliation effect on lion. Findings of this study concentrated on examining retaliation effect on lions only.

CHAPTER TWO

LITERATURE REVIEW

2.1 Lion Ecology, Distribution and Conservation Status

Lions are social felids, living in groups called prides that include two to eighteen related females and a coalition of one to seven males (Bygott *et al.*, 1979). Females live in a pride for communal rearing of offspring and males form a coalition to ensure protection, maximum reproduction, and hunting success (Bygott *et al.*, 1979; Pusey & Packer, 1997). The gestation period of female lion is approximately 110 days where they give birth from one to six litters. Female lions have adapted to synchronous cubs rearing where they most often give birth at the same time and assist each other in rearing of the cubs when some go out to hunt (Bertram, 1973; Packer & Pusey, 1987). The survival rate of the cubs to independent age is influenced by number of individuals both female and male in a pride, location of the pride, availability of resources such as prey population, water source and threats (Mosser, 2008; Mosser & Packer, 2009). Lion's life span ranges from 8 to 12 years in the wilderness, while those in captive, zoo may reach 15 years and above. Within the ecosystem, African lion is among keystone species that regulate the population of herbivores; wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*). Their continuous decline pose a threat to the proper functioning of the ecosystem structure (Sargent *et al.*, 2021). Lions feed on a broad range of prey species between habitats depending on the most common and locally available herbivore (Hayward & Kerley, 2005). They feed on medium size species (100-300 kg) zebra, wildebeest, kudu (*Tragelaphus strepsiceros*) to large species (average 400+ kg) buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*) and hippopotamus (*Hippopotamus amphibius*), also lions feed on small species such as warthog (*Phacochoerus africanus*) (Scheel, 1992; Scheel, 1993). Prey preference by lions may also be influenced by abundance of prey species, size of the prey, temporal and spatial distribution of prey, defense and anti-predatory tactics. Moreover, environmental factors such as vegetation height, time of the day, terrain, may all affect the hunting success and therefore prey preference of lions (Funston *et al.*, 2001; Hopcraft *et al.*, 2005).

Historically, lions occurred throughout the world in Africa, Europe, Middle East and South west Asia with the exception of the desert areas and in moist rainforest (IUCN, 2006). Currently, lions are found mostly on the southern part, eastern parts and some western part of Africa (IUCN, 2006; Riggio *et al.*, 2013; Bauer *et al.*, 2015). Lions are found in protected areas

and in some countries like Tanzania exist also, in open unprotected areas (IUCN SSC Cat Specialist Group, 2018). The current lion population lies between 20 000 to 30 000 exclude lions in breeding farms and in zoos found mostly in South Africa, hence are listed as vulnerable species under IUCN Red list (IUCN SSC Cat Specialist Group, 2018). Current population has been influenced by a number of threat include increase in human population that result in settlement expansion of lion habitat, that goes along with increase in livestock and agricultural activities (Lindsey *et al.*, 2006; Loveridge *et al.*, 2010; Loveridge *et al.*, 2016). These increase in human intervention has led to continuous habitat loss for lions, population fragmentation and accelerated human-lion conflict that result to lion poisoning, shooting, trapping and retaliation.

2.2 Lion Habitat Selection and Home Range

Species habitat selection varies widely depending on the availability of resources: water, forage, shelter and competition (Hopcraft *et al.*, 2005). Lions are most active at night and live in a variety of habitats but prefer grassland, savanna, dense scrub, and open woodland. They have a strong site fidelity throughout their lifetime and prides do occupy the same range of habitat over several generations and may change slightly their habitat depending on the seasons, availability of prey abundance and threat (Patterson, 2014). In Tanzania, where lions occurs both in protected areas and outside, selection of their habitat and home range varies from prey abundance, prey density, hunting efficiency and anthropogenic pressure (Hopcraft *et al.*, 2005; Valeix *et al.*, 2012). Selected habitats are defended through roaring, patrolling and scent marking. In Serengeti larger pride where found to occupy higher quality habitat with adequate resources, water and prey species (Sargent *et al.*, 2021). Lions found in TME have their prides disperse in a wide range of habitat, some prides are situated at the midst of the park while some are at the periphery (Kissui, 2004). Usually, in dry seasons prides located in both midst and periphery of the park their prey are: wildebeest, zebra, buffalo (Kissui & Packer, 2004). In wet seasons prides at the periphery of the protected areas tend to migrate into communal areas where people have their settlement. These prides change their home ranges while following the migrating herds of wildebeest and zebra in turn end up attacking livestock. For prides in the midst of the park switch to hunt warthog (Scheel & Packer, 1991) due to scarcity of preferred prey.

2.3 Male Lion Coalition and Retaliation

Male lions in larger coalitions have a competitive advantage to defend their territories against incoming intruders, enhance their survival and reproductive success compared to single males or those in small groups (Packer & Pusey, 1982; Zabel *et al.*, 1992). In Serengeti National Park, Tanzania, coalitions with large numbers of males had longer tenure in a pride, the survival chances of their cubs were higher and the possibility of dominating a large number of prides was higher compared to smaller coalitions (Bygott *et al.*, 1979). Other than mates and territory, the coalition also provides group protection and advantages in food acquiring (Mosser *et al.*, 2015). Therefore, group size within coalitions determines the strength of the coalition (Mosser & Packer, 2009).

Generally, the lion population declining, is due to an increase in human population causing habitat destruction and fragmentation, which reduces connectivity and increase isolation of the populations (Riggio *et al.*, 2013). Thus, remaining lion populations are restricted to small and isolated protected areas, where, despite concerted protection, they are subject to unusually high mortality due to close interactions with people adjacent to protected areas (Kolowski & Holekamp, 2006). Studies conducted in West Africa showed a linear relationship between the loss of livestock and lower lion populations due to retaliatory killing of lions (Trinkel & Angelici, 2016). Furthermore, a decline of prey abundance forced lions to disperse out of protected areas and depredating on livestock, which led to lions being speared and killed by the pastoral communities living adjacent to the Amboseli National Park (Frank *et al.*, 2006). In Hwange National Park, Zimbabwe, about 88% and 67% mortality rates of male and female lions, respectively, were caused by humans (Loveridge *et al.*, 2016).

2.4 Human-Lion Conflict and Community Understanding on Retaliation Effects

The increase in human population has led to progressive exploitation of natural resources, into agricultural fields, industries and settlements that have decreased habitats for carnivores and their prey species (Karant & Chellam, 2009; Morrison *et al.*, 2007; Ripple *et al.*, 2014). Lions, among those predators that face continuous habitat loss of their home range, have most often interacted with pastoral communities (IUCN, 2006; Riggio *et al.*, 2013). These interactions have led to an adverse impact to the communities as they kill livestock and cause injuries/death to people (Loveridge *et al.*, 2010; Dickman *et al.*, 2014). Losses of property and an associated reduction in family wealth caused people to retaliate by killing lion or any carnivore that was

perceived to cause the loss (Packer *et al.*, 2005; Woodroffe *et al.*, 2005; Kissui, 2008). These retaliatory killings have been shown to threaten the persistence of carnivore populations (Woodroffe & Frank, 2005).

In northern Tanzania, particularly Maasai steppe, has large carnivore populations, which include spotted hyena (*Crocuta crocuta*), African wild dog (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*) as well as natural prey. This area is also known as a potential strong-hold of lions (Riggio *et al.*, 2013). The pastoral community lives in close proximity to the protected areas (Okello *et al.*, 2014). Recent increases in the pastoral population has led to restrictions of wildlife movements and threatened their persistence (Nyahongo, 2007). Prey species such as zebra (*Equus quagga*) and wildebeest (*Connochaetes taurinus*) have seasonal migration routes in the Maasai steppe, where open areas have become dominated by human settlements (Kiffner *et al.*, 2016). Most often, large carnivores such as hyena and Lion (*Panthera leo*) follow the migratory prey and come into contact with human and livestock (Koziarski *et al.*, 2016), which results in livestock depredation and threats to humans, which influences their negative attitude (Hazzah *et al.*, 2009; Romañach *et al.*, 2007). While these conflicts are known, few studies have investigated how retaliatory killing impact the social structure of lions and, especially, the male coalitions, which determine the survival of the population.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

This study was conducted in the Tarangire-Manyara ecosystem as shown in Fig. 1, with an estimated area of 35 000 km² in Northern Tanzania, covering two National Parks, several game reserves, game controlled areas and villages (Prins, 1987). About 10% of the TME is covered by Tarangire (2800 km²) and Manyara (330 km²) National Parks (TNP and LMNP, respectively), which have an average elevation of 950-1500 m.a.s.l, average annual temperature and rainfall of 25°C and 650 mm, respectively (Borner, 1985). About 575 371 people live in Monduli and Babati districts, mostly Maasai communities involved in pastoralism and subsistence agriculture, with a 4.7% and 4.5% population growth rate, respectively (Tanzania Population and Housing Census, 2012). This increase in human population has led to expansion of agricultural fields and livestock numbers (Kiffner *et al.*, 2016). The ecosystem is characterized by an arid woodland savannah climate, dominated by Acacia (*Acacia tortillis* and *Commiphora schimperi*), baobab trees especially in Tarangire National Park. Other vegetation type include riverine grassland, grassland (*Digitaria macroblephara* and *Panicum coloratum*), bushland (*Acacia stuhlmannii* and *Acacia drepanolobium*) and Euphorbia spp (Kahurananga, 1979; Borner, 1985). Tarangire-Manyara Ecosystem (TME) has two major seasons dry that ranges from June to October and wet season from November to May. In dry seasons the ungulate remain within the protected areas, while in wet season wildlife; wildebeest, zebra, hartebeest and fringe eared oryx migrate from the National park to the adjacent dispersal areas for grazing and calving (Kahurananga & Silkiluwasha, 1997).

