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Franco Peniel Mbise

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Contents

Preface

Foremost thanks go to my family for their support and encouragement throughout my academic life. I thank Sharon and Axel (from Canada) for their support during my high school studies. You are the reason for my achievement this far. I would like to thank Professor Eivin Røskaft for making my academic journey possible. We met in 2010 in the Selous Game Reserve, at the time when I was a volunteer with the Wildlife Division and the Tanzania Wildlife Research Institute (TAWIRI). Since then, we became friends, and he opened the door for me to pursue my masters and PhD degrees at the Norwegian University of Science and Technology (NTNU). I thank him a lot for the time he devoted to tirelessly reading my work and discussing issues that needed more clarification. Long life "*maisha marefu*" Professor... Thanks to mama Berit Røskaft for your time in making nice food, desserts and drinks. Thanks for inviting me to your place very often and even letting me bring the nice food back with me. It was especially kind of you when for the first time I arrived in Norway, to make sure that I had everything that I needed to start living at Moholt Studentby. *Asante sana mama*.

I extend my sincere thanks for co-authorship and very good advice to Dr. Robert Fyumagwa, Dr. Craig Jackson, Dr. Richard Lyamuya, Mr. Justin Wanda, Dr. Gine Roll Skjærvø and Dr. Tomas Holmern. I thank the AfricanBioServices family for support and collaboration in my academic journey from Tanzania, Norway and Kenya (driver Juma Mkwizu, Dr. Emanuel Masenga, Dr. Wilfred Njama Marealle, Dr. Emanuel Clamsen Mmassy, Dr. Frode Fosssøy, Mr. Peter Sjolte Ranke, photographer Per Harald Olsen, Ms. Solveig Børresen, Ms. Merceline Ojwala and Mr. Joseph Mukeka). I cannot mention everyone who has been part of my academic and social life, but you should know that I love you all and appreciate your company.

Summary

Human-carnivore conflict occurs in both developed and developing nations all over the world. The problem has existed since medieval times, but presently, due to the increasing human population, which in turn destroys carnivores' habitats and depletes their prey bases, the situation has worsened. Therefore, large carnivores have been placed in the vicinity of people, threatening their lives and livelihoods. Measures to curb the problem involve a variety of approaches depending on culture and livestock keepers. Human-carnivore conflict can be due to livestock depredation and/or human attacks. Livestock depredation and human attacks are intolerable. Livestock depredation can be compensated for, but human attacks and/or kills cannot. The immediate reaction of communities experiencing attacks on humans and/or kills by carnivores is frequently retaliatory killings. At least when livestock depredation occurs, people are aware that compensation can be made under some circumstances.

In the Loliondo Game Controlled Area (LGCA) in northern Tanzania, reported livestock depredation incidences have occurred mostly during the day when livestock are pastured and during the dry season. Spotted hyenas *(Crocuta crocuta)* were the carnivores most commonly reported to cause livestock depredation. The rate of livestock depredation caused by other predators, including lions *(Panthera leo)*, cheetahs *(Acinonyx jubatus)*, leopards *(Panthera pardus)*, African wild dogs *(Lycaon pictus)* and black-backed jackals (*Canis mesomelas schmidti*), is low. In protecting livestock, the Maasai tribe preferred using knives and/or spears, whereas the Sonjo tribe used bows and poisoned arrows. Furthermore, financial compensation for loss is not necessarily an effective and sustainable solution. To explore possible alternatives, one of our objectives tested the willingness of these tribes to coexist with wild carnivores before and after the implementation of a chemoprophylactic program on livestock that served as an alternative form of compensation. The Maasai and the Sonjo tribes expressed more willingness to coexist with wild carnivores if they received tangible benefits due to the presence of these predators in their areas. To test this, we utilised a pre-test and post-test approach following the implementation of a chemoprophylactic program among the Maasai and Sonjo tribes as a potential conservation incentive. Chemoprophylaxis is used to boost animals' immunity against diseases using various drugs. The pre-test results obtained before implementation of the program indicated a low willingness to coexist with wild carnivores. However, the post-test results showed an increase in people's willingness to coexist with wild carnivores in their areas. Livestock loss caused by disease was much higher than the losses caused by depredation.

Therefore, if this program is continued in the long term, willingness to coexist with wild carnivores may improve. In the longer-term, such a project may have undesirable side-effects. Livestock populations have increased dramatically in the study area, to the detrimental fate of the ecosystem and the wildlife populations it formally supported.

Attacks by predators on humans were alarming and drew our attention to exploring the circumstances surrounding human attacks in the area. The Maasai tribe experienced more attacks on humans because they live closer to the park. Most of these attacks occurred during the wet season and in the daytime while people were herding livestock. Youths (males) were most affected by these attacks because they take the responsibility of herding livestock as a family obligation. Fortunately, most of the human attacks caused injuries rather than loss of life. The predators most often responsible for these attacks were lions, followed by leopards and spotted hyenas.

Unlike attacks on humans, coexistence measures are easier to realize in a community when dealing with livestock depredation. It is often possible to provide some conservation incentives that boost locals' morale and increase their willingness to tolerate losses due to the said incentives. However, it is never possible to offer incentives that compensate for human attacks and/or kills. Ideally, there should be studies that provide awareness of how to avoid human attacks based on the circumstances surrounding previous attacks. The findings from this study will be used to propose different strategies that will favour harmonic coexistence between humans and carnivores as well as to support their conservation. The main target for conservation stakeholders in Tanzania is reduction of the decrease in the carnivore population adjacent to many networks of protected areas. When people have negative attitudes towards large carnivores, retaliatory killings will increase. Large carnivores require large home ranges, and due to the shrinking of protected areas due to anthropogenic activities, they end up living close to human-dominated areas. To ensure a promising future for large carnivores, local communities must be able to realize tangible benefits related to the presence of carnivores in their areas.

Furthermore, we assessed the validity of reports by local people concerning the frequency of encountering carnivores in their areas. We double-checked this information by conducting call-in survey in the areas that appeared to have a high probability of being carnivore habitats. The findings matched the reported encounters, confirming the reliability of local people's reports concerning livestock depredation and human attacks. Field observations using call-in surveys in conjunction with questionnaires were used to test whether observations of wild carnivores were consistent with the information reported by local people about the presence of wild carnivores in their areas. At twelve sites at which call-in surveys were conducted in triplicate, we observed 9 lions, 88 spotted hyenas and 47 jackals. The observed and reported frequencies of encountering spotted hyenas and jackals in areas occupied by the Maasai and Sonjo tribes were negatively correlated with the distance from the Serengeti National Park (SNP). On the other hand, observations at call-in sites positively matched what people reported in the same areas. Additionally, the reported frequencies of encountering four other types of wild carnivores (lions, leopards, cheetahs, and African wild dogs) were higher closer to the SNP.

List of papers

This thesis is based on the following papers;

1. **Mbise, F. P.,** Skjærvø, G. R., Lyamuya, R. D., Fyumagwa, R. D., Jackson, C., Holmern, T., & Røskaft, E. (2018). Livestock depredation by wild carnivores in the eastern Serengeti ecosystem, Tanzania. *International Journal of Biodiversity and Conservation,* 10(3), pp. 122-130. doi:10.5897/IJBC2017.1165

2. **Mbise, F. P.,** Skjærvø, G. R., Lyamuya, R. D., Fyumagwa, R. D., Jackson, C., Holmern, T., & Røskaft, E. (2018). Attacks on humans vs. retaliatory killing of wild carnivore in the eastern Serengeti ecosystem, Tanzania. (Submitted)

3. **Mbise, F. P.,** Wanda, J. S., Jackson, C., Fyumagwa, R. D., Lyamuya, R. D., Skjærvø, G. R., & Røskaft, E. (2018). Can conservation incentives promote people's willingness to coexist with large carnivores in the eastern Serengeti ecosystem? (Manuscript)

4. **Mbise, F. P.,** Jackson, C., Lyamuya, R. D., Fyumagwa, R. D., Holmern, T., Skjærvø, G. R., & Røskaft, E. (2018). Do carnivore surveys match reports of carnivore presence by pastoralists? A case of the eastern Serengeti ecosystem. (Manuscript)

Declaration of contributions

Paper I

FPM conceived the idea, designed the study, collected data and led the writing of the manuscript. GRS, RDL, RDF, CJ, TH contributed in the manuscript writing. ER assisted as a supervisor in manuscript writing. All authors contributed accordingly and approved the final draft for publication.

Paper II

FPM conceived the idea, designed the study, collected data and led the writing of the manuscript. GRS, RDL, RDF, CJ, TH contributed in the manuscript writing. ER assisted as a supervisor in manuscript writing. All authors contributed accordingly and approved the final draft for publication.

Paper III

FPM conceived the idea, designed the study, collected data and led the writing of the manuscript. JSW administered chemoprophylaxis and contributed in manuscript writing. RDF assisted in logistic support for field work and manuscript writing. CJ, RDL & GRS contributed in manuscript writing. ER assisted as a supervisor in manuscript writing. All authors contributed accordingly and approved the final draft for publication.

Paper IV

FPM conceived the idea, designed the study, collected data and led the writing of the manuscript. CJ, RDL, RDF, TH & GRS contributed in the manuscript writing. ER assisted as a supervisor in manuscript writing. All authors contributed accordingly and approved the final draft for publication.

Introduction

Human-carnivore coexistence and conflict

Due to human-carnivore conflict, the need to develop good conservation methods for coexistence is vital to the future conservation of large carnivore populations (Woodroffe et al. 2005a, Dickman 2010, Gehring et al. 2010, Souza et al. 2017). A harmonic human-carnivore coexistence will sustain the future of large carnivores (Linnell et al. 2001, Woodroffe et al. 2005c, Inskip and Zimmermann 2009, Yirga et al. 2014). Coexistence will be promising when interdisciplinary strategies are applied by combining ecological and social approaches (Treves and Karanth 2003, Carter et al. 2012, Redpath et al. 2013). For instance, when local people's behaviour is dependent on creating positive attitudes towards large carnivores, willingness to coexist with carnivore species will be improved (Hazzah 2006). Therefore, incidents involving the persecution of carnivores will decline (Treves and Karanth 2003).

When communities living with wild carnivores experience an increasing rate of human attacks and livestock depredation, their attitudes toward these species tend to become more negative. Negative attitudes increase the likelihood that humans will take revenge by killing carnivores (Linnell et al. 2001, Hazzah 2006, Romañach et al. 2007, Kissui 2008, Dar et al. 2009, Lindsey et al. 2013, Mwakatobe et al. 2013, Abade et al. 2014a, Abade et al. 2014b). Due to the costs associated with living and interacting with wild carnivores, the livelihoods of local people are highly compromised (Adams and Hutton 2007, Romañach et al. 2007, Røskaft et al. 2007, Vedeld et al. 2012, Dickman et al. 2014, Nana and Tchamadeu 2014). Therefore, human-carnivore conflicts are often severe for communities that share the same landscape with wild carnivores (Holt 2001, Carter et al. 2012, Lindsey et al. 2017).

It is difficult to devise a win-win solution when humans and large carnivores share the same landscape (Woodroffe et al. 2005c, McShane et al. 2011). However, when proper and strategic management practices are employed by integrating locals' knowledge and researchers' knowledge, the likelihood of fostering human and carnivore coexistence will be enhanced. Although keeping livestock brings conflict between carnivores and people, it actually offers the best alternative for conservation, especially around protected areas, compared to other land use activities such as farming (Vedeld et al. 2012). Conservationists have dedicated their efforts to ensuring that wildlife-based tourism prevails as one of the least invasive land use activities (Songorwa 2004, Walpole and Thouless 2005).

Due to anthropogenic activities and human population increase, habitats for large carnivores are gradually shrinking at the global level (Croes et al. 2011, Schuette et al. 2013, Yirga et al. 2013, Ronnenberg et al. 2017). The edges of protected areas are gradually shrinking due to human population increase, resulting in increased demand for land for settlement and farming. Such demands tend to encroach on arable and fertile lands adjacent to protected areas, which negatively impacts the conservation of carnivores and other wildlife species (Shivik 2006, Nyhus 2010). Thus, frequent interactions between humans and large carnivores increase due to habitat deterioration and prey base depletion (Inskip and Zimmermann 2009, Croes et al. 2011, Yirga et al. 2013, Yirga et al. 2014, Ronnenberg et al. 2017). The correlation between the increase in the human population and the extinction of large carnivores is strong in the African context because human population control in Africa is poor (Linnell et al. 2001, Songorwa 2004). Furthermore, the use of lethal methods to control carnivore populations is uncontrolled, and in many countries resource exploitation to sustain people's livelihoods is not well regulated (Linnell et al. 2001).

In east Africa, management efforts are being made to determine how pastoral activities and wild carnivores can coexist and benefit from each other. Communities engage in livestock husbandry as the only possible way to sustain their lives. When their livestock are depredated by wild carnivores, their livelihoods tend to be compromised (Ogada et al. 2003, Mwakatobe et al. 2013). The incidence of depredation is currently increasing greatly in these communities because habitats for wild carnivores have been destroyed and the abundance of their wild prey has declined tremendously, worsening the human-carnivore conflict (Pirie et al. 2017). It is a well-established fact that when the human population increases, habitats for wildlife become fragmented, requiring urgent intervention. For instance, in the 1960s when Tanzania became independent, her population was approximately nine million people. Presently, the population of Tanzania is nearly six times the 1960s population (NBS 2017). This situation has increased the frequency of human encounters with wild carnivores. Due to habitat loss and fragmentation, these carnivore species frequently tend to come close to residential areas, resulting in human attacks and livestock depredation.