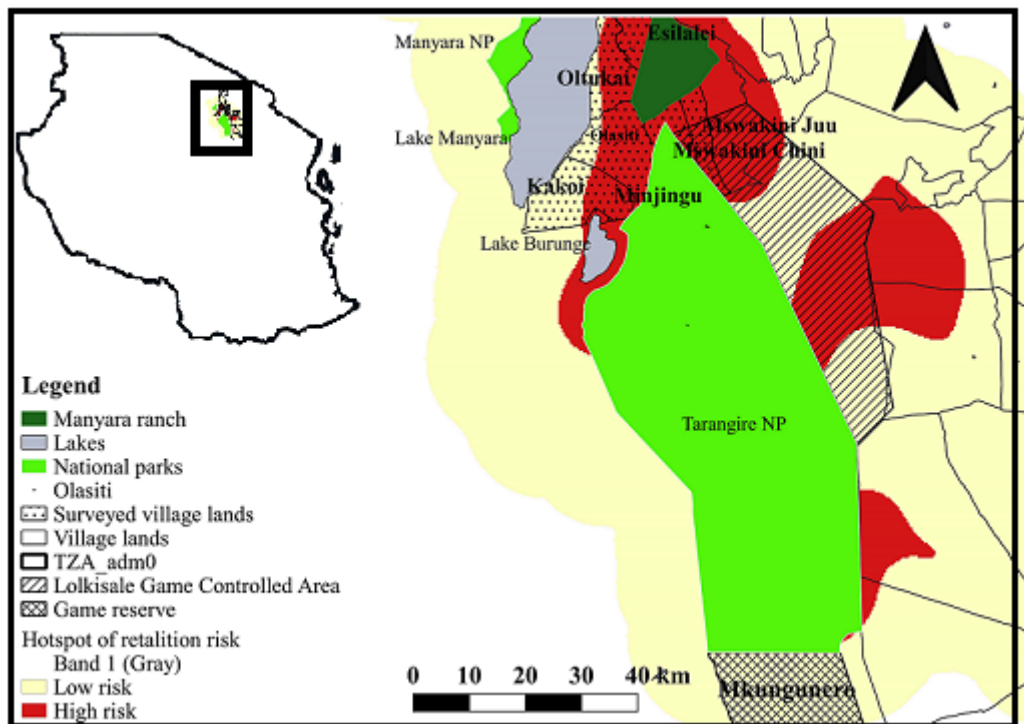


Figure 1: Map of the Tarangire-Manyara Ecosystem with the surveyed villages, hunting blocks and villages with high and low retaliation risk based on retaliatory killing data collected over the years 2004 to 2018 by TLP

3.2 Data Acquisition and Field Protocols

Lion datasets were obtained from long-term lion monitoring studies 2004 to 2018 of the Tarangire Lion Project (TLP). The lion population has been studied continuously since 2004 in 35 000 km² of the TME (Kissui, 2011; Kissui, 2013; Kissui, 2015). The number of lions in the core study area has been fluctuating around 160-200 individuals (unpublished data). In this study, data from 10 prides were used, which had been monitored for 14 years. For each pride, one to two individuals (in most cases females) were fitted with a Very High Frequency (VHF) collar to track and locate lions for direct field observations (Scheel & Packer, 1991; Noon, 2017). Very High Frequency (VHF) collar with Nyloc nuts and bolts are high tech collars equipped with radio transmitters to track animals' movements and understand their territories, home ranges and predator prey interaction. During the process of fitting a collar to a lion, a female lion aged 5 to 6 years is selected from individuals in a pride that will be immobilized and fitted the collar. Prior to fitting the collar to the lion, the radio transmitter is set to the frequency that the collar has and tested for its efficiency. The radio transmitter is required to emit frequency of up to 5 km away to enable tracking and locating the collared lion. The collaring process is done by a veterinary doctor who is responsible to immobilize the lion using

sedative and ensure safety of the lion and the rest of the team before beginning collaring work. After fitting the collar, the lion is given antidote and the vet monitors its progress until it awakes and able to move and meet with the rest of the pride.

3.2.1 Mapping Male Lion Coalitions

Spatio-temporal dynamics of male lion coalitions found in TME were assessed from movement data of ten prides from 2004 to 2018. For each sighted coalition Global Positioning System (GPS) coordinates were recorded and individual males identified. A total of 553 lion sightings were obtained with coalition that had at least 5 sightings within prides. These were used for mapping pride locations overlaying male coalitions with village surrounding protected areas using QGIS version 3.13.

3.2.2 Retaliation Effect on Male Lion Coalitions

Data of 46 male coalitions were extracted from TLP long-term data set of lion monitoring collected for 14 years to examine the effect of retaliation on male lion coalition. All 46 male coalitions were used in order to have a good representation of the sample population and increase accuracy of the findings. From the dataset, the number of males in a coalition group and their tenure period were recorded. Each coalition group was observed from when it was first sighted within a pride until when it was evicted by other males, i.e., the tenure period. The location of male coalition was considered as whether they were inside the protected areas (core) or had migrated into surrounding unprotected areas (periphery). Moreover, some areas where hunting block for trophy hunting thus, some coalitions were considered to be in or adjacent to active hunting blocks. Therefore, the following environmental variables were used in the model to predict the male coalition size and tenure period for male coalition found (i) in core or periphery of the protected areas and, (ii) in high retaliation risk or low retaliation risk village land, as well as (iii) in or adjacent to hunting blocks.

Table 1: Description of variables included in the analysis of the factors influencing retaliatory killing on male coalition in TME

Variable	Explanation
Protected area	Location in the core part of the protected area, midst or periphery
Retaliation risk	Location close to (< 5 km) or far (> 5 km) from villages that had record of retaliation
Male numbers	Number of male lions in a coalition group
Hunting location	Location within active hunting blocks (yes or not)
Tenure period	Duration a coalition group is resident in a pride

3.2.3 Community Perceptions on the Effect of Retaliation to Lion Population

A survey of seven villages was done to assess community awareness on the effect of retaliation to lion population from March 2019 to May 2019. Villages were selected based on the frequency of retaliation risk (Appendix 3). Semi-structured questionnaires were used to 214 households. Systematic sampling technique was used in choosing an interviewee, in which every sixth household head in each sub-village was interviewed (Muriuki *et al.*, 2017). Criteria of inclusion in the interview were: a) the household head had lived in the village for more than five years and b) was an adult of ≥ 18 years. Additionally, key informant interviews were conducted with rangers from Tarangire National Park, Burunge Wildlife Management Area, and Manyara Ranch. Key informants' interviews were conducted to people with the knowledge of lion retaliation, aiming to get an in-depth understanding of incidences of lion killing and preventions. Interviews and questionnaires aimed at determining peoples' perception towards wildlife challenges and retaliatory killing incidences that occurred over the last five years. The questionnaire was piloted and tested with 10 individuals living in TME in February, 2019. The questionnaire was in English and translated into Swahili or Maasai language by a translator. People's knowledge was investigated on the status of lion population, recent lion attacks and retaliatory killing events. The questionnaire had four parts; the first assessed socio-demographic information of the respondent (age, occupation, sex, education, resident time and benefits from conservation), the second part consisted of respondent awareness on wildlife related challenges and ranking of the problem animals, the third part assessed awareness, knowledge and effectiveness of measures used to protect livestock, and the last part assessed the respondent's attitude and perception towards lion populations, their trends, effect of

retaliatory killing on the TME lion population and reports of lion killings in the past three years (Appendix 4).



Figure 2: Interviewing villagers from March to May 2019 in TME

3.3 Data Analysis

Data analysis was performed in R version 3.6.3 (R coreTeam, 2014) where descriptive statistics of male coalition size and tenure period as response variable were calculated. In testing for normality of the response variables, data were not normally distributed hence Generalized Linear Model (GLMM) with a Poisson family of distribution was used. For each response variable prior candidate models were constructed and tested using GLMM with Poisson distribution. To determine whether predictor variables of retaliation risk, location in protected area (PA), and closeness to a hunting block significantly influenced response variables. Interaction of the predictors; retaliation risk, location in PA, and hunting block on number of males in a coalition and tenure period respectively were considered. For each response variable seven priori candidate models were created and models with the lowest AICc and highest Akaike weights (ω_i) values as the best approximating model in the set of candidate models (Anderson & Burnham, 2002). Models with $\Delta AICc < 2$ had strong support and represented a confidence set of the best model, while $\Delta AICc$ values of > 2 showed weak support (Anderson & Burnham, 2002).

On understanding community attitude towards effect of retaliation to lion population data were tested for collinearity on each variable using corrplot package and usdm package in R version 3.6.3 (Appendix 1). From each question, prior candidate models were constructed from response variables identified. Data of the response variables were not normally distributed and, hence, GLMM with a Poisson distribution was used to analyze the variation of community attitude towards the effect of retaliatory killing on the lion population. All statistical tests were two-tailed with a 5% level of significance.

Table 2: Predictor variables used in the analysis of generalized linear mixed model to understand community attitude towards the effect of retaliatory killing on lion population in TME

Predictors	Explanations
Occupation	Agro-pastoralist, pastoralist, farmer, business owner, employee
Age class	18-35 years, 36-45 years, 46-55 years, >55 years
Sex	Male, female
Education	Illiterate, primary, secondary, tertiary
Resident time	5 years, 5-15 years, >15 years
Benefit	Employment, business opportunity, community development, no benefit

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1 Results

4.1.1 Spatio-Temporal Dynamics of Male Lion Coalition

A total of 113 individual males were identified across 10 prides that belonged to 46 different coalitions. These male coalitions had their life history recorded from when they started being with the pride until last seen, hence obtained the months a coalition lasted with the pride (Appendix 2). These numbers excluded the nomadic males that were sighted only once with the prides. On average 2 males older than 4 years of age formed coalitions in prides. During the study period, the largest coalition group had 5 males.

Figure 3 shows the male coalition groups mapped on different prides in Tarangire National Park (TNP). Some coalitions in a pride are found in the midst of the park include; Kuro, New Tarangire hill, Old Silale, and Silale Minyonyo while some at the periphery such as Altipiano, Boundary hill, New Silale, New Wazi, Tarangire hill and Wazi where they are close hunting block of Lolkisale Game Controlled Areas (GCA) and to village settlement hence are at a risk of retaliation.

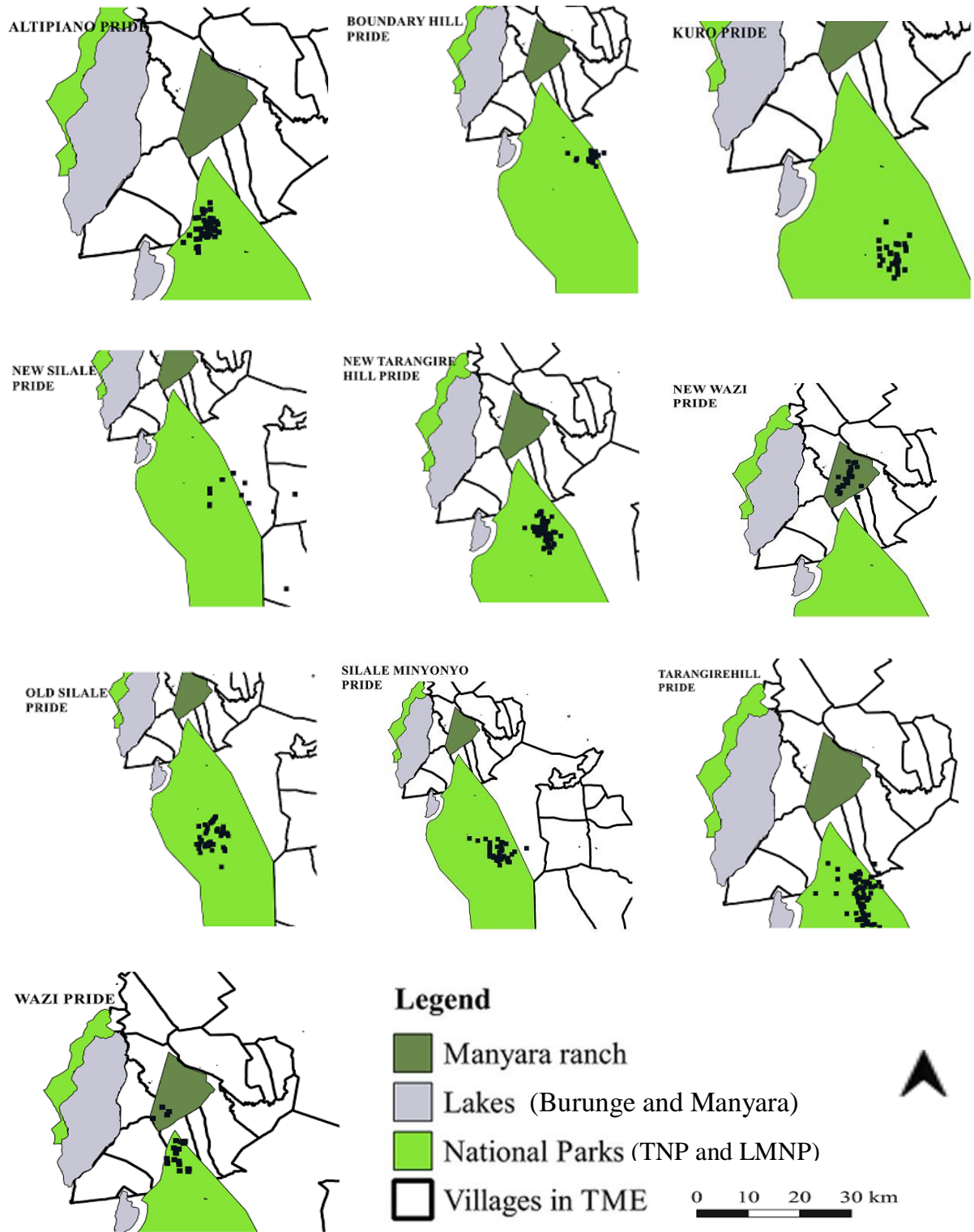


Figure 3: Maps showing spatial distribution of male lion coalitions and village surrounding the protected areas of the study site in TME based on data collected from 2004 to 2018

4.1.2 Effect of Retaliatory Killing on Male Lion Coalition

(i) Effect of Retaliatory Killing on Male Lion Coalition Size

Male coalitions in areas with high retaliation risk had smaller group sizes with few individuals. In Table 3, the $\Delta AICc$ revealed that models 2 and 3 had values <2 , thus constituting the confidence set of the best model. The Akaike weights (ω_i) showed that the best model was only slightly (1.1 times) as likely as model 2 and 3. These two models showed that if the coalition was in the periphery of the protected area and within a hunting block as well as in a village with high retaliation frequencies the coalition size was small, while male coalitions inside the PA core part were larger. Candidate models consists of coalition ID as random effect. df: degree of freedom; AICc: Akaike's Information Criterion corrected; $\Delta AICc$: difference in AICc values between the best performing model and the model of interest; ω_i : Akaike model weights.

Table 3: A priori generalized linear mixed models representing the effect of retaliatory killing on coalition size in TME

S/N	Candidate models	df	AICc	$\Delta AICc$	ω_i
1.	Retaliation risk	43	151.5	0.00	0.28
2.	Hunting location	43	151.9	0.53	0.22
3.	Protected area location	43	152.0	0.56	0.21
4.	Hunting location, retaliation risk	42	153.7	2.32	0.09
5.	Protected area location, retaliation risk	42	153.8	2.40	0.08
6.	Protected area location, hunting location	42	154.3	2.89	0.06
7.	Retaliation risk, hunting location, Protected area location	41	156.2	4.83	0.02

(ii) Effect of Coalition Size, Lion Hunting and Retaliation on Coalition Tenure Period

The average ($\pm SD$) tenure of a coalition group within a pride was (19.9 ± 15.4) months and was strongly related to the number of males and the location of the coalition. Larger coalitions located far away from areas with high risk of retaliation had a longer tenure period than those close to high retaliation risk areas. In GLMM, $\Delta AICc$ revealed that models 2, 3 and 4 had values <2 (Table 4), thus constituting the confidence set of the best model. The Akaike weights (ω_i) showed that the best model was only 2.2 times as likely as models 2, 3 and 4 (Table 4).

From model 5 interaction of the variables revealed no effect on tenure period. Thus, number of males, PA location and retaliation influence the time period a coalition last in a pride (Table 5). Candidate models consists of coalition ID as random effect; df: degree of freedom; AICc: Akaike’s Information Criterion corrected for small sample size (n=46); Δ AICc: difference in AICc values between the best performing model and the model of interest; ω_i : Akaike model weights (Commas separate independent factors while * denotes interactions).

Table 4: Candidate models under generalized linear mixed models for determining the effect of retaliatory killing on the tenure period of male coalitions in TME

S/N	Candidate Models	df	AICc	Δ AICc	ω_i
1.	Male numbers, PA location	42	351.0	0.00	0.21
2.	PA location	43	351.1	0.12	0.20
3.	Male numbers	43	351.3	0.38	0.17
4.	Retaliation risk	43	351.8	0.84	0.14
5.	Male numbers*retaliation risk, PA location	40	352.8	1.84	0.08
6.	Male numbers, PA location, retaliation risk	41	353.0	2.09	0.07
7.	Male numbers, PA location, retaliation risk, hunting location	40	355.7	4.71	0.02

Table 5: Parameter estimates and 95% confidence intervals (CI) of the top-ranking model for the effect of retaliatory killing on the tenure period of male coalition in TME

Parameter	Estimate	SE	Lower CI	Upper CI	P
Male numbers	0.13	0.08	-0.03	0.31	0.236
PA location	-0.34	0.20	-0.75	0.06	<0.001
Retaliation risk	0.34	0.21	-0.09	0.77	0.221

4.1.3 Community Awareness and Attitude on the Effect of Retaliatory Killing to Lion Population

A total of 214 respondents were interviewed from the selected villages based on the data of lion retaliation collected from 2004 to 2018 (Appendix 3).