When predators attack humans and kill livestock, human-carnivore conflict escalates and mutual coexistence is lost, both of which hamper carnivore conservation initiatives (Treves and Karanth 2003, Woodroffe et al. 2005a, Holmern et al. 2007, Gehring et al. 2010, Karlsson and Johansson 2010, Mwakatobe et al. 2013, Megaze et al. 2017). In response to this, retaliation by poisoning and/or direct attacks will increase. Thus, providing satisfactory conservation incentives is key to ensuring the future of wild carnivore conservation (Naughton-Treves et al. 2003). Creating tolerance for livestock predation using conservation incentives may play a greater role (Hazzah 2006, Maclennan et al. 2009).

To achieve a sustainable conservation goal for predators, harmonious coexistence between these species and people should be improved (Cocks et al. 2012, Schuette et al. 2013, Ronnenberg et al. 2017). Despite the habitat loss and fragmentation, the main target should be dedicated to merging human activities and conservation activities (Treves and Karanth 2003). If local communities dealing with livestock depredation problems receive conservation incentives, the level of tolerance for carnivores will increase (Bagchi and Mishra 2006, Yirga et al. 2014). Thus, when communities receive benefits related to the presence of large carnivores, tolerance towards the losses of their livestock will improve. Communities living with predators in their landscapes have adopted a variety of techniques to safeguard their livestock against depredation. Although some of these techniques are temporary and ineffective, more advanced multiple techniques should be employed as countermeasures (Ed and John 2001, Dickman 2010, Mwakatobe et al. 2013, Lyamuya et al. 2016b).

Assessing the circumstances surrounding livestock depredation incidents and evaluating techniques that are used by communities to protect their livestock will enhance the future of carnivore species (Spira 2014). In developing countries in which compensation for livestock loss due to predators is not a government priority, herders are mainly used to safeguard livestock (Lyamuya et al. 2016b). In developed countries, government agencies receive a lot of pressure from people in rural areas as they bear conservation costs such as human attacks and livestock depredation by living with these carnivores (Miquelle et al. 2005). Therefore, due to this pressure, they conduct carnivore culling to reduce livestock depredation incidences. For instance, in Sweden and Norway, culling for predators is mainly due to pressure by rural people who are claiming their rights; this forces governments to reduce the number of wild carnivores to please the locals (Swenson and Andren 2005). If the number of wild carnivores were as high in Norway as it is in east Africa, depredation cases would likely be extremely numerous because sheep are allowed to roam freely unattended by shepherds due to high labour costs (Widman et al. 2017).

Human attacks increase when the rate of encounters with predators increases, and the situation differs depending on factors such as terrain, habitat, and prey abundance (Carter et al. 2012). Attacks on humans fall on the extreme end of the human-carnivore conflict as they may result in serious injuries and/or loss of human life (Löe and Røskaft 2004, Packer et al. 2005, Quigley and Herrero 2005, Gurung et al. 2008, Ikanda and Packer 2008). Assessing and understanding the circumstances surrounding previous human attacks is vital to developing insight into how various strategies can be employed to avoid and mitigate such attacks (Packer et al. 2005, Smith 2005, Kissui 2008, Lagendijk and Gusset 2008, Dorresteijn et al. 2014, Penteriani et al. 2016). For instance, identifying hiding habitats and preferred habitats for these predators will help communities sharing the same landscape with these species to be careful and/or avoid such places (Abade et al. 2014a). Creating awareness on the part of the local people living with carnivores regarding the likelihood of where and when human attacks might occur will help reduce the number of these attacks (Campbell et al. 2014).

In anthropogenically modified landscapes that include wild carnivores, the human-carnivore encounter rate increases, increasing the likelihood of human attacks (Ikanda and Packer 2008, Penteriani et al. 2016, Pooley et al. 2017). Countermeasures such as separating human activities and conservation activities help create zones for each activity, especially in areas where wildlife and humans interact (Breitenmoser 1998, Shivik 2006, Mbau 2013, Packer et al. 2013). Wild carnivores play an important role in ecosystem functioning and economically for people living with these species (Durant et al. 2011, Valkenburgh and Wayne 2011, Koziarski et al. 2016). Therefore, more effort should be dedicated to fostering coexistence between humans and predators; this will ultimately enhance their future conservation.

Livestock depredation and human attacks

Large carnivores have a long history of conflict with humans involving human attacks and livestock depredation (Löe and Røskaft 2004, Packer et al. 2005, Bagchi and Mishra 2006, Ikanda 2009, Inskip and Zimmermann 2009, Linnell et al. 2012, Schuette et al. 2013). Human attacks and livestock depredation have resulted in retaliatory killings of carnivores (Kissui 2008, Ikanda 2009, Kuiper et al. 2015). This conflict needs to be addressed with all means to get conservation support for large carnivores from local people interacting with these species (Gurung et al. 2008, Ronnenberg et al. 2017). For instance, a study of the feeding and seasonal preferences of lions *(Panthera leo)* in Tsavo National Park in Kenya found that livestock depredation incidences increased during the dry season (TLP 2015). During the wet season, carnivores' prey are evenly distributed across the habitat, in contrast to the dry season when most herds of prey are found around water sources. This enables lions to hide and prey on the approaching herds (TLP 2015). However, during the wet season it requires more effort and energy to chase individuals when all prey are evenly distributed due to many shallow water points. When it is difficult for predators to hunt wild prey, they look for easily hunted prey such as livestock (TLP 2015). Additionally, in the Tsholotsho Communal Land and Ngamo Forest adjacent to Hwange National Park in Zimbabwe, it was found that livestock depredation incidences increased during the wet season (Kuiper et al. 2015). During the wet season, communities normally grow crops; at this time, their livestock are taken further from the crop fields to graze adjacent to protected areas where there are higher densities of wild carnivores (Kuiper et al. 2015).

Carnivore retaliatory killings

Globally, carnivores face a serious threat of extinction mainly due to direct or indirect retaliatory killings by humans (Hazzah 2006, Ikanda and Packer 2008, Kissui 2008, Inskip and Zimmermann 2009). Currently, the rate of persecution of large carnivores is higher than their capacity to re-establish their populations. Furthermore, mortality is higher when a given protected area is surrounded by a high-density human population (Woodroffe et al. 2005c). The establishment of protected areas provides protection for these species and their habitats (Woodroffe et al. 2005c). However, the areas outside the borders of protected areas, which may have high biodiversity, ironically are not protected. For instance, due to their larger home ranges, large carnivores also occupy outside protected areas, where they may tend to attack humans and livestock. In response, local people often retaliate directly by spearing the animals or shooting them with arrows or indirectly by poisoning them with pesticides or insecticides (Hazzah 2006, Kissui 2008, Omoya and Plumptre 2011, Masenga et al. 2013, RCP 2018). Recently, due to technological developments that have provided easy access to poisons, this has become detrimental to several carnivore species.

Conservationists are extremely concerned about the fate of large carnivores as pastoralists increasingly continue to use poison to get rid of carnivores that prey on their livestock (Omoya and Plumptre 2011, Masenga et al. 2013, RCP 2018). Pastoralists have developed harmful techniques of applying insecticides and pesticides to carcasses whether wild or domestic; these techniques ultimately kill large carnivores such as lions, hyenas, wild dogs, and jackals that feed on carcasses (Omoya and Plumptre 2011, Masenga et al. 2013, RCP 2018). A recent deadly and depressing retaliatory incident, in which 11 lions and 74 vultures died after feeding on a cattle carcass poisoned by pastoralists, occurred adjacent to Ruaha National Park in southern Tanzania (RCP 2018). The case is under investigation to determine the type of poison used and to identify the suspect (RCP 2018). Sometimes the killing occurs indirectly, as when herbivores eat grasses contaminated with pesticides and die and the carnivores feed on their carcasses (Omoya and Plumptre 2011). A commonly used pesticide in Kenya and Uganda is carbofuran, the use of which is restricted in Europe and the United States due to its toxicity to animals. In Africa, especially in east Africa, carbofuran is widely available and inexpensive (Omoya and Plumptre 2011).

People's willingness to coexist with large carnivores

Livestock depredation has occurred since time immemorial, and in most cases people express low willingness to coexist with carnivores (Woodroffe et al. 2005c, Lagendijk and Gusset 2008). There is a great need to involve local people who bear conservation costs such as human attacks and livestock depredation (Inskip and Zimmermann 2009, Schuette et al. 2013, Yirga et al. 2014, Ronnenberg et al. 2017). Providing compensation after livestock loss tends to increase tolerance of large carnivores (Hazzah 2006). Although the compensation improves tolerance of livestock loss due to carnivore depredation in specific areas, there is a need to increase personal responsibility for livestock (CDPNews 2003, Rodriguez 2007) and to decrease reliance on compensation when depredation occurs. Additionally, if local people realize tangible benefits related to the presence of large carnivores in their areas rather than only experiencing problems such as livestock depredation and human attacks, their willingness to coexist with these carnivores will be improved.

Land use changes associated with human population increase

As the human population continues to grow, particularly in Africa, wild prey species are depleted and natural habitats for large carnivores are displaced; currently, these habitats are limited to small patches (Yirga et al. 2013). Ideas on managing wild prey abundance are needed to reduce the chances of carnivores hunting livestock (Karlsson and Johansson 2010, Yirga et al. 2014). Thus, a proper management structure and policy designed to conserve large carnivores is urgently needed (Linnell et al. 2001, Hazzah 2006, Hazzah et al. 2017, Ronnenberg et al. 2017). When areas surrounding protected areas are human-dominated, their activities tremendously negatively impact wildlife (Yirga et al. 2013). An example of such an edge effect can be seen in Algonquin Park, Canada, where the wolf population was severely persecuted when the animals crossed the park border (Woodroffe et al. 2005c). Presently, habitats for wild carnivores face great challenges due to human population increases and the expansion of agricultural activities for global food security. Due to anthropogenic activities, land cover and land use are greatly changed, which negatively affects biodiversity in any ecosystem (Wessels et al. 2000). For instance, in the Serengeti ecosystem, large carnivore populations are higher within the Serengeti National Park (SNP) than in the Loliondo Game Controlled Area (LGCA) (Craft et al. 2015), whereas in past decades large carnivore abundance was similar in the two areas (Maddox 2003). This change is a result of the increase in pastoral community populations that reside inside the LGCA together with their livestock.

Thesis aims

General objective

The main objective of this thesis is to assess human-carnivore coexistence and conflict in the eastern Serengeti ecosystem. Human-carnivore conflict being the ever-increasing problem in the Loliondo Game Controlled Area (GCA), harmonic coexistence is an urgent need to secure the future of carnivore species in the area. Currently, the major threat facing the future of wild carnivores is conflict with people. When such conflict escalates the level of retaliation increases. Understanding the root-cause of these problems and suggesting intervention measures to the conservation authorities and the general public will enhance the conservation of wild carnivores.

Specific objectives

1. Assess the local circumstances surrounding livestock depredation and identify a way forward to curb depredation incidences (Paper I).
2. Assess attacks by wild carnivores on humans and retaliatory killings after attacks (Paper II).
3. Test the willingness of humans to coexist with wild carnivores before and after implementing a conservation incentive (chemoprophylactic program) (Paper III).
4. Correlate carnivore surveys to determine whether observations of wild carnivores match what people report (Paper IV).

Study area

The study was conducted in a designated reserve, the Loliondo Game Controlled Area (LGCA). The area lies between 1 ° 40′S and 2 ° 50′S and 35 ° 10′E and 35 ° 55′E, covering a total area of approximately 4,500 km^2 (Masenga 2011, Lyamuya et al. 2014a) (Fig. 1). The area borders Narok County in Kenya on the north, the SNP on the west, and Ngorongoro Conservation Area (NCA) on the south. The surveyed villages included three belonging to the Maasai tribe (Ololosokwan, Soitsambu, and Oloipiri) and three belonging to the Sonjo tribe (Sale, Samunge, and Yasimdito). The Maasai people are pastoralists and are dominant in the area, while the Sonjo people are agro-pastoralists (Maddox 2003, Masenga and Mentzel 2005, Lyamuya et al. 2014a). The LGCA contains diverse vegetation types including forests, woodlands, wooded grasslands, shrublands, and grasslands (Lyamuya et al. 2016a). Furthermore, the area harbours a rich diversity of ungulate species, including impala (*Aepyceros melampus*), zebra (*Equus burchelli)*, wildebeest (*Connochaetes taurinus),* Grant's gazelle (*Nanger granti)*, and Thomson's gazelle *(Eudorcas thomsonii*). The wild carnivores; lions (*Panthera leo*)*,* leopards *(Panthera pardus)*, cheetahs *(Acinonyx jubatus)*, spotted hyenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*) and black-backed jackals (*Canis mesomelas schmidti*) in the area help regulate the ungulate population (Maddox 2003, Holdo et al. 2010, Valkenburgh and Wayne 2011).

Administratively, the area belongs to the Ngorongoro district. The human population of the area is increasing rapidly. For instance, in 2012 the population of the district was 174,278, and it is projected to reach 199,879 after five years (NBS 2017). Due to the human population increase, the demand for land for livestock keeping, farming, and settlement has increased. Thus, habitats for carnivores are deteriorating and are being displaced by other activities (Maddox 2003, Lyamuya et al. 2014a).

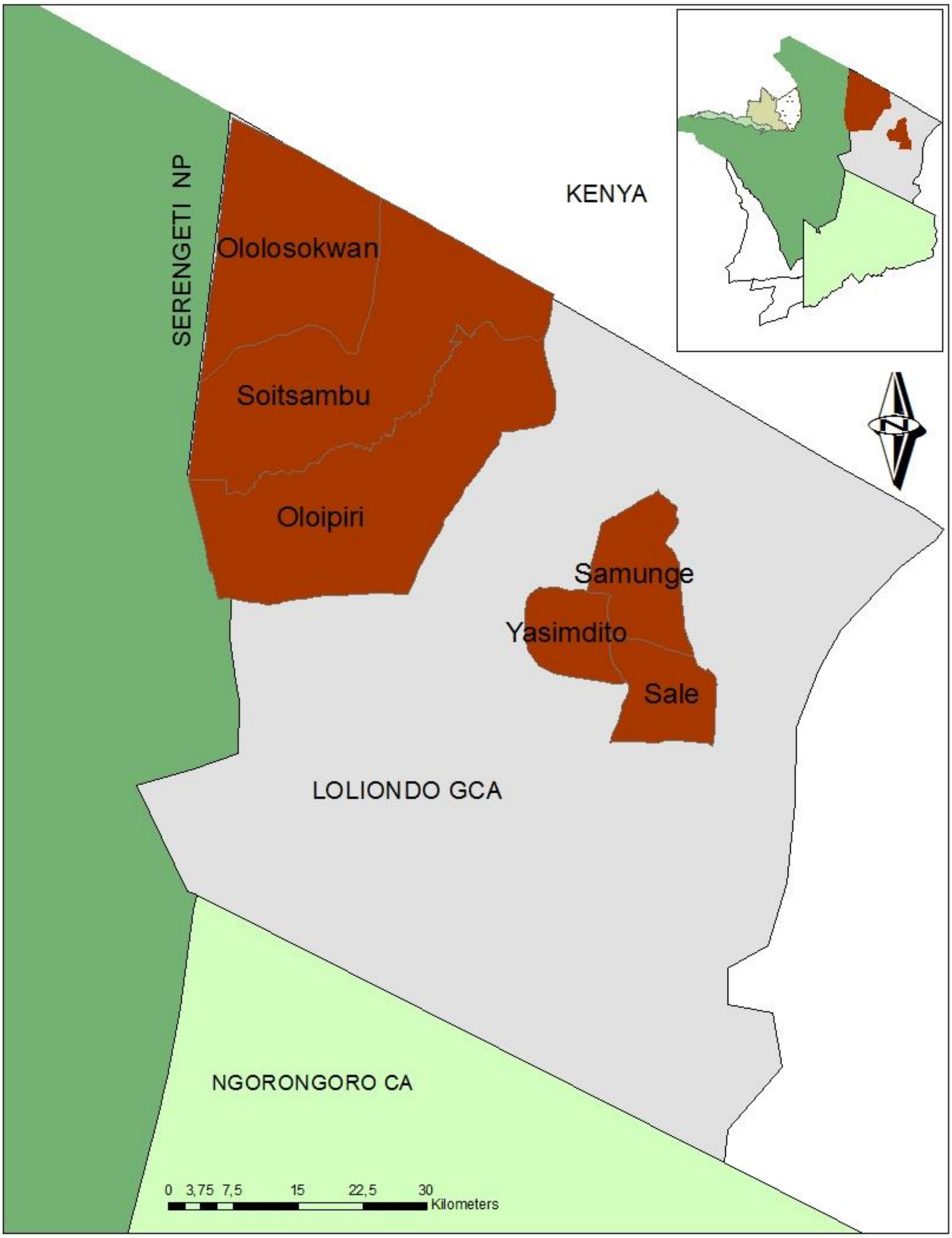

Figure 1: Study area showing the six surveyed village areas in the eastern Serengeti

Carnivore species

The studied wild carnivores belong to three families: Felidae (lion, leopard, and cheetah), Hyaenidae (spotted hyena) and Canidae (African wild dog and black-backed jackal) (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018).

Lion

Lions are active especially during the cooler hours and during the night and are territorial animals (Kennedy and Kennedy 2014, ADW 2018). They live in prides; males can dominate a pride from 3-5 years of age (Kennedy and Kennedy 2014, ADW 2018). During this time, territorial males actively defend their territories against other male intruders, and this may result in intense fighting (Kennedy and Kennedy 2014, ADW 2018). Lions practice infanticide; when adult males find females with young cubs, they kill the cubs, and the females soon ovulate (Kennedy and Kennedy 2014, ADW 2018). Siring normally requires up to 2-3 days; males normally at this time become weak but still copulate frequently for fertilization assurance (Kennedy and Kennedy 2014, ADW 2018). Females usually give birth to 5-8 cubs, of which only a few reach maturity (Kennedy and Kennedy 2014, ADW 2018). Adult males have manes and are larger in size than females (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). The gestation period of lions is 15 weeks (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Lionesses (females) commonly are the ones that hunt (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). They prefer plain grasslands and are rarely found in dense vegetation (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Lions feed on a variety of herbivores ranging from hares to buffalo (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). In SNP, for instance, wildebeest, zebra, impala, and Grant’s and Thomson’s gazelles are mostly preferred (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018).

Lions are species that attracts iconic attention from animal lovers across the globe (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Many tourists are highly interested in seeing them before leaving the bush (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Due to human population increases and depletion of their prey base, lions are now being forced out of their habitats, and sometimes they prey on livestock (Hazzah 2006, Lyamuya et al. 2016b, AWF 2018, Mbise et al. 2018). Rarely, upon encounters with humans they may cause serious injuries or loss of human lives (Packer et al. 2005, Kissui 2008, RCP 2018). Pastoralists and farmers who live in close range of these species often kill them in retaliation (Packer et al. 2005, Kissui 2008, RCP 2018). Current data show that only approximately 23,000 individuals remain in the wild in Tanzania, and lions are now classified as a vulnerable species by the IUCN (AWF 2018).

Leopard

The gestation period of leopards is 13-14 weeks (Kennedy and Kennedy 2014, ADW 2018). Normally, leopards are stealthy animals and take their prey up into a tree after hunting (Kennedy and Kennedy 2014, ADW 2018). The leopard's hunting technique involves stalking, and it is normally active during the night and early morning (Kennedy and Kennedy 2014, ADW 2018). The leopard is a cat with beautiful spots, short legs, a white-tipped tail and white whiskers (Kennedy and Kennedy 2014, ADW 2018). Leopards are found in a variety of habitats ranging from open savanna to woodland and forest (Kennedy and Kennedy 2014, ADW 2018). They prey on a variety of herbivores, preferably impala, warthog (*Phacochoerus africanus),* baboon (*Papio* spp.) and sometimes bird species such as Galliformes (Kennedy and Kennedy 2014, ADW 2018). Leopards are listed as "near threatened" on the IUCN Red List of Threatened Species (Stein et al. 2016). With the increase in the human population, the total leopard population is declining due to habitat loss and fragmentation, persecution and hunting for trade (Stein et al. 2016). The majority of African leopards live outside protected areas and are highly tolerant of human disturbances (Stein et al. 2016). The species is widely distributed in sub-Saharan Africa but is found only in limited numbers in small suitable habitats (Ray et al. 2005, Stein et al. 2016). It is locally extinct in areas with many anthropogenic activities (Hunter et al. 2013). For instance, in sub-Saharan Africa, its habitat loss over the last 25 years has been 21 %, and a prey loss of 59 % has occurred, resulting in a species decline of > 30 % (Jacobson et al. 2016, Stein et al. 2016).

Cheetah

The cheetah is the fastest running terrestrial animal on earth, reaching a speed of 112 kmh^{-1} and is the only feline with non-retractable claws (Kennedy and Kennedy 2014, ADW 2018). The gestation period of cheetahs is 13 to 13.5 weeks (Kennedy and Kennedy 2014, ADW 2018). When mature at two years of age, females may hunt and live alone within a home range, whereas males mature earlier (Kennedy and Kennedy 2014, ADW 2018). Males normally hunt together with other members of the territory (Mills and Hes 1997, Valkenburgh and Wayne 2011, Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). Cheetahs are promiscuous; thus, litters have different fathers (Mills and Hes 1997, Valkenburgh and Wayne 2011, Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). They give birth to up to six cubs, of which unfortunately only one or two survive to maturity due to predation by other predators such as lions and hyenas (Mills and Hes 1997, Valkenburgh and Wayne 2011, Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). The cheetah is mostly active during the daytime (Kennedy and Kennedy 2014, ADW 2018). It has beautiful spots and a long tail and is a long-legged, streamlined cat with a small head and prominent black tears on the face (Kennedy and Kennedy 2014, ADW 2018). Cheetahs are often found on the open grass plain, where they preferably hunt hares (*Lepus* spp.), springbok (*Antidorcas marsupialis*), Thomson's gazelles, and larger prey when they hunt in a group (Mills and Hes 1997, Valkenburgh and Wayne 2011, Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). Prey abundance determines the size of the home range; the smaller the number of prey in the area, the larger the home range (Mills and Hes 1997).

The cheetah is classified as a vulnerable species by the IUCN (Durant et al. 2015). Estimates show that only 10,000 individuals remain in the wild (AWF 2018). The species is currently threatened by the increase in the population of humans demanding land for settlement and farming, which in turn destroys their habitat and depletes their prey (Durant et al. 2015). Unlike other predators, cheetahs hardly strive to coexist with humans (Laurenson and Caro 1994). The presence of humans tends to interfere with cheetahs' feeding and reproductive patterns (Nowak and Kays 2005). When cheetahs occur outside protected areas, farmers and pastoralists often intentionally kill them for the sake of their livestock (Durant et al. 2015). Cheetahs are also threatened by road networks that pass through their habitats, as many are killed by tourist vehicles and supply trucks (Kennedy and Kennedy 2014, Durant et al. 2015, ADW 2018).

Spotted hyena

Three species of hyena are found in Africa: the spotted hyena, the stripped hyena (*Hyena hyena*) and the brown hyena (*Hyena brunnea*) (Holekamp 2004). In our study area and during call-in surveys, we observed only spotted hyenas (Holekamp 2004, Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Spotted hyena females normally dominate the group, and they are larger than males (Holekamp 2004, Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). The gestation period is between 16 and 17 weeks (Kennedy and Kennedy 2014, ADW 2018). The hyena is a predator with a muscular, sloping back and large round ears (Holekamp 2004, Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). It has strong jaws that help it tear bones (Holekamp 2004, Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018), and it hunts and scavenges for prey ranging from small insects to big game (Holekamp 2004, Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Hyenas are found in all types of habitats in their ranges, including open grassland, shrubland, woodland and forest (Holekamp 2004, Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). Hyenas are good indicators of ecosystem health (Holekamp 2004). They can survive in environments that other large carnivore species cannot tolerate (Holekamp 2004). In the Serengeti ecosystem, hyenas are present in larger numbers than any other predators in both protected and unprotected areas (Holmern et al. 2007, Kissui 2008, Nyahongo and Røskaft 2012, Mwakatobe et al. 2013, Yirga et al. 2014, Lyamuya et al. 2016b, Mbise et al. 2018). Outside protected areas, where they struggle to live with humans, they are the predators that are most frequently reported to cause livestock depredation, and most are killed in revenge (Holmern et al. 2007, Kissui 2008, Nyahongo and Røskaft 2012, Mwakatobe et al. 2013, Yirga et al. 2014, Lyamuya et al. 2016b, Mbise et al. 2018).

African wild dog

Wild dogs live in packs in which breeding is dominated by an alpha pair (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). While the alpha pair dominate the breeding (Frame et al. 1979), subordinates also gives birth. Genetic studies show that many litters are of mixed paternity (Spiering et al. 2010). The females give birth to 5-12 pups (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). The gestation period is 10 weeks. African wild dogs have attractive black, tan and white blotched coats, large ears and bushy white-tipped tails (Valkenburgh and Wayne 2011, Kennedy and Kennedy 2014, ADW 2018). They are sociable animals, living in packs of up to 15 individuals (Gusset and Macdonald 2010, Masenga 2017). The effective group size is > 5 individuals, as it eases the hunting (Gusset and Macdonald 2010, Masenga 2017). They are found in savanna, open grassland, and woodland habitats (Kennedy and Kennedy 2014, ADW 2018). They hunt small, medium and larger antelopes (Kennedy and Kennedy 2014, ADW 2018). Their hunting behaviour normally involves exhausting their prey; they are able to reach speeds of 64 kph (Kennedy and Kennedy 2014, ADW 2018). Smaller and medium-sized prey can be subdued by one individual (Kennedy and Kennedy 2014, ADW 2018). Larger prey are usually torn apart from abdomen to tail until they become unconscious (Kennedy and Kennedy 2014, ADW 2018). Hunting success is very high when hunting occurs in packs (Kennedy and Kennedy 2014, ADW 2018). The African wild dog is classified as an endangered species by the IUCN (Woodroffe and Sillero-Zubiri 2012). Only approximately 6,600 adults remain in the wild (AWF 2018). Due to the human population increase, their population continues to decrease as they require a vast land area due to their large home range (Woodroffe et al. 2005a, Woodroffe 2011, Masenga et al. 2016). Wild dogs are found in both protected and unprotected areas. Adjacent to protected areas, especially when their prey abundance is low, they often prey on livestock, which causes retaliation in return (Woodroffe et al. 2005a, Masenga 2017).