Table 6: A descriptive statistics of the data obtained from the interviews conducted in villages surrounding TME

Variable	Summary description of the variables	
Gender	Male	45%
	Female	55%
Age	Mean	40
Resident time	Mean	16
Occupation	Agro-pastoralist	89%
	Employees	5%
	Farmers	3%,
	Business	2%
	Pure pastoralist	1%
Education	Illiterate	44%
	Literate	56%
Benefit from conservation	Community development	50%
	No support	43%
	Employment	5%
	Business	3%

(i) Community Awareness on Effect of Retaliation to Lion Population

A total of 12 lions were recorded to be killed as a revenge for livestock depredation over the last three years (July 2016 to May 2019). In addition, 15 attempts to kill lions had been organized by pastoral communities but had been unsuccessful because of intervention from local government leaders, conservation officers from the National Park Authorities, Wildlife Management Areas (WMA), and Non-Governmental Organizations (NGOs). About 55% of all 214 respondents acknowledged that retaliatory killing has negative effects on lion populations while 43% suggested that it has no effect. Key informants suggested that human-lion conflict has decreased due to increase in human population into migratory areas of the wildlife, blocking migration corridors. Moreover, they claimed that lion killings conducted in the villages adjacent to the national parks over the past five years have led to a general decline in the lion population.

(ii) Attitude Towards Lion Presence

Almost three quarters (72%) of all (n = 214) respondents from villages of both high and low retaliation frequencies had a positive attitude towards lion existence, while 28% had a negative attitude and did not wish lions to exist. Out of the former, 116 acknowledged that wildlife (lions) has led to natural resource protection and increased cultural tourism activities within their villages. The remaining 38 respondents had a positive attitude but suggested that wildlife should be restricted to protected areas and not allowed to migrate into villages.

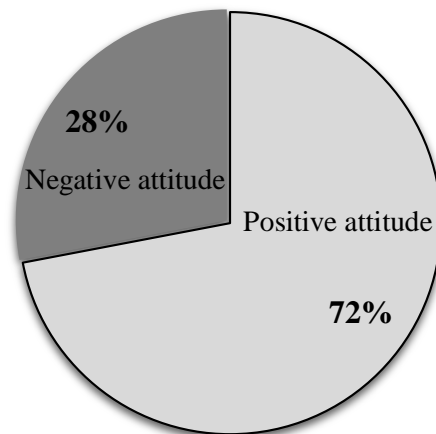


Figure 4: Percentage of the respondents with positive attitude and negative attitude towards lion presence in TME

A priori generalized linear mixed models for whether lions have the right to live or not (Table 7). Candidate model consist of village ranks as random effect, df: degree of freedom; AICc: Akaike's Information Criterion corrected for sample size (n = 214); Δ AICc: difference in AICc values between the best performing model and the model of interest; ω_i : Akaike model weights. Younger respondents of 18-35 years old and 36-45years, which were almost half of the interviewee 49% (n = 116) had positive attitude towards lions (Estimate = 0.87, SE = 0.43, Z = 2.02, p = 0.04). Also, people that had no formal education were more positive towards lions than those with primary or secondary education (illiterate: Estimate = 0.34, SE = 0.32, Z = 1.06, p = <0.001; primary: Estimate = 0.03, SE = 0.34, Z = 0.11, p = 0.909; secondary: Estimate = 1.44, SE = 0.68, Z = 2.1, p = 0.035).

Table 7: Candidate models under generalized linear mixed models for whether lions have right to live or not in TME

S/N	Candidate models	df	AICc	Δ AICc	ω_i
1.	Age class, education	4	254.2	0.00	0.18
2.	Benefit	3	254.3	0.11	0.17
3.	Occupation	3	254.8	0.54	0.14
4.	Benefit, occupation	4	255.0	0.83	0.12
5.	Education, age class, sex	5	256.0	1.82	0.07
6.	Age class, sex	4	256.2	1.98	0.06
7.	Education, occupation	4	256.2	2.03	0.06
8.	Resident	3	256.8	2.58	0.05
9.	Education	5	257.1	2.9	0.04
10.	Resident, age class, sex	5	258.2	3.97	0.02
11.	Education, occupation, resident	5	258.3	4.12	0.02
12.	Age class, education, benefit, occupation, sex, resident	8	259.5	5.33	0.01

(iii) Human and Livestock Attacks by Lion and Lion Killing

Respondents mentioned that six lion attacks on seven people had occurred from July 2016 to May 2019, all of which happened in bushy areas and close to the protected area border. Moreover, 20 attacks on 64 individual livestock (51 cattle, 8 sheep, and 5 goats), had been reported within the last 3 years by interviewees. Of all respondents, 45% (n = 96) claimed that livestock depredation was the second most common cause of livestock loss after diseases, followed by drought. More than half (55%, n = 118) of the respondents suggested that lions and other carnivores should be killed when they attack livestock or humans and 50% (n = 117) suggested that not only lions but any wildlife that causes damage should be killed, while 45% claimed that lions should be translocated to other areas in these cases. Most community members 42% (n = 90) are highly dependent on livestock as their source of income and they claimed that the loss of livestock by a predator threatened the family status and income. Some (15%, n = 96) respondents suggested that lion attacks on livestock had decreased while those

caused by hyena (*Crocuta crocuta*) had increased while the remaining 85% claimed that livestock attacks by lions have increased.

From Table 8, were priori generalized linear mixed models for whether lions should be killed due to livestock depredation constructed. Candidate models consists of village name as random effect; df: degree of freedom; AICc: Akaike's Information Criterion corrected for small sample size; Δ AICc: difference in AICc values between the best performing model and the model of interest; ω_i : Akaike model weights. The GLMM reveals that education levels significantly determined whether respondents wanted lions to be killed in return for their attacking livestock. Respondents with primary and secondary level of education were less tolerant towards livestock losses by lion compared to those without any formal education. (Primary: Estimate = -0.68, SE = 0.30, Z = -2.25, p= 0.024; Secondary: Estimate = -0.92, SE = 0.46, Z = -1.98, p = 0.046; Illiterate: Estimate = 0.58, SE = 0.21, Z = 2.78, p = <0.001).

Table 8: Prior candidate models under generalize linear mixed models for whether lions should be killed due to livestock depredation in TME

S/N	Candidate models	df	AICc	Δ AICc	ω_i
1.	Education	3	293.8	0	0.29
2.	Benefit	3	294.1	0.27	0.25
3.	Education, occupation	4	295.7	1.88	0.11
4.	Benefit, occupation	4	296.0	2.15	0.10
5.	Occupation	3	297.1	3.25	0.05
6.	Resident	3	297.4	3.55	0.04
7.	Education, occupation, resident	5	297.6	3.74	0.04
8.	Education, age class, sex	5	297.6	3.75	0.04
9.	Age, sex	4	299.6	5.74	0.01
10.	All	8	300.6	6.79	0.00
11.	Resident, age class, sex	5	301.3	7.48	0.00

4.2 Discussion

4.2.1 Spatio-Temporal Dynamic of Male Lion Coalition

Human-carnivore conflict represents a universal problem that is negatively impacting lion (*Panthera leo*) populations and local livelihoods (Constant *et al.*, 2015; Morrison *et al.*, 2007; Ripple *et al.*, 2014). From the study male lions were dispersed around the TME. Some dominated prides whose home range were at the midst of the park, hence were least affected by retaliation and the coalition groups within the pride lasted longer, example New Tarangire hill pride. While other coalitions are at the periphery with few coalitions that had short tenure period, example Altipiano pride. Findings of the number of males in a coalition and their tenure period can be found in Appendix 2 which is showing the time period a coalition lasted in each pride.

4.2.2 Effect of Retaliation and Lion Hunting on Coalition

(i) Effect of Retaliation and Lion Hunting on Coalition Size

Results from the study showed that male coalitions located in the periphery of the protected area, close to villages with high retaliation risk and in active hunting blocks of Lolkisale GCA had small coalition sizes as seen in prides altipiano, kuro, boundary hill, new silale, new wazi, tarangire hill and wazi (Appendix 2). In TME, lions migrate into communal areas, following migrating ungulates such as wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) during wet season (Kiffner *et al.*, 2016; Kissui, 2008). Hence, they spend about 6 months outside of protected areas and become vulnerable to retaliation due to livestock predation.

In accordance with Whitman *et al.* (2004), the study found that coalition sizes are negatively affected by lion hunting led to reducing social stability and causes cascading effect to lion abundance at large (Whitman *et al.*, 2004; Trinkel & Angelici, 2016; Yamazaki, 1996). This aligns with the hypothesis that male coalitions close to hunting blocks and villages with high retaliation risk would be small. With respect to male coalition responsibility in prides, small coalition groups are at risk of not ensuring protection against intruders and persistence of the pride. This increases the risk of pride take over by other intruder males in areas where male competition is high (Bygott *et al.*, 1979). Not only local hunting might reduce lion fitness, in Zimbabwe the lion population outside Hwange National Park faced a continuous decline due to trophy hunting (Loveridge *et al.*, 2007). In northern Tanzania, trophy hunting around

Serengeti and Ngorongoro Conservation Area, showed to have devastating impact on lion population (Whitman *et al.*, 2004; Creel *et al.*, 2016). Therefore, lion hunting affect coalition sizes, leading to few coalition groups with few individuals that reduce social stability within a pride and affecting lion abundance at large.

(ii) Influence of Coalition Size and Location on Tenure Period

Findings of the study showed that tenure period of male coalitions depends on the number of males in a coalition and its location in a protected area, as predicted by the study expectation. Prides in the periphery with coalition size of two males had a short tenure period less than 12 months due to retaliation and hunting. While, prides in the midst of the protected areas with similar coalition size or even singleton, lasting more than 12 months likely due to absence of human disturbance. This is similar to studies conducted in northern Tanzania (Bygott *et al.*, 1979; Pusey & Packer, 1997) where large coalition groups had a significant advantage of having longer tenure period within prides, also ensuring pride and offspring survival. Male coalitions will remain longer in a pride of females located in areas with adequate habitat quality, prey abundance and water sources (Personal Observation). In Zambia, at Kafue National Park, both female and male lions that had their home range closer to the border of the park disappeared due to trophy hunting and retaliation (Becker *et al.*, 2012; Midlane, 2013) supporting the study results of reduced coalition size and tenure period at the periphery.

4.2.3 Community Attitude and Awareness on the Effect of Retaliatory Killing to Lion Population

(i) Community Awareness on Effect of Retaliation to Lion Population

From the study lion retaliation incidences had declined during the study period by 2019. In recent years, more attempts of retaliation had been stopped through the cooperation of government officials and NGOs, who received information from local government leaders and informers living in the village areas (pers. comm). This agrees with Mkonyi *et al.* (2017b) that fewer cases of livestock predation by lions had led to little involvement of people to retaliate or kill lions. Moreover, in TME studies about lions have increased recently and led to broadened knowledge of the study population (Mkonyi *et al.*, 2017b; Eustace & Tarimo, 2018; Kissui *et al.*, 2019; Beck *et al.*, 2020).

(ii) Attitude Towards Lion Presence

From the study attitudes of the local community towards carnivores, in particular lions, were positive as long as lions stayed away from human settlements. Results showed that younger people had a more positive attitude towards lions, as do the illiterate people. This is contrary to the study expectation, and what has been reported by other studies as well. In TME knowledge of wildlife conservation is taught to young Maasai warriors while they are in primary and secondary schools (Mkonyi *et al.*, 2017a). Although this is the case but most of the young people feel that they have not being given opportunities to participate in resolving conflicts of livestock attacks which might led to their negative attitude.

Training and having young people as local guards to protect livestock from wildlife attacks in communal areas, will assist to resolve human-lion conflict and raise positive attitude as observed in Lion Guardian and Ruaha Carnivore project (Hazzah *et al.*, 2014). This engagement aimed to increase benefit that communities directly receive from conservation include employment and to raise tolerance level of livestock loss by lions (Dickman *et al.*, 2014; Mkonyi *et al.*, 2017a; Treves & Karanth, 2003). From the study people who lived in TME for ten years and above adopted measure to coincide with wildlife by improving their livestock enclosure with chain-link fence and using adult herders when grazing livestock in identified risk areas (Mkonyi *et al.*, 2017b).

Over the last three years key informants reported an increase in positive attitude towards lions' conservation. This had been observed with increase in women groups that were engaged in cultural tourism which promote their income and positive attitudes. In northern Tanzania, around TME livestock losses influence negative attitude and perception while employment opportunities in tourism activities, sport hunting stimulate positive attitude and increase tolerance level (Woodroffe & Frank, 2005; Kissui, 2008). This aligns with findings from this study where people understood the importance of wildlife and associated benefits but still wishes wildlife to be controlled and remote from humans.

(iii) Human and Livestock Attack by Lion and Lion Killing

From the study lions attacks on livestock occurred mostly in the bush/grazing areas that were proximity to park boundaries while attacks by hyena (*Crocuta crocuta*) were common in the enclosures/boma which is similar to what was reported by Kissui (2008), Mponzi *et al.* (2014) and Mkonyi *et al.* (2017b). Moreover, during rainy seasons were conflict between human and

lion occurs often due to seasonal migration of carnivores and ungulates, can be anticipated and measures taken to reduce livestock loss and retaliation of lions. The use of participatory approach measure will assist to increase tolerance level of the community with primary and secondary education on losses of livestock by lions or any carnivore as they will learn ways to protect their livestock and increase their knowledge. Approaches such as regular monitoring the locations of lions, particularly when they roam outside of the parks and conducting frequent patrols in the identified conflict hotspot areas. These activities can help alerting communities on the presence of predators in their settlements in order to increase vigilance by both protected area officers and community members for protecting lions and livestock.

CHAPTER FIVE

CONCLUSION AND RECOMMENDATIONS

5.1 Conclusion

This study has identified hotspot areas where lion retaliation occurred over the past fourteen years and set these hotspots in relation to environmental and socio-economic factors. Findings showed that retaliatory killing negatively impacts number and tenure of male lion coalitions, which are crucial for protecting the entire lion pride and ensuring survival of the cubs. Also, small male coalitions have shorter tenure periods than larger coalitions, thus the location of a particular male coalition influences its tenure period. The study has highlighted that retaliatory killing negatively affects lion social structure as well as long-term lion survival and that awareness-raising and strategies (i.e., policies) need to be established and implemented at TME to protect the declining lion population as pointed out by Mkonyi *et al.* (2017b).

The local community around TME had little knowledge on the effect of retaliatory killings on the lion populations, depicting the need for better communication and awareness raising among local communities, conservation agencies and park management. From the study, many local communities acknowledged that the number of livestock attacks by lions had decreased over the last years, compared to other carnivore species such as hyena (*Crocuta crocuta*). Lastly, the attitude of people towards lions and other carnivores was dependent on the level of education and age, therefore, more environmental education programs, should be organized and conducted particularly to the villages around protected areas.

5.2 Recommendations

Since, this study assessed the effect of retaliation on male lion coalitions, there is a need for further investigation and monitoring to observe the trend of male coalition size and their tenure period. Because male coalitions have an essential role within a pride of ensuring the survival of lion population. Moreover, this study identified hotspot areas where retaliation risk is high, particularly close to human settlements and in hunting blocks. Therefore, this should alert protected area management, including National parks, WMAs, and NGOs, to organize and monitor lion prides continuously that have established their home range in these risk areas to prevent livestock loss to the community and lion attack. Furthermore, as suggested by Minin *et al.* (2016) that for sustainable human-carnivore (lion) coexistence a need of landscape-level

planning is inevitable, which includes identifying areas for lions, and established frameworks and policies that will secure the areas without neglecting human demands. Kissui (2008), Mponzi *et al.* (2014) and Mkonyi *et al.* (2017b) reported livestock depredation and retaliation events simultaneously occur in the wet seasons, and this study observed a similar pattern. Therefore, pro-active measures have to be prepared particularly during this season to secure and protect the declining lion population.

From the study, communities in the TME showed positive attitudes towards lions and other carnivores dependent on their level of education and age. Therefore, this study suggests more environmental education programs to be given to the communities in TME. Immediate effort should be directed to the villages that have records of high retaliation incidences. Both government and NGOs should collaborate and prepare programs that will fit different stakeholder groups in the community i.e., for young people who are attending school; environmental clubs should be active and prepare programs that involve physical activities and recreations that will attract more students to join and become future ambassadors of carnivores/wildlife in general. For adult group programs/activities have to be established, where a village will be rewarded when its people report conflict animal presence in the villages immediately.

REFERENCES

- Anderson, R., & Burnham, P. (2002). Avoiding Pitfalls when using Information Theoretic Methods. *Journal of Wildlife Management*, *66*(3), 912–918.
- Bauer, H., & Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, *38*(1), 26–31. <https://doi.org/10.1017/S0030605304000055>.
- Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T., Macdonald, W., & Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, *112*(48), 14894-14899. <https://doi.org/10.1073/pnas.1500664112>.
- Beck, J. M., Moll, R. J., Kissui, B. M., & Montgomery, R. A. (2021). Do pastoralist cattle fear African lions? *Oikos*, *130*(3), 422-430.
- Becker, S., Watson, R., Droge, E., Leigh, K., Carlson, S., & Carlson, A. (2012). Estimating past and future male loss in three Zambian lion populations. *Journal of Wildlife Management*, 1–15. <https://doi.org/10.1002/jwmg.446>.
- Bertram, C. (1973). Lion population regulation. *Ecological African Wildlife Journal*, *11* (1972), 215–225.
- Borner, M. (1985). The Increasing Isolation of Tarangire National Park. *Oryx*, *19*(2), 91–96. <https://doi.org/10.1017/S0030605300019797>.
- Borrego, N., Ozgul, A., Slotow, R., & Packer, C. (2018). Lion population dynamics: Do nomadic males' matter? *Behavioral Ecology*, *29*(3), 660-666.
- Bygott, J., Bertram, B. C., & Hanby, J. P. (1979). Coalition of male lions has a reproductive advantage. *Nature*, *282*, 839–841.
- Chakrabarti, S., & Jhala, Y. V. (2017). Selfish partners: Resource partitioning in male coalitions of Asiatic lions. *Behavioral Ecology*, *28*(6), 1532-1539.
- Constant, L., Bell, S., & Hill, A. (2015). The impacts, characterisation and management of human-leopard conflict in a multi-use land system in South Africa. *Biodiversity and Conservation*, *24*(12), 2967–2989. <https://doi.org/10.1007/s10531-015-0989-2>.