Jackal

Jackals are territorial and fox-like, with three common species found in the Serengeti ecosystem: black-backed jackals, side-stripped jackals (*Canis adustus notatus*) and golden jackals (*Canis aureus*) (Walton and Joly 2003, Kingdon and Hoffman 2013, Hoffmann 2014, Kennedy and Kennedy 2014, ADW 2018). In our study area, black-backed jackals were present (Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). Their flanks and legs bear a reddish-brown coat, and the belly part is whitish (Walton and Joly 2003, Kingdon and Hoffman 2013, Hoffmann 2014, Kennedy and Kennedy 2014, ADW 2018). The backside shows a mix of silver and black hairs (Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). The gestation period is 9 weeks, the lifespan in the wild is approximately 8 years, and the adult body weight ranges from 6.8 to 13.8 kg (Walton and Joly 2003, Kingdon and Hoffman 2013, Hoffmann 2014, Kennedy and Kennedy 2014, ADW 2018). Males and females bond and mate for life, and they live with their offspring (Hoffmann 2014, ADW

2018). They are normally found in the open grassland, shrubland and sometimes in woodland habitats (Walton and Joly 2003, Kingdon and Hoffman 2013, Hoffmann 2014, Kennedy and Kennedy 2014, ADW 2018). The black-backed jackal is an omnivore that feeds on grass, insects, lizards, snakes, rodents, hares and young antelope (Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). Sometimes they scavenge on carcasses (Kingdon and Hoffman 2013, Kennedy and Kennedy 2014, ADW 2018). Occasionally they prey on domestic animals such as sheep (*Ovis aries*) and goats (*Capra hircus*) (Walton and Joly 2003). Because they are small in size, they normally target young individuals (Walton and Joly 2003). This brings them into conflict with local people, by whom they may be killed with spears, arrows or poison (Walton and Joly 2003). Jackals are listed as a species of "least concern" on the IUCN Red List of Threatened Species (Hoffmann 2014). The species is widely distributed across eastern and southern Africa (Hoffmann 2014, ADW 2018). Jackals carry a variety of diseases such as canine distemper, rabies, and African horse sickness (Walton and Joly 2003). They also carry trematodes, cestodes, nematodes, and protozoans (Walton and Joly 2003).

Data collection

We collected our data from August 2016 to July 2017 (**Papers I - IV**).

Reported livestock depredation and human attacks

A survey was conducted through a semi-structured questionnaire employing a face-to-face interview (*Photo 1*). Both closed-ended and open-ended questions were included for comparison purposes and to obtain additional details that were not captured by our questions. Our respondents were older than 18 years of age; as a result, they had experience and reliable information to tell. The survey was conducted in six villages, including three villages (Ololosokwan, Oloipiri, and Soitsambu) of the Maasai tribe and three (Yasimdito, Samunge, and Sale) of the Sonjo tribe. Each respondent was randomly selected from a household, and a total of 180 respondents were interviewed. More males than females were interviewed because in the Maasai and Sonjo tribes men speak on behalf of the household. Due to this challenge, it was difficult to interview equal numbers of males and females. Therefore, our sample consisted of 144 males and 36 females. To respect the norms of the tribes, interviewing females was only possible in the absence of the husband. The Tanzanian national language, Swahili, was used with respondents who spoke it fluently. Where necessary, we engaged local translators (Maasai and Sonjo) when respondents were not comfortable with the Swahili language. The language used in the interview was Swahili for those respondents who spoke it well; a mixture of the Maasai and Sonjo languages was used by local translators for those respondents who did not speak Swahili fluently.

Photo 1: Listening attentively while talking with local Maasai people at Oloipiri village (Photo: P. H. Olsen)

Chemoprophylactic program

We conducted a pre-test survey of people's willingness to coexist with wild carnivores that aimed to gather responses from individuals before the conservation incentive (chemoprophylactic program) was applied. An assessment was performed to determine whether people's willingness to coexist with carnivores was positive, neutral or negative. To avoid influencing their responses and answers, we did not mention the incentive that would be offered. For justification purposes, we recorded the reported livestock loss caused by carnivore depredation and disease. A post-test survey was conducted after four months (February 2017) together with chemoprophylaxis administration to the same respondents who participated in the pre-test survey (*Photo 2*). Chemoprophylaxis is a measure that is used to boost the immunity of animals to diseases (Jibbo et al. 2010). Common diseases in the area were coenurosis, East Coast fever (ECF), contagious bovine pleuropneumonia (CBPP), and anthrax. The drugs were administered by the veterinary officer of the Tanzania Wildlife Research Institute (TAWIRI). Oxytetracycline hydrochloride 20 % and albendazole 10 % were administered. However, at this time of the year it was the dry season, and some respondents moved their livestock to other villages searching for green pastures. Therefore, in the end 120 households received this incentive. The same questions were asked as in the pre-test survey to assess the changes in people's willingness to coexist with wild carnivores.

Photo 2: Conservation incentive: Administering chemoprophylaxis to the livestock (Photo: F. Mbise)

Call-in surveys

Call-in surveys were conducted three times, in November 2016, February 2017 and July 2017. A total of 36 call-in surveys were conducted between 6:00 am and 9:00 am. The locations of the call-ins were selected by local people based on the higher chances of encountering these carnivore species in these locations (*Photo 3*). The call-in surveys were performed three times at each site; the sites included grassland, shrubland, wooded grassland and woodland habitats. Two call-in surveys were performed in the dry season, and one was performed in the wet season. We broadcasted the sound from two speakers on the roof of a Land Cruiser. After the first round of call-in was broadcasted for 15 minutes, we rotated the speakers to cover all directions. In the 15-minute call-in, the first 3 minutes broadcasted the distressed crying of a wildebeest calf followed by 12 minutes of hyenas squabbling over a kill. Thus, the total time effort was 30 minutes, and we counted all attracted hyenas and jackals within a range of 100 meters. Comparisons with what local people reported (180 respondents) concerning the presence of wild carnivores in their areas were only made for hyenas and jackals, as they were the most common carnivore species in the area and were easily attracted to the call-in sites. Lions were only attracted to one of the twelve call-in sites.

Photo 3: After a call-in survey at one of our sites (Photo: J. Yuda)

Summaries of papers

Paper 1

Livestock depredation by wild carnivores in the eastern Serengeti ecosystem, Tanzania

The Maasai and the Sonjo, who practice pastoralism and agro-pastoralism, respectively, are the main tribes living in the eastern Serengeti ecosystem (*Photo 4*). Targeting human-carnivore coexistence, which in return will assure the future of carnivores in the area, is the main goal of conservation stakeholders. When livestock depredation occurs, it induces negative attitudes towards large carnivores and promotes actions such as persecution (Naughton-Treves et al. 2003, Røskaft et al. 2007, Kissui 2008). "Keeping livestock is purposely for sustaining our livelihood and not for sake of feeding wild carnivores" (*Anonymous, 2016*). Spotted hyenas are responsible for most reported livestock depredation in the areas occupied by the Maasai and Sonjo tribes; this depredation typically occurs during the day when the livestock are in pastures and during the dry season. Livestock depredation caused by lions and cheetahs has only been reported on the Maasai side, which is close to the SNP. However, leopards, black-backed jackals, and African wild dogs were found to cause more depredation in the Maasai tribe than in the Sonjo tribe. Both tribes preferred using a combination of techniques to safeguard their livestock against depredation. This paper concludes that there are significant differences between the Maasai and Sonjo tribes in livestock depredation rates and patterns. The Maasai tribe lives closer to the park; thus, the livestock depredation rate correlated with the higher carnivore densities in the area. Therefore, an understanding of depredation patterns and their contributing factors is very important for these tribes in choosing and developing possible countermeasures.

Photo 4: Maasai herders herding their livestock adjacent to the SNP (Photo: P. H. Olsen)

Paper 2

Attacks on humans vs. retaliatory killing of wild carnivores in the eastern Serengeti ecosystem, Tanzania

Due to the increase in the human population, habitats for large carnivores that demand vast amounts of land are increasingly deteriorating. Therefore, large carnivores are restricted to small patches; this often leads to human attacks due to the high frequency of encounters (Packer et al. 2005, Thirgood et al. 2005). Following such attacks, communities normally hold negative attitudes towards large carnivores, and persecution of these important species tends to increase (Thirgood et al. 2005, Røskaft et al. 2007, Ikanda 2009). Managers and policymakers have to employ several countermeasures to reduce the incidence of human attacks as a way forward to save these species from extinction due to retaliation (Kissui 2008, Ikanda 2009). Based on the past circumstances of human attacks, communities should be educated on how to avoid attacks and on how to share this information with their children (Packer et al. 2005, Thirgood et al. 2005). The reported incidences of human attacks among the Maasai and Sonjo tribes show that the former tribe has experienced more attacks because they are close to the SNP. Human attacks have occurred frequently when herding livestock in daytime in the wet season, and young males were most often attacked, as herding livestock is their main task (*Photo 5*). Lions, leopards and spotted hyenas were the most common species causing these attacks, and most victims were injured rather than killed. This paper concludes that the Maasai tribe experienced most of the human attacks and that these attacks occurred while people were herding livestock rather than performing other activities. However, the Sonjo tribe performed most of the retaliatory killings of carnivores. Finding the means to avoid such attacks is vital as it will foster harmonic coexistence between people and predators.

Photo 5: Subject of a recent attack by a lion; his thigh, arm and finger were terribly wounded (Photo: F. Mbise)

Paper 3

Can conservation incentives promote people's willingness to coexist with large carnivores in the eastern Serengeti ecosystem?

When communities sharing the landscape with large carnivores realize tangible benefits due to the presence of these species in their areas, they may change their negative attitudes into positive attitudes (Walpole and Thouless 2005). The chemoprophylactic program, which increases the immunity of livestock to diseases that cause more loss than depredation by predators, was implemented as a conservation incentive (Jibbo et al. 2010, Nyahongo and Røskaft 2012). More livestock loss in the eastern Serengeti was caused by disease than by depredation. Thus, when appropriate procedures such as the chemoprophylactic programs are used to bring tangible benefits to the community, people's willingness to coexist with large carnivores will be improved. Conservation incentives for local people who bear the conservation costs are of paramount importance to promote their willingness to coexist with large carnivores in their areas. This paper concludes that because the Maasai and Sonjo tribes bear the conservation costs for carnivores living in their areas, providing tangible benefits such as chemoprophylactic programs will improve their willingness to coexist with wild carnivores. However, caution must be taken when implementing this program as in a long-term will increase the livestock number, which destroy habitat for carnivores and their wild prey.

Paper 4

Do carnivore surveys match reports of carnivore presence by pastoralists? A case of the eastern Serengeti ecosystem

Based on the nature of the ecosystem, wild carnivores can be distributed independently of the season and their habitats (Cozzi et al. 2013). However, when seasonal factors determine the distribution of prey densities, predators follow the prey movement (Ogutu and Dublin 1998). Field observations and the reported information on encountering lions, leopards, cheetahs, spotted hyenas, and black-backed jackals were higher closer to the SNP. Both call-in surveys and questionnaire data were used, and the reported information on the presence of wild carnivores matched the field observations. What people reported about the frequencies of encountering these species, matched the observations made at call-in sites for two carnivore species (spotted hyenas and jackals). The validity of the reported information was higher when it matched the field observations. Thus, this paper (IV) provides insight on the reported frequencies of livestock depredation and human attacks in relation to the actual number of carnivores species observed. The paper concludes that in areas in which people and wild carnivores share the same landscape, the information provided by local people should be verified using various techniques, as we did using call-in surveys. This will provide a necessary tool for obtaining ecological and social information about the presence of wild carnivores and their impact on people.

General discussion

Understanding local human problems caused by wild carnivores can bring insight into what managers can do to reduce and mitigate human-carnivore conflicts (Treves and Karanth 2003, Thirgood et al. 2005, Hazzah 2006, Koziarski et al. 2016). Communities that are located in protected areas or share the landscape with large carnivores bear direct and indirect costs (Quigley and Herrero 2005, Kidegesho 2008). Direct costs occur through livestock depredation and human attacks, while indirect costs occur when people use their time and money to protect against damage such as livestock depredation (Thirgood et al. 2005). The Maasai and Sonjo tribes keep cattle, sheep, and goats for their subsistence adjacent to the SNP.

Living closer to protected areas increases the chances of carnivores attacking livestock. Adjacent to the park, there are higher numbers of carnivore species, and this correlates with the number of livestock depredation incidences, as in the case of the villages around Jigme Singye Wangchuck National Park in Bhutan (Wanga and Macdonald 2006). Because the Maasai tribe live close to the SNP, they had more reported incidences of livestock depredation than their neighbours, the Sonjo tribe. Incidences of depredation were most common during the daytime when the livestock were in the fields grazing and browsing. During the dry season, herders take their livestock away from the normal grazing grounds in search of green pasture; this, in turn, became a primary contributing factor to depredation by wild carnivores.

Livestock predation patterns in the Maasai and Sonjo tribes have changed after seven years; originally, the predators most responsible for livestock depredation were wild dogs. In the Serengeti ecosystem, the abundance of hyenas is greater than that of other carnivore species, and hyenas have higher tolerance for human-dominated areas (Goymann et al. 2001). Thus, the reported livestock depredation caused by hyenas is greater than that caused by leopards, lions, cheetahs, wild dogs, and jackals. Similarly, in 2007 in the western Serengeti, hyenas were the carnivores most often reported as responsible for livestock depredation. Leopards were the second most reported predator causing depredation in the eastern Serengeti ecosystem; incidences of predation by leopards were common during the dry season when herders wander in the bushy and dense woodlands looking for green pasture to sustain their livestock. Lions and cheetahs were only reported to cause livestock depredation in areas occupied by the Maasai tribe, due to their proximity to the SNP. As habitat degradation occurs coupled with increased human activities, as in the Sonjo tribe, the home ranges of predators such as lions and cheetahs will be displaced by humans (Paper I).