- Creel, S., M'soka, J., Dröge, E., Rosenblatt, E., Becker, M. S., Matandiko, W., & Simpamba, T. (2016). Assessing the sustainability of African lion trophy hunting, with recommendations for policy. *Ecological Applications*, 26(7), 2347-2357.
- Dickman, J. (2010). Complexities of conflict : The importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, 13, 458–466. <https://doi.org/10.1111/j.1469-1795.2010.00368.x>.
- Dickman, A. J., Hazzah, L., Carbone, C., & Durant, S. M. (2014). Carnivores, culture and contagious conflict: Multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biological Conservation*, 178, 19-27.
- Dickman, A. J., Macdonald, E. A., & Macdonald, D. W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, 108(34), 13937-13944. <https://doi.org/10.1073/pnas.1118014108>.
- Dickman, A. J. (2009). *Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania* (Doctoral Dissertation, University College London (University of London)).
- Eustace, A., & Tarimo, D. (2018). Maasai and lion killings in the Tarangire-Manyara Ecosystem. *African Journal of Ecology*, 57, 140–143.
- Frank, L., MacLennan, S., Hazzah, L., Bonham, R., & Hill, T. (2006). Lion killing in the Amboseli-Tsavo Ecosystem, 2001-2006, and its implications for Kenya's lion population. *Living with Lions, Nairobi, Kenya*, 9.
- Funston, P., Mills, M., & Biggs, H. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *The Zoological Society of London*, 253, 419–431.
- Hayward, M., & Kerley, G. (2005). Prey preferences of the lion (*Panthera leo*). *The Zoological Society of London*, 267, 309–322. <https://doi.org/10.1017/S0952836905007508>.
- Hazzah, L., Mulder, M. B., & Frank, L. (2009). Lions and warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in

- Kenya. *Biological Conservation*, 142(11), 2428-2437.
- Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C. T., Mwebi, O., Kearney, F., & Frank, L. (2014). Efficacy of two lion conservation programs in Maasailand, Kenya. *Conservation Biology*, 28(3), 851–860.
- Holmern, T., Nyahongo, J., & Røskaft, E. (2007). Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation*, 135(4), 518–526. <https://doi.org/10.1016/j.biocon.2006.10.049>.
- Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74(3), 559–566. <https://doi.org/10.1111/j.1365-2656.2005.00955.x>.
- Ikanda, D., & Packer, C. (2008). Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania. *Endangered Species Research*, 6(1), 67–74.
- IUCN. (2006). *Regional Lion Conservation Strategy for the African Lion (Panthera leo) in Eastern and Southern Africa*.
- IUCN, & Group, S. C. S. (2018). *Guidelines for the Conservation of Lions in Africa* (December).
- Kahurananga, J. (1979). The vegetation of the Simanjiro Plains, Northern Tanzania. *African Journal of Ecology*, 17, 65–83.
- Kahurananga, J., & Silkiluwasha, F. (1997). The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, Northern Tanzania, in 1972 and recent trends. *African Journal of Ecology*, 35, 179–185.
- Karanth, K. U., & Chellam, R. (2009). Carnivore conservation at the crossroads. *Oryx*, 43(1), 1-2. <https://doi.org/10.1017/S003060530843106X>.
- Kellert, S., & Berry, J. K. (1987). Attitudes, Knowledge and Behaviors toward Wildlife as affected by Gender. *Wildlife Society Bulletin*, 15, 363–371.
- Kerley, G., Pressey, R. L., & Cowling, R. M. (2003). Options for the conservation of large and medium-sized animals in the Cape Floristic Region hotspot, South Africa. *Biological*

- Conservation*, 112, 169–190. [https://doi.org/10.1016/S0006-3207\(02\)00426-3](https://doi.org/10.1016/S0006-3207(02)00426-3).
- Kiffner, C., Nagar, S., Kollmar, C., & Kioko, J. (2016). Wildlife species richness and densities in wildlife corridors of Northern Tanzania. *Journal for Nature Conservation*, 21, 1–12. <https://doi.org/10.1016/j.jnc.2016.02.006>.
- Kissui, B. (2011). *Research and conservation report*.
- Kissui, B. (2013). *Lion research and conservation*.
- Kissui, B. (2015). *Human-lion conflict mitigation in the Maasai steppe, Northern Tanzania* (June).
- Kissui, B. (2008). Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation*, 1–11. <https://doi.org/10.1111/j.1469-1795.2008.00199.x>.
- Kissui, B. M., Kiffner, C., König, H. J., & Montgomery, R. A. (2019). Patterns of livestock depredation and cost-effectiveness of fortified livestock enclosures in northern Tanzania. *Ecology and Evolution*, 9(19), 11420-11433.
- Kissui, B. M., & Packer, C. (2004). Top–down population regulation of a top predator: Lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1550), 1867-1874.
- Kissui, B. M. (2008). *Demography, Population Dynamics, and The Human-lion Conflicts: Lions in The Ngorongoro Crater and The Maasai Steppe, Tanzania* (Doctoral Dissertation, University of Minnesota, Major: Ecology, Evolution, and Behavior.).
- Kolowski, J., & Holekamp, K. (2006). Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation*, 128(4), 529–541. <https://doi.org/10.1016/j.biocon.2005.10.021>.
- Koziarski, A., Kissui, B., & Kiffner, C. (2016). Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. *Biological Conservation*, 199, 41–50. <https://doi.org/10.1016/j.biocon.2016.04.029>.
- Lindsey, P. A., Alexander, R., Frank, L. G., & Mathieson, A. (2006). Potential of trophy

- hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Animal Conservation*, 9, 283–291. <https://doi.org/10.1111/j.1469-1795.2006.00034.x>.
- Lindsey, P. A., Roulet, P. A., & Roman, S. S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, 134, 455–469. <https://doi.org/10.1016/j.biocon.2006.09.005>.
- Loveridge, A J, Searle, A. W., Murindagomo, F., & Macdonald, D. W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Science Direct*, 4, 548–558. <https://doi.org/10.1016/j.biocon.2006.09.010>.
- Loveridge, Andrew J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2016). The landscape of anthropogenic mortality: How African lions respond to spatial variation risk. *Journal of Applied Ecology*, 54(3), 815–825. <https://doi.org/10.1111/1365-2664.12794>.
- Loveridge, A. J. S. W., Wang, S. W., Frank, L., & Seidensticker, J. (2010). People and wild felids: Conservation of cats and management of conflicts. *Biology and Conservation of Wild Felids*, 161-195.
- Maddox, T. M. (2003). *The ecology of cheetahs and other large carnivores in a pastoralist-dominated buffer zone*. University of London (United Kingdom).
- Midlane, N. (2014). *The conservation status and dynamics of a protected African lion Panthera leo population in Kafue National Park, Zambia*. University of CapeTown.
- Minin, E., Slotow, R., Hunter, L., Pouzols, F., Toivonen, T., Verburg, P., Leader-williams, N., Petracca, L., & Moilanen, A. (2016). Global priorities for national carnivore conservation under land use change. *Nature*, 6, 1–9. <https://doi.org/10.1038/srep23814>.
- Mkonyi, F. J., Estes, A. B., Msuha, M. J., Lichtenfeld, L. L., & Durant, S. M. (2017). Local attitudes and perceptions toward large carnivores in a human-dominated landscape of northern Tanzania. *Human Dimensions of Wildlife*, 22(4), 314-330.
- Mkonyi, F. J., Estes, A. B., Msuha, M. J., Lichtenfeld, L. L., & Durant, S. M. (2017b). Socio-economic correlates and management implications of livestock depredation by large carnivores in the Tarangire Ecosystem, Northern Tanzania. *International Journal of*

- Biodiversity Science, Ecosystem Services & Management*, 13(1), 248–263.
<https://doi.org/10.1080/21513732.2017.1339734>.
- Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S., & Lamoreux, J. F. (2007). Persistence of Large Mammal Faunas as Indicators of Global Human Impacts. *Journal of Mammalogy*, 88(6), 1363–1380. <https://doi.org/10.1644/06-mamm-a-124r2.1>.
- Mosser, A. (2008). *Group territoriality of the African lion: Behavioral adaptation in a heterogeneous landscape*. University of Minnesota, USA.
- Mosser, A. A., Kosmala, M., & Packer, C. (2015). Landscape heterogeneity and behavioral traits drive the evolution of lion group territoriality. *Behavioral Ecology*, 26(4), 1051–1059. <https://doi.org/10.1093/beheco/arv046>.
- Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78(2), 359–370.
- Mponzi, B. P., Lepczyk, C. A., & Kissui, B. M. (2014). Characteristics and distribution of livestock losses caused by wild carnivores in Maasai Steppe of Northern Tanzania. *Human-Wildlife Interaction*, 8(2), 1–11.
- Muriuki, M. W., Ipara, H., & Kiringe, J. W. (2017). The cost of livestock lost to lions and other wildlife species in the Amboseli ecosystem, Kenya. *European Journal of Wildlife Resource*, 63(60), 1–11. <https://doi.org/10.1007/s10344-017-1117-2>.
- National Bureau of Standard. (2013). Population and Housing Census. *Ministry of Finance*.
- Noon, B. R. (2017). Radio Tracking and Animal Populations. *Auk*, 119(2), 580–582. [https://doi.org/10.1642/0004-8038\(2002\)119](https://doi.org/10.1642/0004-8038(2002)119).
- Nyahongo, J. W. (2007). *Depredation of Livestock by Wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania*. (Doctorate Thesis, Norwegian University of Science and Technology).
- Okello, M. M., Kiringe, J. W., & Warinwa, F. (2014). Human-Carnivore Conflicts in Private Conservancy Lands of Elerai and Oltiyiani in Amboseli Area, Kenya. *Natural Resources*, 5, 375–391.