Communities sharing a landscape with carnivores have developed local techniques to protect their livestock against depredation (Patterson et al. 2004, Wanga and Macdonald 2006, Dickman 2010, Jacobs and Main 2015), and the use of multiple techniques seems to be rewarding (Ed and John 2001, Lyamuya et al. 2016b). In protecting against livestock depredation, the Maasai tribe prefers the use of spears, whereas the Sonjo tribe uses arrows tipped with poison from *Acokanthera spp*. In Europe and America, livestock keepers have been successful in using trained dogs to frighten off predators (Gehring et al. 2010, Spira 2014). In South Africa and Namibia, the use of domestic dogs is common; however, in the eastern Serengeti, domestic dogs are not trained, and most of them are in poor health and cannot do the job of protection effectively (Lyamuya et al. 2014a). Precaution is extremely important in enabling communities to coexist with wild carnivores; thus, to develop effective countermeasures, it is imperative to understand the circumstances and patterns of the previous depredations (Patterson et al. 2004, Spira 2014).

As anthropogenic activities continue to increase in the area, prey abundance has declined. Predators find it easier to switch and hunt for domestic animals, as animals are easier to hunt when they are hungry and exhausted (Patterson et al. 2004, Lyamuya et al. 2016b). In areas where prey abundance is higher, the likelihood that predators will look for domestic animals is lower (Patterson et al. 2004, Woodroffe et al. 2005a, Lindsey et al. 2013), which enhances harmonic coexistence with locals (Carter et al. 2012). In a given area, especially one in which wild and domestic animals are both present, higher wild prey abundance and diversity enhances choices for predators (Per et al. 2009, Lyamuya et al. 2016b). Hunting for domestic animals is a learned behaviour that occurs after predators struggle to find wild prey with no success; in turn, as a survival trade-off, they may even kill humans (Paper I).

Attacks on humans by wild carnivores have a long history (Thirgood et al. 2005, Inskip and Zimmermann 2009). The incidence of human attacks has been reported in many cases, and most reported incidents involved people living in proximity to protected areas. In the eastern Serengeti, most attacks occurred to the Maasai tribe as they live close to the SNP; lions, leopards and hyenas were responsible for these attacks. Gaining insight on how, when and where these human attacks occur will enhance management measures in dealing with the problem (Brantingham 1998, Woodroffe et al. 2005c, Nyhus 2010). If local people are educated on how to avoid encounters with predators and what to do when a predator is encountered, this will provide a necessary tool for reducing the incidence of human attacks that result in serious injuries and sometimes loss of human life. Such attacks bring fear to the community, and people are likely to respond to them by killing predators in their surroundings (Røskaft et al. 2003, Thirgood et al. 2005, Nyhus 2010). Most attacks on humans in Africa occur to men, as they perform most of the outdoor activities (Packer et al. 2005) (Paper II).

A variety of factors contribute to predation on humans. When their habitats are fragmented and their prey base is depleted, large carnivores may end up wandering, which increases their chances of encountering humans (Brantingham 1998, Packer et al. 2005, Woodroffe et al. 2005c, Ikanda 2009, Nyhus 2010). A recent attack in the eastern Serengeti was caused by an old male lion, which was probably unable to hunt (*Photo 5*). Following an attack on humans, retaliation against lions and spotted hyenas is common because these species are fearless and may often appear during the daytime in human-dominated areas (Kissui 2008). Retaliation can be direct or indirect. Arrows can be smeared with poison sap from *Acokanthera spp.* or poison can be applied to a carcass; this, in turn, targets carnivores such as lions and hyenas who also feed on carrion. Currently, the use of agrochemical poisons to kill carnivores in east Africa is a serious concern (RCP 2018) (Paper II).

The frequency of livestock depredation is higher when farmers and pastoralists coexist in the same landscape with large carnivores (Spira 2014, Durant et al. 2015, Mbise et al. 2018). In recent years, the Maasai and Sonjo tribes have increased their persecution of wild carnivores, which could potentially cause the extinction of these species if no urgent intervention is made. Local people living with wildlife is the determining factor in these species' survival (Carter et al. 2012, Mbau 2013). Due to livestock depredation and human attacks, these communities hold negative attitudes towards large carnivores. These incidents become negative and dramatic in any society as they may result in serious injuries or loss of human life (Packer et al. 2005, Quigley and Herrero 2005, Carter et al. 2012). In most cases, when individuals encounter predators, they tend to kill them with arrows or spears or indirectly by applying poison to a carcass (Hazzah 2006, Ikanda and Packer 2008, Kissui 2008) (Paper I & II).

Species interactions with humans should be in harmony for sustainable future conservation. Integrating research and conservation is a necessary tool in reaching management goals (Caro et al. 2013). Intervention due to the dwindling of the wild carnivore populations must be situation-specific to ensure their future survival (Treves and Karanth 2003, Carter et al. 2012). In areas where humans and wild carnivores intersect, there is a need to enhance local people's motivation to coexist with wild carnivores and ultimately support conservation initiatives (Hazzah 2006, Lindsey et al. 2013, Lyamuya et al. 2014b, Spira 2014). These people display increased carnivore conservation support if they receive conservation-related benefits (Lagendijk and Gusset 2008, Lindsey et al. 2013). Through conservation initiatives, local communities provide local knowledge that is supportive, can be specifically applied in a particular ecosystem and is consistent with the culture of the people surrounding protected areas (Hazzah et al. 2017) (Paper III).

Encouraging willingness for coexistence between people and large carnivores through measures such as chemoprophylactic programs is very important. Livestock loss induced by diseases is higher than the loss caused by depredation (Nyahongo and Røskaft 2012). The latter most deeply affects the livelihoods of pastoralists because they depend on livestock for their survival (Gifford-Gonzalez 2000, Nyahongo and Røskaft 2012). Chemoprophylaxis helps boost immunity against diseases (Jibbo et al. 2010). Therefore, treating livestock against disease provides a tangible benefit that will improve tolerance to livestock depredation. However, this measure should be examined closely as it will support increased numbers of livestock in the area, which may exacerbate the current problems of habitat destruction and human-carnivore conflict. Another alternative that may bring harmonic coexistence between people and predators is the use of compensation schemes (Rodriguez 2007, Spira 2014), although people's efforts to protect their livestock against depredation might decrease due to the expected compensation (CDPNews 2003, Rodriguez 2007) (Paper III).

Higher numbers of spotted hyenas and jackals were observed at call-in sites close to the SNP. Habitat and season were not important indicators of the frequency of observing carnivore species; this concurs with the findings of Cozzi et al. (2013) in northern Botswana, who found that hyenas were evenly distributed independent of the habitat and season. However, in Maasai Mara National Reserve, Kenya, Ogutu and Dublin (1998) found that the carnivore response tended to vary seasonally with the presence or absence of migratory prey. Additionally, the reported frequencies of encountering lions, leopards, cheetah, hyenas, African wild dogs and jackals were higher closer to the SNP. The future of large carnivore conservation requires a well-structured management plan that will attract the support of local communities, as these species have no physical borders due to their large home ranges (Linnell et al. 2001, Hazzah 2006). Conservation of large carnivores is the goal and aspiration of global concerns that need both local and international support. These carnivores play a great role both ecologically and economically for local people who live with these keystone species (Treves and Karanth 2003, Durant et al. 2011, Valkenburgh and Wayne 2011, Koziarski et al. 2016). Ecologically, they control the prey species abundance, which when absent results in the total collapse of any ecosystem, a phenomenon that is referred to as the cascade effect (Woodroffe et al. 2005c, UWA 2010, Valkenburgh and Wayne 2011, Yirga et al. 2013) (Papers IV).

Due to the increase in the human population, most habitats have been destroyed and displaced by settlements and croplands. Anthropogenic activities are a global menace to the future of wild carnivores, who demand vast land in which to roam (Shivik 2006, Markovchick-Nicholls et al. 2008, Mbau 2013). Furthermore, persecution of large carnivores is also one of the causes of the carnivores' decline in areas adjacent to the SNP. The area adjacent to SNP is becoming a sink for wild carnivores, as many disappear when they go outside the park due to hunting and retaliatory killings (mostly by poisoning) (Masenga et al. 2016). The major threat facing the future of large carnivores globally is conflict with people. When human-carnivore conflicts occur, people's motivation to protect these species declines, and the incidence of persecution also increases tremendously (Woodroffe and Ginsberg 1998) (Paper II & IV).

Harmonic human-carnivore coexistence can be achieved only if conflicts related to livestock depredation and human attacks are mitigated. Proper mitigation measures should be thoroughly implemented to create a promising future for wild carnivores, especially in landscapes where they co-occur with humans. Globally, the main target for conservation stakeholders for large carnivore conservation is to achieve harmonic coexistence with people. Public pressure forces governments to find possible mitigation measures that will reconcile species existence and the local people's need to protect their livestock, lives and lifestyles (Woodroffe et al. 2005b). For instance, in Tanzania in the face of human population increase, separating human activities and conservation activities offers a promising and effective tool for mitigating human-carnivore conflict (Songorwa 2004). However, the only promising practical measure is to promote coexistence between people and large carnivores, especially in the landscapes where the two interact. Control methods can be applied to wild carnivore species when they disturb the livelihoods, lives or lifestyles of people. In the case of the eastern Serengeti ecosystem, many species such as hyenas and jackals will strive to survive, and some will be prone to endangerment like African wild dogs and cheetahs.

Conclusions and recommendations

Many protected areas in Africa are facing great challenges, and the areas adjacent to their borders pose a serious threat to large carnivores and other species (Caro et al. 2013). The source-sink scenario for large carnivores is very strong along the Serengeti borders (Masenga et al. 2016). With the increase in the human population of the Loliondo Game Controlled Area, northern Tanzania, pastoralists are now switching to agro-pastoralism (Mbise et al. 2018). Outside SNP, wild carnivore populations are declining enormously, and habitats conducive to carnivores are also being displaced by farming activities. Presently, the major threat facing large carnivore conservation is retaliation due to problems associated with human attacks and livestock depredation.

Understanding the circumstances and the factors that contribute to human attacks and livestock depredation will help give local communities awareness of how to mitigate such incidences. Large carnivores play an important role, both ecologically and economically, in the lives of local people living with these keystone species. Retaliatory killing of carnivores due to conflicts with people is the major threat facing their future globally. For instance, human attacks are the most irritating and intolerable. In the Maasai and Sonjo tribes, most human attacks occur while people are herding their livestock rather than performing other daily activities. Investigating the circumstances of previous attacks will be the necessary tool for mitigation by raising awareness of where carnivores may be hiding and of what should be done when they are encountered.

Furthermore, employing interdisciplinary techniques will help management develop plausible measures, especially when it comes to livestock depredation and human attacks. For instance, studying livestock depredation, wild prey availability, where livestock graze, and where wild carnivores move in and out of protected areas (using GPS collars and aerial tracking) are possible measures that can be used to reduce human-carnivore conflict. Additionally, when animals are collared, it can be easier for management to determine when they die and to know the cause of their mortality. This monitoring tool can also provide a means of estimating the number of retaliation incidences if many large carnivores are collared.

In the case of the eastern Serengeti ecosystem, living close to the national park (Maasai tribe) results in a higher depredation rate than living far away (Sonjo tribe). There are higher carnivore densities in the villages that are closer to the SNP. In the twelve surveyed call-in sites, the reported frequencies of encountering spotted hyenas and jackals by local people matched the observed numbers over a gradient of distance from the SNP border. Considering the high validity of what local people reported, this confirms other reported cases. Therefore, it is imperative in research endeavours to use interdisciplinary techniques that combine field observation and reports from local people. Additionally, to better safeguard livestock from predators, there is a need to use multiple techniques. Thus, understanding depredation patterns and contributing factors will provide a basis for developing the best countermeasures.

Modern and traditional measures can be used to minimize and/or avoid livestock depredation by wild carnivores. Currently, around Tarangire National Park in northern Tanzania, there is a running project supporting the use of fortified bomas by Maasai communities during the night, and this has proven to be successful to some extent. In the eastern Serengeti ecosystem, most livestock depredation occurs during the daytime, so a different alternative is needed to reduce livestock depredation by wild carnivores. In Kenya, solar power lights around bomas have been used successfully to frighten off wild carnivores during the night. Some bomas in my study area were using these techniques, and it was rewarding compared to other households. For justification purposes, we did not perform statistical analyses because relatively few households used the above-mentioned techniques.

Our future research will attempt to increase awareness of and later to assess the effectiveness of these countermeasures in mitigating livestock depredation in the area. Other measures that these pastoralist communities should consider are the use of adult individuals to herd their livestock and the use of trained domestic dogs. The use of trained domestic dogs, if done wisely, has been successful in Europe and North America and in some African countries including Namibia and South Africa. Although livestock losses caused by disease in the Maasai and Sonjo tribes are higher than the losses caused by depredation, there is a need to improve livestock safeguarding measures coupled with tangible benefits to the local people such as treating their livestock against diseases. If both types of measures are applied wisely, there is a promising goal of improving people’s willingness to coexist with wild carnivores in the area.

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Livestock depredation by wild carnivores in the eastern Serengeti ecosystem, Tanzania

by

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Livestock depredation by wild carnivores in the Eastern Serengeti Ecosystem, Tanzania

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Livestock losses caused by wild carnivores foster negative attitudes and promote retaliatory killings, threatening the future of carnivore populations. Measures to bring about coexistence between humans and carnivores are of great importance to carnivore conservation. The study questionnaire survey involved 180 respondents from Eastern Serengeti tribes (Maasai and Sonjo), all of which owned livestock. Reported livestock depredation in 2016 by the Maasai tribe (pastoralists) was higher than that by the Sonjo tribe (agropastoralists) because the Maasai own many livestock and live closer to the Serengeti National Park boundary. Most livestock depredation occurred during the day when livestock were out feeding and during the dry season. Spotted hyenas *(Crocuta crocuta)* were the most commonly reported carnivore responsible for livestock depredation. Livestock depredation caused by lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) was only reported by the Maasai tribe. Leopards (*Panthera pardus*), jackals (*Canis spp.*), and African wild dogs (*Lycaon pictus*) were responsible for more livestock depredation of the Maasai livestock. A similar study was performed six years earlier, in 2010. Therefore, this study brings insight to the temporal changes of livestock depredation patterns and changes of carnivorous species causing livestock depredation in the Eastern Serengeti ecosystem. The Maasai and Sonjo are the main tribes living in the Eastern Serengeti ecosystem. The Maasai preferably use knives and/or spears, whereas the Sonjo use bows and poisoned arrows to protect their livestock against depredation by wild carnivores, and both tribes prefer the use of multiple techniques to increase the efficiency of livestock protection.

Key words: Boma, herding, Maasai, preferences, Sonjo, tribe, weapons.

INTRODUCTION

Human-wildlife conflict presents an increasing challenge to conservation biology worldwide, and developing novel solutions for the coexistence between humans and different species, particularly carnivores, has been a research focus (Dickman, 2010; Gehring et al., 2010; Woodroffe et al., 2005).

Conflicts escalate when carnivores attack livestock, thereby hampering carnivore conservation (Gehring et al., 2010; Megaze et al., 2017; Treves & Karanth, 2003; Woodroffe et al., 2005). Livestock depredation by large carnivores negatively impacts coexistence between humans and such species (Holmern et al., 2007; Karlsson and Johansson, 2010; Mwakatobe et al., 2013). Livestock represents a source of income to pastoralist communities (Mwakatobe et al., 2013). Hence, if depredation incidences increase, household livelihood quality tends to be compromised (Ogada et al., 2003). Additionally, as the human population grows, particularly in third world countries, human-carnivore conflict increases (Pirie et al., 2017) which hampers the future of large carnivores.

In rural areas, especially those close to protected areas, land for livestock husbandry is open access, which attracts pastoralists to such places. Most people in Africa live in rural areas and there are many trade-offs encountered by people living adjacent to protected areas. The livelihoods of such societies have been compromised due to the costs associated with wildlife interactions (Adams and Hutton, 2007; Nana and Tchamadeu, 2014; Vedeld et al., 2012). Thus, people living adjacent to protected areas tend to have negative attitudes towards wildlife as they impact their livelihoods negatively (Dickman et al., 2014; Romanach et al., 2007; Røskaft et al., 2007). For instance, some communities tend to respond to attacks on their livestock by killing carnivores (Kissui, 2008; Lindsey et al., 2013; Mwakatobe et al., 2013).

Living close to protected areas may have enormous costs, and the human-carnivore conflict in such communities is high (Carter et al., 2012; Holt, 2001; Lindsey et al., 2017). To reduce livestock depredation, local people may employ various traditional husbandry techniques to kill problematic carnivores, with certain techniques being more effective than others (Ed and John, 2001; Lyamuya et al., 2016b; Mwakatobe et al., 2013). Most of these techniques are temporary and inefficient, therefore a long-term solution is needed (Dickman, 2010).

Measures to curb livestock depredation by wild carnivores includes different approaches depending on the culture and livestock keepers (Dickman, 2010). Countries with no consolation schemes for livestock losses from predators use herders, who have developed different guarding techniques. Guarding livestock against depredation has been a successful tool in countries where labour is cheap (Lyamuya et al., 2016b). In the modern world, however, as in Norway, livestock are allowed to roam freely without shepherds because labour costs are high (Widman et al., 2017).

Livestock guarding elsewhere, for instance in the Maasai and Sonjo communities in Tanzania, is a family obligation and is mostly performed by boys and girls who are denied access to school by their parents (Ikanda and Packer, 2008). Thus, they might be less motivated to perform their duties effectively due to lack of incentives (Maclennan et al., 2009). Additionally, the Maasai and Sonjo communities own large flocks of livestock, and herding a large flock might reduce protection from predation. It is easier for carnivores, such as African wild dogs, which normally move in packs, to sneak in and attack large herds of livestock (Lyamuya et al., 2016b).

Many studies in Africa have focused on quantification of reported livestock depredation by wild carnivores in relation to the distance from protected areas. Such studies have been conducted in low human density areas adjacent to protected areas (Holmern et al., 2007; Kissui, 2008; Mwakatobe et al., 2013; Patterson et al., 2004; Rasmussen, 1999). Few studies have evaluated how tribe, age and education may affect how people report numbers of depredated livestock. Each tribe has its own way of living which may influence how people report livestock depredation by wild carnivores. Age can be a predictor of wealth associated with livestock in pastoralist tribes, while education will elucidate whether educated people have more efficient methods of protecting their livestock against depredation. We performed a comparison study between the two tribes (Maasai and Sonjo) to quantify reported livestock depredation by wild carnivores and assess the techniques preferred by both communities in protecting their livestock against depredation.

The presence of large carnivores in any ecosystem is important due to their vital ecological and economical roles (Durant et al., 2011). Monitoring livestock depredation (Spira, 2014) and assessing the preferred techniques used by local communities to safeguard their livestock is therefore relevant to develop good, solid coexistence measures that will enhance the future of all existing carnivore species in the face of human populations. In this study, we addressed three objectives:

(1) To assess if tribe (Maasai and Sonjo), age and education have an effect on the number of livestock reported depredated in a questionnaire;
(2) To determine wild carnivore species responsible for livestock depredation and;

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(3) To assess the preferred techniques of protecting livestock from carnivores within the two ethnic groups.

MATERIALS AND METHODS

Study area

The study was conducted in the Eastern Serengeti ecosystem, in the Loliondo Game Controlled Area (LGCA; Figure 1). The LGCA lies between 1°40′S and 2°50′S and 35°10′E and 35°55′E, covering a total area of about 4,500 km^2 in the Maasai land (Lyamuya et al., 2014a). On the northern side, it borders Narok County (Kenya), on the western side it borders Serengeti National Park (SNP), and on the southern side it boarders the Ngorongoro Conservation Area (NCA). The area includes diverse vegetation types, ranging from forests, woodlands, wooded grasslands, shrub lands, and grasslands (Lyamuya et al., 2016a). Administratively, the area is under control of the District Council, and the District Game Officer (DGO) manages tourism hunting in the LGCA. Hunting without a licensed permit is illegal (MNRT, 2013), and hunting concessions are under the Ortello Business Company of Saudi Arabia. LGCA is the home to the Maasai and Sonjo tribes, the former tribe being dominant. The Maasai people are pastoralists, whereas the Sonjo people are agro-pastoralists (Lyamuya et al., 2014a; Maddox, 2003), where both tribes keep cattle, sheep and goats. An increase in the human population has reduced the available grazing space and resulted in the increasing livestock population grazing on a smaller piece of land results in land and environmental degradation (Lyamuya et al., 2014a). The Maasai people live close to the park boundary, while the Sonjo people live slightly further away (Lyamuya et al., 2016b). Thus, carnivore abundance is higher in the Maasai land compared to the Sonjo land (Maddox, 2003).

Data collection

Data collection was performed from September to November 2016. A sample size above 100 respondents tends to give a broader idea about the information given by respondents, and reduces the biasness of the data (Delice, 2010). We collected data from six villages, in each of which we randomly selected 30 respondents to acquire better details and to ease the data collection work. To be objective we employed a random sampling technique which reduces bias and allows us to cover most of the villages.

A total of 180 respondents were interviewed from six villages, including three villages from the Maasai tribe (Ololosokwan, Oloipiri, and Soitsambu) and three from the Sonjo tribe (Yasimdito, Samunge, and Sale). From each village, 30 respondents were randomly selected. Only one respondent was interviewed from each household. We used local people to introduce us to all interviewed households to acquire confidence and readiness to speak openly. After arriving at a household, we introduced the project and asked if they were ready to answer the questions regarding livestock depredation by wild carnivores. All interviewed persons agreed to give the requested information and we assured them to use their information only for the purpose of our research and as advice to the government. Additionally, we assured their anonymity by hiding their identities. More males were interviewed than females because in the Maasai and Sonjo tribes, men speak on behalf of the household. Females are never allowed to speak openly in the presence of their husband.

Therefore, the sample included more male ($n = 144$) than female ($n = 36$) respondents, as females were interviewed only in the absence of their husband. The survey was conducted through a semi-structured questionnaire employing face-to-face interviews, and questions were in both closed-ended and open-ended. The language of the interview was Swahili for those respondents who spoke it well, and sometimes, a mix of Maasai and Sonjo languages were used by local translators for those respondents who did not understand Swahili clearly.

The information gathered from the respondents was: tribe, gender, age, education level, whether their livestock had been attacked by large carnivores over the last twelve months in the boma or in the pasture (yes, no), when was the last livestock depredation (year), what was the time of depredation, where did the depredation occur, what type of livestock were depredated (cattle, sheep, and goats), what was the number of livestock depredated, what was the carnivore species responsible for the depredation, and what were their herding equipment preferences (Figure 1).

Data analysis

Statistical analysis was performed using the Statistical Package for the Social Sciences (SPSS) version 21 (IBM, 2012).The significance level was set to be below 0.05 ($p < 0.05$). Binary logistic regression analysis (enter method) was performed to determine the probabilities of perceived number of carnivore-induced depredations. Independents variables in the model were (tribe, age and education).

One-way analysis of variance (ANOVA) tests were carried out on the perceived number of livestock depredation and depredation rate between the Maasai and the Sonjo tribes. Chi-square tests determined the differences between the two ethnic groups on the following variables: year of livestock depredation, time (day/night) of depredation, where (boma/pasture) depredation occurred, season (dry/wet) of depredation, type of livestock that was depredated, number of livestock that were depredated, identity of the carnivore responsible for the depredation and herding equipment preferences.

RESULTS

Demographic variables

The sampled population was from two ethnic groups (Maasai and Sonjo), and respondents were above 18 years old. Age categories were youth (18 to 35 years; Maasai; n = 45, Sonjo; n = 37), adult (36-49 years; Maasai; n = 21, Sonjo; n = 37) and elder (>50 years; Maasai: n = 24, Sonjo; n = 16). Educational level for the respondents ranged from no education (Maasai; n = 32, Sonjo; n = 12), primary education (Maasai; n = 48, Sonjo; n = 72) and secondary education (Maasai; n = 10, Sonjo; n = 6).

We interviewed 180 household members (90 respondents from each tribe), of which 135 (75.0 %) had experienced livestock depredation and 45 (25.0 %) had not experienced livestock depredation over the previous 12 months. A total of 662 livestock (cattle = 105, goats = 310, and sheep = 247) were depredated by wild carnivores ($\bar{x} = 13.2 \pm 23.9$, $n = 135$ per household, excluding zeros).

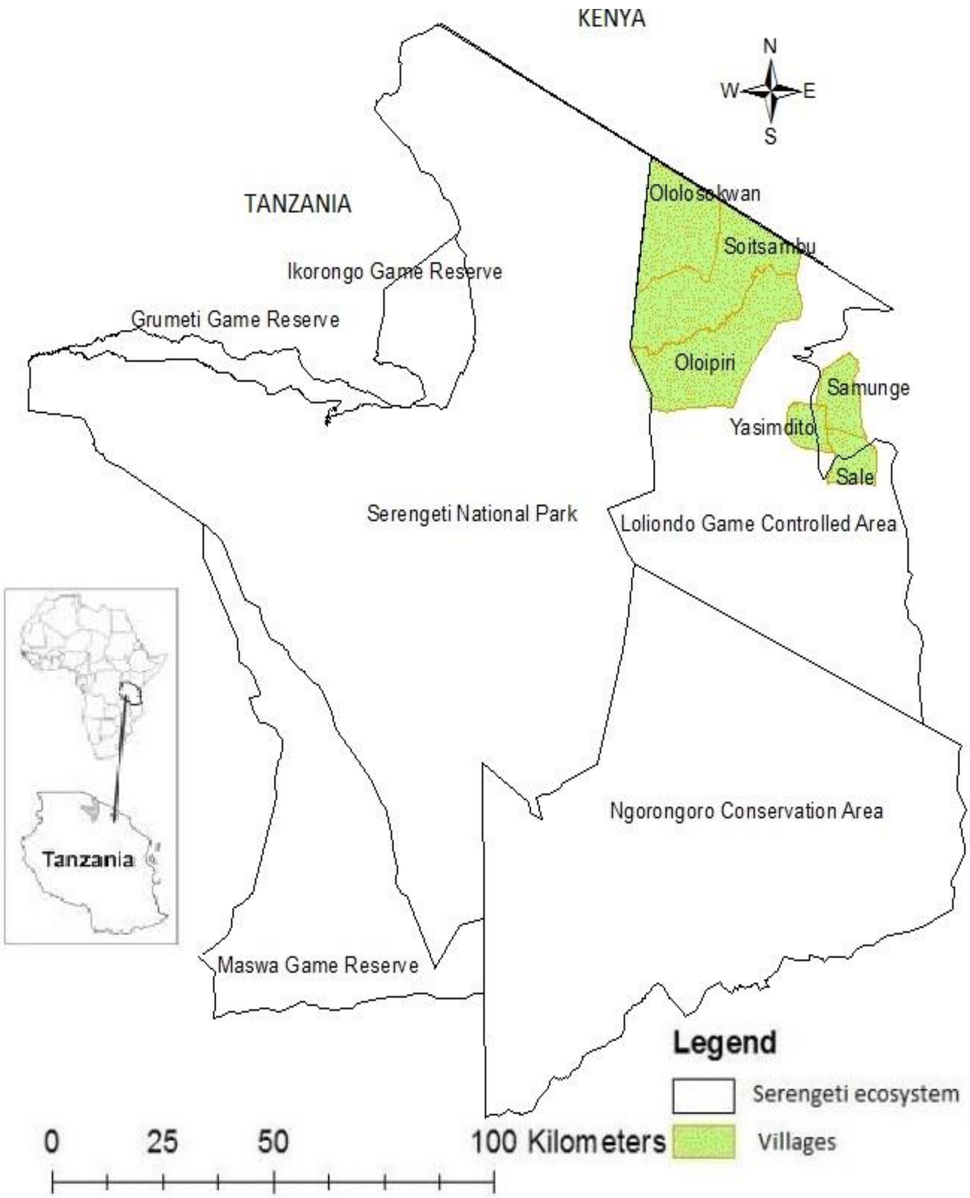

Figure 1. Map showing the study villages (Ololosokwan, Soitsambu, Oloipiri, Samunge, Sale, and Yasimdito) in the Eastern Serengeti ecosystem.