- Ontiri, E. M., Odino, M., Kasanga, A., Kahumbu, P., Robinson, L. W., Currie, T., & Hodgson, D. J. (2019). Maasai pastoralists kill lions in retaliation for depredation of livestock by lions. *People and Nature*, *1*, 59–69. <https://doi.org/10.1002/pan3.10>.
- Packer, C., Brink, H., Kissui, B. M., Maliti, H., Kushnir, H., & Caro, T. (2010). Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conservation Biology*, *25*(1), 142–153. <https://doi.org/10.1111/j.1523-1739.2010.01576.x>.
- Packer, C., Ikanda, D., Kissui, B., & Kushnir, H. (2005). Lion attacks on humans in Tanzania. *Nature*, *436*(7053), 927–928. <https://doi.org/10.1038/436791a>.
- Packer, C., & Pusey, A. E. (1982). Cooperation and competition within coalitions of male lions: Kin selection or game theory? *Nature*, *296*(5859), 740–742.
- Packer, C., & Pusey, A. E. (1987). Intrasexual cooperation and the sex ratio in African lions. *The American Naturalist*, *130*(4), 636–642.
- Patterson, B. D. (2007). On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology*, *34*, 55–60. <https://doi.org/10.1007/s11692-007-9003-6>.
- Prins, H. H. T. (1987). Nature conservation as an integral part of optimal land use in East Africa: The case of the Masai Ecosystem of Northern Tanzania. *Biological Conservation*, *40*(2), 141–161. [https://doi.org/10.1016/0006-3207\(87\)90064-4](https://doi.org/10.1016/0006-3207(87)90064-4).
- Packer, C., & Pusey, A. E. (1997). Divided we fall: Cooperation among lions. *Scientific American*, *276*(5), 52–59.
- Ray, J. C., Hunter, L., & Zigouris, J. (2005). *Setting conservation and research priorities for larger African carnivores*, *24*(24), 1–203. New York: Wildlife Conservation Society. <https://doi.org/10.1017/s0952836905007508>.
- Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., Hans, I., Pimm, S., & Lichtenfeld, L. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. <https://doi.org/10.1007/s10531-012-0381-4>.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W.,

- Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484.
- Romañach, S. S., Lindsey, P. A., & Woodroffe, R. (2007). Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. *Oryx*, *41*(2), 185–195.
- Roskaft, E., Händel, B., Bjerke, T., & Kaltenborn, B. R. P. (2007). Human attitudes towards large carnivores in Norway. *Wildlife Biology*, *13*(2), 172-185.
- Sargent, R., McGowan, P. J. K., Bunnefeld, N., & Pfeifer, M. (2021). Room to roam for African lions *Panthera leo* : A review of the key drivers of lion habitat use and implications for conservation. *Mammal Review*, 1–13. <https://doi.org/10.1111/mam.12262>.
- Scheel, D. (1992). Profitability, encounter rates, and prey choice of African lions. *Behavioral Ecology*, *4*(1), 90–97.
- Scheel, D. (1993). Watching for lions in the grass: The usefulness of scanning and its effects during hunts. *Animal Behaviour*, *46*, 695–704.
- Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions : A search for cooperation. *Animal Behaviour*, *41*, 697–709.
- Team, R. C. (2014). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Treves, A., & Karanth, K. U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, *17*(6), 1491–1499.
- Trinkel, M., & Angelici, F. M. (2016). The decline in the lion population in Africa and possible mitigation measures. *Problematic Wildlife: A Cross-Disciplinary Approach*, 45-68. <https://doi.org/10.1007/978-3-319-22246-2>.
- Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., & Macdonald, W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, *49*(1), 73–81.
- Whitman, K., Starfield, A. M., Quadling, H. S., & Packer, C. (2004). Sustainable trophy

hunting of African lions. *Nature*, 428(6979), 175–178.

Woodroffe, R., & Frank, L. G. (2005a). Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation*, 8, 91–98.

Woodroffe, R., & Frank, L. G. (2005b). Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation*, 8(1), 91–98. <https://doi.org/10.1017/S1367943004001829>.

Woodroffe, R., Thirgood, S., & Rabinowitz, A. (2005). The impact of human-wildlife conflict on natural systems. *People and Wildlife: Conflict or Coexistence?* 1–10. Cambridge University Press.

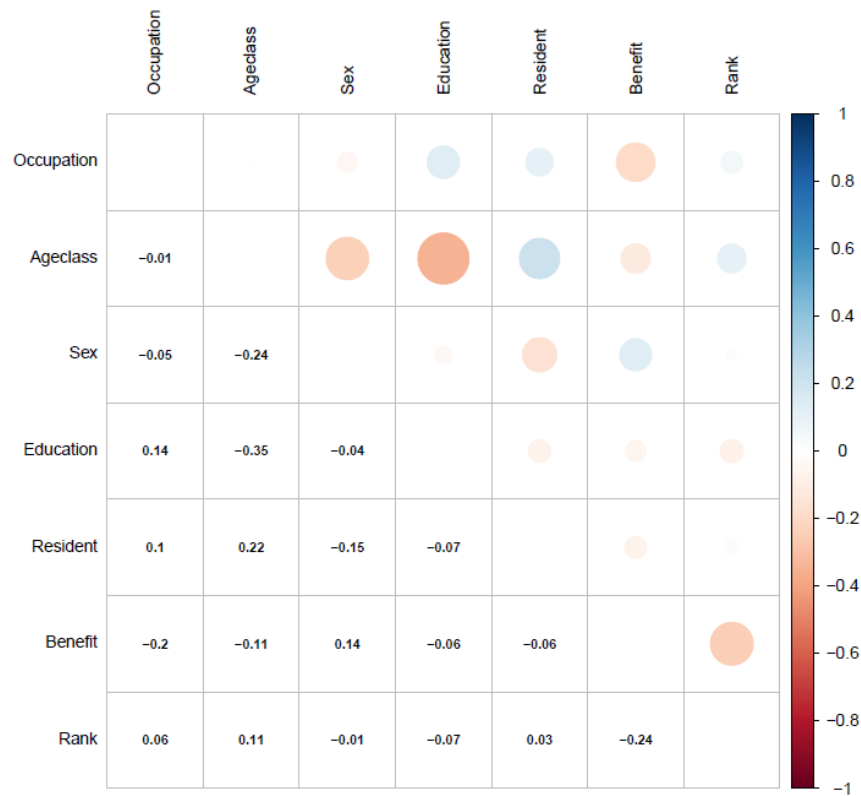
Yamazaki, K. (1996). Social Variation of Lions in a Male-Depopulated Area in Zambia. *The Journal of Wildlife Management*, 60(3), 490–497.

Zabel, C., Glickman, S. E., Frank, L. G., Woodmansee, K. B., & Keppel, G. (1992). Coalition formation in a colony of prepubertal spotted hyenas. *Coalitions and Alliances in Human and Other Animals*, 13–136. Oxford University Press.

APPENDICES

Appendix 1: Matrix Plot of Spearman Correlation Coefficient for predictor Variables

Matrix showing pairwise Spearman rank correlation coefficient values for considered predictor variables. Color intensity and the size of the circle are proportional to the correlation coefficients (Kissui *et al.*, 2019). Correlation coefficient values of less than 0.5 are not correlated and were used as independent variable in our model. Categories are shown in (Table 2). Positive correlations are shown in blue, negative ones in red.



Appendix 2: Male Lion Coalition Found in Tarangire-Manyara Ecosystem

A summary of the male lion coalition groups for 10 prides in the Tarangire-Manyara Ecosystem. The pride name, Coalition ID and the number of males in the coalition is shown as well as the tenure period shows (time period that coalition group lasted in the pride) and the location, indicating the home range area of the coalition group in the park (either in the middle or the periphery of the park).