Tribe

Different tests (excluding zeros) were carried out with reported livestock depredation number versus age, education and tribe. Tribe was the only predictor variable that significantly explained the number of livestock

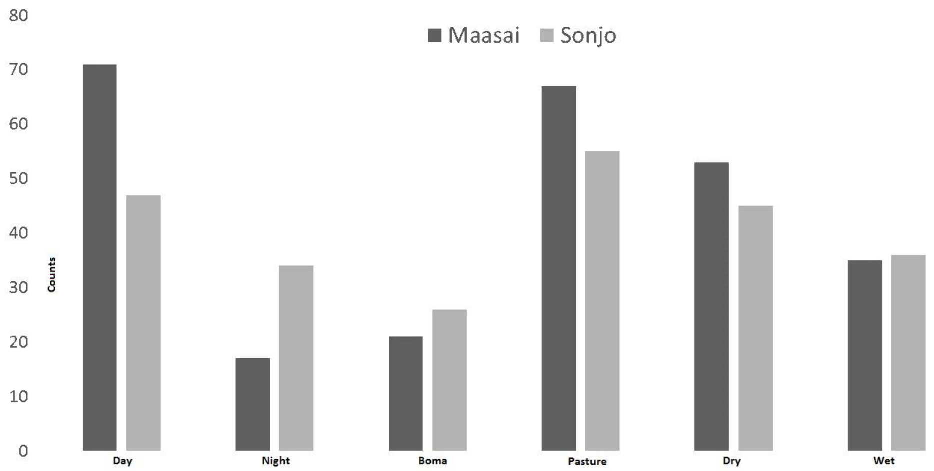

Figure 2. Livestock depredation depending on the time of depredation, where it occurred and in what season it occurred.

Table 1. Carnivore species reported for livestock depredation.

Tribe	Spotted hyena	Leopard	Jackal	Lion	African wild dog	Cheetah	Total depredation
Maasai N	51	33	34	38	14	11	181
%	28.2	18.2	18.8	20.9	7.7	6	100
Sonjo N	32	16	6	0	10	0	64
%	50	25	9.4	0	15.6	0	100

*Some respondents had more than one attack.

depredations (t-test; $t = 6.696$; df = 133, $p < 0.0001$). The other two variables were insignificant (age; rho = -0.014, $p = 0.869$; education; $F = 1.379$, df = 2 and 132, $p = 0.255$). The reported rate of depredated livestock (yes, no) was significantly different between the two tribes (yes: Maasai=60%, Sonjo=40%; and no: Maasai=20%, Sonjo=80%) ($\chi^2 = 23.1$, df = 1, $p < 0.0001$). The Maasai tribe ($\bar{x} = 19.1 \pm 29.2$, n = 81) experienced much higher livestock depredation than the Sonjo tribe ($\bar{x} = 4.3 \pm 4.0$, n = 54) (F =13.6, df = 1 and 133, $p < 0.0001$). The Maasai own more livestock ($\bar{x} = 295 \pm 306.5$, n = 90) than the Sonjo ($\bar{x} = 72.2 \pm 55.4$, n = 90). Additionally, the livestock depredation rate per 1000 livestock was significantly higher in the Maasai ($\bar{x} = 6.9 \pm 10.8$, n = 78) than in the Sonjo ($\bar{x} = 0.4 \pm 0.5$, n = 54) (F = 19.8, df = 1, $p < 0.0001$). More incidences of depredation occurred during 2016 (75%), compared to previous years (25%) ($\chi^2 = 32.3$, df = 1, $p < 0.0001$). Depredation occurred most frequently during the day in both tribes; however, it was significantly more common during the night in the Sonjo tribe ($\chi^2 = 10.3$, df = 1, and $p = 0.001$) (Figure 2). In addition, livestock depredation occurred more frequently in the pasture land than in the boma ($\chi^2 = 6.2$, df = 1, $p = 0.046$; Figure 2). Finally, livestock depredation occurred more frequently during the dry season (Figure 2).

Carnivore species responsible

A significant difference was found in the frequency of attacks by different carnivore species (that is, lion, cheetah, leopard, spotted hyena, African wild dog, and jackal) between the two tribes ($\chi^2 = 27.7$, df = 5, $p = 0.002$; Table 1). In both ethnic groups, spotted hyena was the most common predator (Table 1). Lions and cheetahs were only found to cause livestock depredation in the Maasai land (Table 1), while leopards and jackals caused more livestock depredation in the Maasai tribe than the Sonjo tribe (Table 1). Similarly, livestock depredation by African wild dogs was higher in the Maasai tribe than the

Table 2. Herding equipment preferences with the responses (yes or no) regarding whether the household had experienced livestock depredation.

Livestock depredation	Tribe	Spear and/or knives and club	Combination	Bow and poisoned arrows	Use of domestic dogs	No equipment	Total
-	Maasai N	25	49	0	14	2	90
	%	27.8	54.4	0	15.6	2.2	100
	Sonjo N	0	41	33	15	1	90
	%	0	45.6	36.7	16.7	1.1	100
Yes	-	23	70	20	21	1	-
%	-	92	77.8	60.6	72.4	33.3	-
No	-	2	20	13	8	2	-
%	-	8	22.2	39.4	27.6	66.7	-

Sonjo tribe, though the difference was not statistically significant (χ^2 = 0.8, df = 1, p = 0.38; Table 1).

Preferences of herding equipment

The study results revealed a difference in the preferences of herding equipment between Maasai and Sonjo herders (χ^2 = 69.9, df = 5, p < 0.0001; Table 2). Only three herders did not use any weapon (Table 2). Maasai herders (n = 25) used more spears and/or knives and clubs (Table 2), whereas Sonjo herders (n = 33) preferred to use bows and poisoned arrows (Table 2). Both tribes rarely used domestic dogs, which would alert them to the incoming carnivores during the night or while in the pastures (Table 2). There was a statistically significant difference in the use of herding equipment and the livestock depredation frequencies (yes, no) (χ^2 = 10.7, df = 4, p = 0.03; Table 2).

DISCUSSION

A study similar to the present study was performed in 2010 by Lyamuya et al. (2016b) who studied livestock and herding efficiencies in relation to the livestock loss caused by wild carnivores. This study adds value in assessing the temporal change six years after the last study and providing insight into predation patterns. African wild dogs at that time were the main predator causing livestock losses in the Sonjo land; however, our results found a different pattern. Spotted hyenas were the most common predator among both tribes due to their higher density in the Serengeti ecosystem and ability to commute in both protected and unprotected areas (Goymann et al., 2001). The frequency of livestock depredation by hyenas was higher than that of any other predator (i.e. lion, cheetah, leopard, African wild dog and jackal), as also found in the western Serengeti by Holmern et al. (2007) and Mwakatobe et al. (2013). Maasai herders used knives and/or spears whereas Sonjo used bows and poisoned arrows to protect their livestock against depredation by wild carnivores. Both tribes preferred the use of multiple, rather than single, techniques to increase the efficiency of livestock protection.

Tribe

The study results revealed that more attacks were found to occur in the Maasai tribe lands than in the Sonjo tribe lands because the Maasai own more livestock and live closer to the Serengeti National Park boundary, where there are higher influxes of different wild carnivores (Lyamuya et al., 2016b; Lyamuya et al., 2014b). The frequency of livestock depredation was higher during daytime while herding, with increased rates during the dry season. During the dry season, herders normally take livestock far from home in search of green pastures, which is a predisposing factor for livestock depredation.

Compared to Lyamuya et al. (2016b), this study recorded a higher rate of livestock depredation. Lindsey et al. (2013) found that human tolerance towards carnivores was higher in areas with high wildlife densities. With wild prey numbers declining in the area, carnivores will switch to the available prey (that is, livestock) (Patterson et al., 2004; Souza et al., 2017). Areas with low numbers of wild prey tend to experience increased livestock depredation compared to areas with large numbers of wild prey (Woodroffe et al., 2005). Prey diversity and abundance enhance choices and where different carnivore species will find their favourite wild prey (Per et al., 2009).

Furthermore, prey diversity enhances carnivore-human coexistence due to low livestock depredation incidences (Carter et al., 2012). In some instances, areas with low diversities of wild prey may experience skewed livestock predation (sheep and/or goat) (Woodroffe et al., 2005). Prey preferences of some carnivores, such as hyenas and jackals, which are common in the Maasai and Sonjo areas, are biased towards goats and sheep because of their higher numbers than cattle; thus, the chance of depredation is density dependent (Okello et al., 2014).

Previous studies have found that the absence of compensation and/or consolation schemes worsens the relationship between these communities and carnivores (Dickman et al., 2014; Wanga and Macdonald, 2006). Areas with livestock husbandry see carnivores as a threat to their livelihood (Musiani and Paquet, 2004) and not as tourist benefits, as perceived by the government and investors. In the Maasai and Sonjo communities, there has been a long-standing consolation claim over livestock depredation to the authorities with no rewards, and currently, these communities have developed reporting fatigue to such attacks due to ongoing disappointments.

Responsible carnivore species

Livestock depredation is higher in the Maasai land than the Sonjo land, which correlates with greater numbers of livestock and higher carnivore densities. Similar findings were found in villages around Jigme Singye Wangchuck National Park in Bhutan, where high carnivore densities correlated with increased livestock depredation (Wanga and Macdonald, 2006). Livestock depredation occurred more frequently in pastures than in bomas and during the daytime. Livestock depredation was mainly caused by spotted hyenas, followed by leopards. Livestock depredation by leopards increased during the dry season (Lyamuya et al., 2014a), and this might be due to the fact that livestock are taken into thick bushes and forested areas while searching for green pastures at this time of the year, which are preferred habitats for leopards. The frequency of livestock depredation by African wild dog was minimal and different from previous findings, in which the Sonjo experienced more livestock depredation (Lyamuya et al., 2016b). Livestock depredation by lions was skewed to cattle in the Maasai land, which is similar to the findings of Lyamuya et al. (2016b) in 2010. Livestock depredation by lions and/or cheetahs did not occur in the Sonjo land due to habitat degradation, which has displaced their home ranges. With regard to the livestock numbers, as noted before, the Maasai have greater numbers of livestock than the Sonjo (Lyamuya et al., 2016b). Thus, even a small loss among the Sonjo will have a large impact on household livelihood. This means that the livestock depredation costs are much higher in the Sonjo.

Preferences in herding equipment

Mitigation measures to foster coexistence with carnivores and to tolerate livestock losses should be in place to cultivate positive attitudes towards carnivore conservation (Dickman, 2010; Jacobs and Main, 2015). The use of multiple livestock guarding techniques was rated as the best method to reduce livestock depredation, which agrees with other findings (Lyamuya et al., 2016b). Different communities have different techniques to keep their livestock safe from carnivores (Patterson et al., 2004; Wanga and Macdonald, 2006). Hence, non-lethal techniques to inhibit livestock depredation need to be thoroughly investigated to minimize dwindling carnivore population trends (Ed and John, 2001). For instance, the use of sticks by the Maasai and Sonjo is only for herding livestock, while carrying defensive weapons helps to scare predators away and can sometimes be used to kill them. However, carnivore killing is very challenging because they silently sneak into groups of livestock that are out in the pasture or inside a boma at night. Although the herding equipment preferences differ between the Maasai and Sonjo communities, the use of weapons is biased to men because they are the ones who take on livestock protection responsibilities. While herding livestock, the Maasai people use spears and/or knives, whereas the Sonjo prefer the use of bows and poisoned arrows. The use of domestic dogs can help to deter predators from attacking livestock (Gehring et al., 2010; Spira, 2014). However, in pastoral communities in Eastern Serengeti, dogs are inadequate at performing this task (Lyamuya et al., 2014a), probably because most of them are in poor condition from starvation and lack of health care. The use of a single method to guard livestock is not effective compared to the use of multiple techniques (Ed and John, 2001). Therefore, implementing livestock surveillance and monitoring practices will help to predict depredation patterns and to develop management measures over time (Patterson et al., 2004; Spira, 2014).