Pride name	Coalition ID	No. of males	Tenure period (months)	Location
Altipiano	ALC5	2	6	Periphery
Altipiano	ALC2	3	10	Periphery
Altipiano	ALC4	2	11	Periphery
Altipiano	ALC6	2	12	Periphery
Altipiano	ALC3	2	19	Periphery
Altipiano	ALC1	2	24	Periphery
Altipiano	ALC7	2	4	Periphery
Boundary hill	BC31	3	14	Periphery
Kuro	KC37	2	4	Midst
Kuro	KC32	1	12	Midst
Kuro	KC34	1	12	Midst
Kuro	KC39	2	12	Midst
Kuro	KC38	5	17	Midst
Kuro	KC35	3	20	Periphery
Kuro	KC33	2	22	Periphery
Kuro	KC40	3	26	Midst
New Silale	NSC42	2	4	Periphery
New Silale	NSC41	2	12	Periphery
New Silale	NSC43	1	12	Periphery
New Tarangire hill	NTC21	2	37	Midst
New Tarangire hill	NTC20	3	52	Midst
New wazi	NWC9	3	8	Periphery
New wazi	NWC12	4	24	Midst
New wazi	NWC10	2	25	Periphery
New wazi	NWC11	1	39	Periphery
Old Silale	OSC46	1	12	Periphery
Old Silale	OSC45	5	24	Periphery
Old Silale	OSC44	2	36	Periphery
Silale/Minynyo	SM47	2	14	Midst
Silale/Minynyo	SM48	1	16	Midst
Silale/Minynyo	SM49	3	26	Midst
Silale/Minynyo	SM50	5	38	Midst
Tarangire hill	TC23	3	3	Periphery

Tarangire hill	TC27	3	4	Periphery
Tarangire hill	TC29	3	6	Periphery
Tarangire hill	TC28	2	10	Periphery
Tarangire hill	TC25	2	12	Periphery
Tarangire hill	TC26	2	19	Periphery
Tarangire hill	TC30	4	25	Periphery
Tarangire hill	TC22	2	35	Midst
Tarangire hill	TC24	5	55	Periphery
Wazi	WC13	3	6	Periphery
Wazi	WC15	2	12	Periphery
Wazi	WC17	1	12	Periphery
Wazi	WC16	2	16	Periphery
Wazi	WC14	2	38	Periphery

Appendix 3: Data of Retaliatory Lion Killing in Tarangire-Manyara Ecosystem

Summary of the data on retaliatory killing of lions from the year 2004 to 2018 in villages within the Tarangire-Manyara Ecosystem and Tarangire-Simanjiro Ecosystem. Selected villages for interview are marked by an asterix. Villages with a frequency of attacks of ≥ 5 were classified as high retaliation villages (Esilalei, Mswakini chini, Kakoi and Olasiti), those of ≤ 5 (Mswakini juu, Minjingu, and Oltukai) were classified as low.

Villages	Frequency	Number of lions killed
Esilalei *	21	27
Loibor Soit	11	22
Olasiti *	11	11
Loibor Siret	10	11
Mswakini chini *	8	7
Tarangire National Park	6	6
Kakoi *	5	5
Kimotorok	5	5
Naitolia	3	3
Oltukai *	3	3
Manyara ranch	4	4
Mswakini juu *	2	4
Makuyuni	2	4
Lolkisale	2	5
Emboret	1	1
Minjingu *	1	1
Mbuyuni	1	2
Lemoti	1	4
Engaruka	1	2
Losirwa	1	1

Source data: Tarangire Lion Project

Appendix 4: Questionnaire to Communities Found in Tarangire-Manyara Ecosystem

Questionnaire that was given to 214 households in the villages around Tarangire-Manyara Ecosystem and 15 key informants.

1. Date (day/month/year)	2. Survey no	3. Interviewer (s) name	4. Other people present at start of interview? (describe)
5. Household GPS		6. Village and sub village	
S:		E:	

PART I: SOCIO- DEMOGRAPHIC CHARACTERISTICS OF THE RESPONDENT

7. Occupation (√) Pure Pastoralist Farmers Agro-pastoralist Employees Business	8. Age class (√) 18- 35 36- 45 46-55 Above 55 years	9. Gender (M/F) Me=1 Fe=2	10. Education level 1 = illiterate, 2 = Primary 3 = Secondary 4 = Tertiary	11. How long have you been living in TME (√) < 5 years 5-15 years More than 15 years	12. Benefit from Conservation 1. Employment 2. Business Opportunity 3. Community Development 4. No benefit
--	---	---------------------------------	--	---	--

PART 2: AWARENESS AND ATTITUDE ON THE EFFECT OF RETALITORY KILLING OF LIONS

13a. Please rank the wildlife challenges below from the highest to the lowest (1, 2 , 3) Livestock predation (), Crop raiding (), Human attacks ()
13b. Rank the problem animals below 1=most problematic, 2= problematic, 3=least problematic and 4=not problematic Lion (), hyena (), leopard (), Jackal (), elephant (), zebra (), warthog (), wilderbeest (), tortoise ()
13c. From the list above, how often do the problem animals cause problems? Daily (), season dry (), season wet (), rare ()
14. What measures do you use for protecting livestock Chain-link fence (), guard & dogs (), tree branches and thorns (), having adult herders and not children (), having at least two herders (), no action ()

15. How do you rate the of problem animals? Increasing (), Decreasing (), Stayed the same ()
16. Who is responsible with the problem caused by wildlife ?Government (), Community ()
17. How do you see the lion population trend in TME Increasing (), decreasing (), stayed the same (), disappear (), I don't know ()
18. Do lions have right to live ? Strongly agree (), agree (), neutral (), disagree (), Strongly disagree ()
19. Should wildlife be punished when they attack livestock? Strongly disagree (), disagree (), neutral (), agree (), strongly agree ()
20. Has retaliation cause a decline in lion population? Strongly disagree (), disagree (). Neutral (), agree (), strongly agree ()
21. Has there been a report of lion killing over the following time eriod? Within 6 month (), every year (), every five years (), I don't know (), no current record ()

RESEARCH OUTPUTS

(i) Research Paper

Felix, N., Kissui, B. M., Munishi, L., & Treydte, A. C. (2022). Retaliatory killing negatively affects African lion (*Panthera leo*) male coalitions in the Tarangire-Manyara Ecosystem, Tanzania. *Plos One*, 17(8), e0272272.

(ii) Poster Presentation


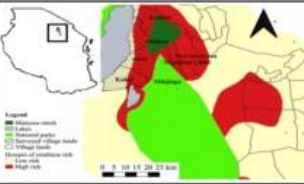

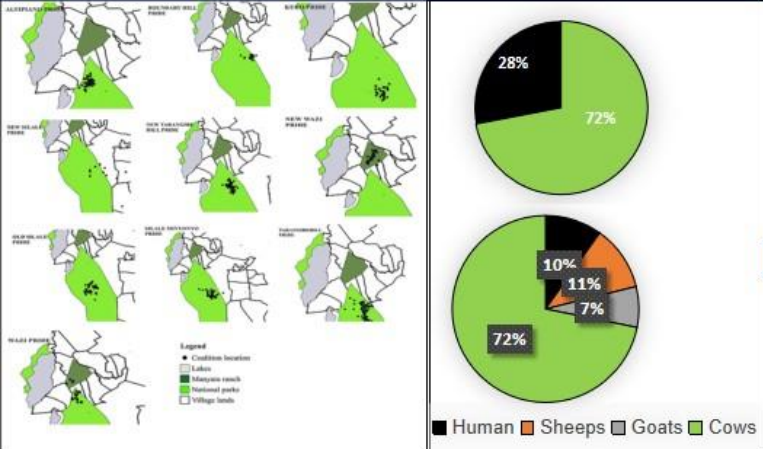


Appendix 5: Poster Presentation

Retaliatory killing negatively affects African lion (*Panthera leo*) male coalitions in the Tarangire-Manyara Ecosystem, Tanzania

Nancy Felix^{1*}, Bernard M. Kissui^{2,3}, Linus Munishi¹, Anna C. Treydtel^{1,4,5}

¹ Department of Sustainable Agriculture, Biodiversity and Ecosystem Management, The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania, ² School for Field Studies, Center for Management Studies, Karatu, Tanzania, ³ Tarangire Lion Project, Arusha, Tanzania, ⁴ Department of Physical Geography, Stockholm University, Stockholm, Sweden, ⁵ Ecology of Tropical Agricultural Systems, Hohenheim University, Stuttgart, Germany

* nancyfelix25@gmail.com

ABSTRACT	INTRODUCTION	STUDY AREA	METHODS
<p>In landscapes where people and lions coexist, conflicts are common due to livestock predation and threats to human safety. Retaliatory lion killing by humans is often a consequence and is one of the leading causes of lion population declines across Africa. We assessed the effects of retaliatory lion killing on male lion coalitions in the Tarangire-Manyara Ecosystem (TME) using a long-term dataset of lion monitoring for ten lion prides, spanning over a fourteen year-period from 2004–2018. We also interviewed 214 respondents about their attitudes and awareness of the effects of retaliatory killing on lions. We found that male lion coalitions were larger and lasted for a longer tenure period in locations with low risk of retaliatory killing, as well as far away from active hunting blocks</p>		 <p>Fig 1: Location of surveyed villages and protected areas heat map of low and high risk</p>	
RESULTS	DISCUSSION AND CONCLUSION		ACKNOWLEDGEMENT
 <p>Legend: Coalition location, Lakes, Manyara reach, National park, Village lands</p> <p>■ Human ■ Sheeps ■ Goats ■ Cows</p>	<ul style="list-style-type: none"> Coalition size are small at high risk areas and active hunting block Tenure period are longer for large coalition at midst Location of a coalition influence the coalition size and tenure period Community have little awareness on the effect of retaliatory killing to lion population Retaliatory killing and hunting negatively impact coalition size and tenure period Awareness raising and strategies need to be established and implemented to protect the declining population of African Lion 		 
REFERENCE			
<ul style="list-style-type: none"> Anderson, R., & Burnham, P. (2002). Avoiding Pitfalls when using Information-Theoretic 959 Methods. <i>Journal of Wildlife Management</i>, 66(3), 912–918. Bygott, J., Bertram, B. C., & Hanby, J. P. (1979). Coalition of male lions has a reproductive 977 advantage. <i>Nature</i>, 282, 839–841 IUCN, & Group, S. C. S. (2018). <i>Guidelines for the Conservation of Lions in Africa</i> (Issue December). Pusey, A. E., & Packer, C. (1997). Divided We Fall : Cooperation among Lions. <i>Scientific</i> 1138 American Inc, May 1997, 51–59. 			