Conclusion

This study concludes that there are significant differences in the livestock depredation rates and patterns between the Maasai and Sonjo areas. Livestock depredation was more common among the Maasai tribe, which correlated with higher carnivore densities. Understanding livestock depredation patterns and contributing factors will help pastoralists to adopt the best coexistence measures. Protecting livestock against depredation requires further research, which will unravel the long history of human-carnivore conflict. For protection, it is recommended that both tribes use multiple techniques to herd their livestock.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Paper II

Manuscript

Paper II

Attacks on humans vs. retaliatory killing of wild carnivore in the eastern Serengeti ecosystem, Tanzania

by

Mbise, F. P., Skjærvø, G. R., Lyamuya, R. D., Fyumagwa, R. D., Jackson, C., Holmern, T., & Røskaft, E.

Attacks on humans and retaliatory killing of wild carnivores in the eastern Serengeti ecosystem, Tanzania

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Running head: Attacks on humans and retaliatory killing of wild carnivores

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ABSTRACT

Attacks on humans by wild carnivores are a serious problem, especially where communities and carnivores share the same landscape. When people are injured or killed, community members commonly retaliate by killing the carnivores. Awareness of how to minimize the risk of attacks is important and dependent on an understanding of the circumstances surrounding previous attacks and communicating them back to society. We randomly selected 180 households from both the Maasai and Sonjo tribes. Our findings are based on the reported incidences among the Maasai and the Sonjo tribes living in the eastern Serengeti. Because the Maasai tribe lives close to the Serengeti National Park, they reported a higher frequency of human attacks than the Sonjo tribe over the last 50 years. Most of the human attacks occurred in the wet season during the daytime while herding livestock as opposed to performing other daily activities. Young males from both tribes responsible for herding family livestock were more susceptible to attack by wild carnivores. Fortunately, while most of the attacked victims sustained injuries, none were killed. Lions (*Panthera leo*) were responsible for most of the reported human attacks, followed by leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*). Currently, the trend in human attacks by carnivores is decreasing in both tribes. It was also established that in many incidences, carnivores escaped after attacking humans. Retaliatory killings for lions was most common among the Maasai, while retaliatory killings for hyenas was most common among the Sonjo. Factors associated with these retaliatory killings were as follows: both lions and hyenas feeding on a carcass, lions being fearless of humans, hyenas being frequently seen, and hyena's tendency to run and look back. Our findings provide insight into the circumstances surrounding human attacks in the eastern Serengeti and the fate of these carnivores.

Key words: *attacks, injured, humans, killed, retaliatory killing, wild carnivore*

Word count: 3,943

INTRODUCTION

Globally, attack on humans is a shocking phenomenon as it can lead to serious injuries and/or loss of human life (Löe and Røskaft 2004, Packer et al. 2005, Quigley and Herrero 2005, Thirgood et al. 2005, Gurung et al. 2008, Nyhus 2010, Penteriani et al. 2016). Attacks on humans by wild carnivores exacerbate frustrations following livestock depredation and may persist for a long time after the actual event (Löe and Røskaft 2004, Quigley and Herrero 2005, Thirgood et al. 2005, Røskaft et al. 2007). Human attacks provoke a strong response and are rarely tolerated by communities, who may call for immediate measures to address the problem animals (Packer et al. 2005, Gurung et al. 2008, Ikanda and Packer 2008, Penteriani et al. 2016). With the availability of robust strategies that can reduce or eliminate human attacks (Löe and Røskaft 2004, Nyhus 2010), governments are frequently willing to support such initiatives (Nyhus 2010, Okello et al. 2014). However, understanding the timing and circumstances surrounding human attacks and/or mortalities will assist in the development of implementable strategies to reduce the likelihood of attacks (Löe and Røskaft 2004, Packer et al. 2005, Kissui 2008, Penteriani et al. 2016). Communities living with wild carnivores should be educated on how to reduce human-carnivore encounters and how to behave upon such encounters, especially when sharing the same landscape with these species (Löe and Røskaft 2004, Woodroffe et al. 2005, Penteriani et al. 2016). According to the Wildlife Conservation Act of Tanzania, it is illegal to kill wildlife unless it is necessary (MNRT 2013). Therefore, local communities are expected to report any human attack to the wildlife authority as soon as human attack occurs. Responsible authorities can either relocate problem animals to other areas or kill them. While the Tanzanian government has devoted much effort to promote tourism (Turner 2015), it has failed to solve local problems related to wildlife (Vedeld et al. 2012).

Due to human population growth, development and technological advancements, wild carnivore populations are threatened and have been severely reduced worldwide (Nyhus 2010). Population expansion adjacent to African protected areas has led to carnivore habitats being destroyed and a tremendous decline in prey abundance. Here, carnivores encounter humans in anthropogenically modified landscapes, which may lead to human attacks and/or deaths (Löe and Røskaft 2004, Ikanda and Packer 2008, Penteriani et al. 2016, Pooley et al. 2017). Consequently, conflict escalates and eventually leads to retaliatory killing of carnivores. These incidences are now more commonplace due to the expansion of human populations (Packer et al. 2005, Ikanda and Packer 2008). Thus, a proper management structure and policy to conserve wild carnivores is urgently needed (Pooley et al. 2017).

Retaliatory killing is a major threat facing wild carnivores worldwide (Treves and Karanth 2003, Ray et al. 2005, Zimmermann et al. 2005, Ripple et al. 2014) and urgent intervention is needed at local levels (Kissui 2008). For example, in Kenya, lion populations are declining because lions are frequently killed by local people co-existing with these species (Dickman 2017). The retaliatory killing of carnivores can be accomplished either directly (e.g., spearing) or indirectly (e.g., poisoning) (Hazzah 2006). Improving carnivore management is necessary because of their important ecological and economic role (Treves and Karanth 2003). In addition, their existence provides emotional, intellectual and spiritual benefit to some (Kellert et al. 1996).

In the areas where people and predators share the same landscape, it is imperative to understand and assess the circumstances surrounding human attacks and what should be done to reduce human-carnivore encounters (Löe and Røskaft 2004). Reducing human-attack incidences will foster a better co-existence between people and carnivores, which will ultimately reduce the carnivore's persecution. We hypothesized the following: (1) More human attacks will occur on Maasai land than on Sonjo land because the Maasai will encounter a higher number of carnivores from Serengeti National Park (SNP). (2) Most human attacks will occur while herding livestock because herders sometimes lead livestock into areas of thick bush and forest seeking green pasture, which predisposes them to attacks. (3) Retaliatory killing of carnivores will be greater in the Sonjo areas than in the Maasai areas because of the more frequent use of poisons in the Sonjo community.

METHODS

Study area

We conducted our survey east of Serengeti National Park (SNP), in the Loliondo Game Controlled Area (LGCA) which lies between 1° 40′ S and 2 ° 50′ S and 35° 10′ E and 35° 55′ E (Fig. 1). The main residents in the area consist of the Maasai and Sonjo tribes, and the population is increasing rapidly, leading to major habitat deterioration and change. The human population in Ngorongoro district was 174,274 in 2012 and was projected to be 199,879 by 2017 (NBS 2017). An increasing number of people and their associated activities will result in major habitat changes and compromise the future of wildlife species living in the area.

Data collection

Respondents were randomly selected and sometimes were met in the field, village centres or while visiting friends. Thus, mapping the location of each participating household to make a distribution map was not realistic. A total of 180 respondents from the Maasai (n = 90) and Sonjo (n = 90) tribes were interviewed from September to November 2016. People were asked about any reported and/or witnessed human attacks by wild carnivores in the vicinity of the village and how the attack occurred. It was difficult for many respondents to remember the attack year, so we excluded this from our analyses. Respondents older than 18 years of age were interviewed because they have a broader experience and provide reliable information. The ages of respondents ranged from 20-76 years old. Only eight respondents were older than 68 years of age. Our findings were therefore based on human attacks occurring over the past 50 years. The age categories for attacked victims were as follows: children (< 18 years), youth (18–35 years), adults (36–49), or elders (> 50 years). We interviewed 30 respondents from each village, and our sample totalled 144 males and 36 females. The interview was administered in 6 villages, three from the Maasai tribe (Ololosokwan, Oloipiri, and Soitsambu) and three from the Sonjo tribe (Yasimdito, Samunge and Sale). Swahili, Maasai and Sonjo languages were used during our interview, therefore, we engaged local translators to assist with the interview when vernacular languages were used.

Our survey had open-ended and closed-ended questions for comparison purposes and for acquiring more details that were not captured by our specific questions. Information obtained from respondents was based on age group (youth, adult, elder), gender (male, female), tribe

(Maasai, Sonjo), and education level (never been to school, primary school, secondary school). The key questions were as follows: do you know anyone in this village who has been attacked (injured, killed) by wild carnivores? (yes, no), his/her age group? (child, youth, adult, elder), time of human attack? (day, night), place of the attack? (home, pasture), what was the person doing? (herding livestock; other activities such as fetching water and searching for firewood and/or medicinal plants), human attack season? (wet, dry), carnivore species responsible for human attacks? (lion, leopard, hyena), carnivore's fate after the attack? (escaped or killed), and human attack and/or killing trend? (decreasing, stable or increasing).

Data analysis

Chi-squared and logistic regression analyses were performed using the Statistical Package for the Social Sciences (SPSS) version 24 (IBM 2016). Chi-squared tests were used to determine significant differences between the Maasai and the Sonjo tribes. Logistic regression analysis was used to determine the predictor variable explaining the variation in incidences of human attack.

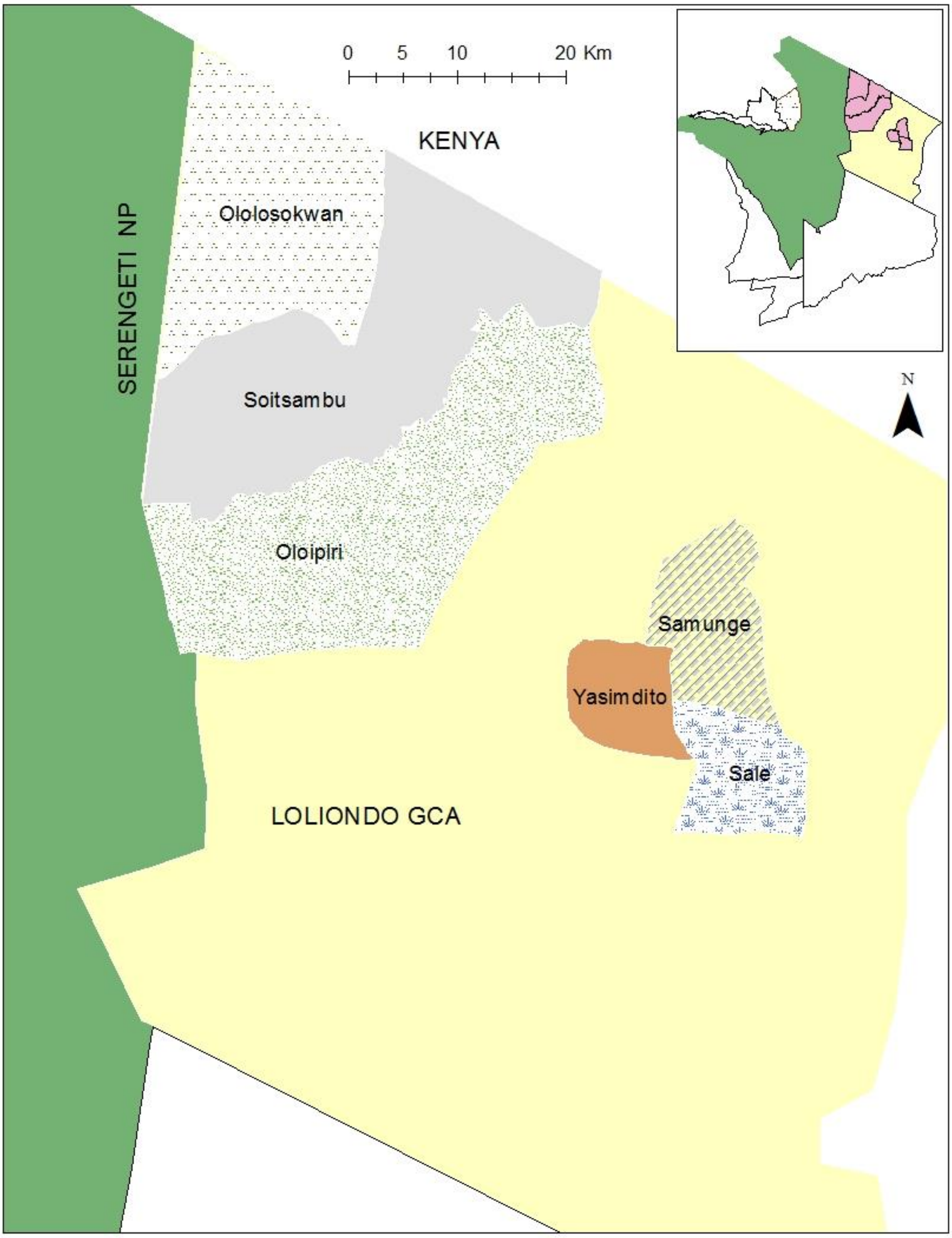

FIG. 1 Map showing the villages included in this study in the eastern Serengeti ecosystem. Upper right; the green area is the Serengeti National Park and the pink area is the study area.

RESULTS

a) Carnivore attacks on humans

Attacks on humans occurred more frequently during the day than at night in both tribes, but the differences between the two tribes were not statistically significant (Pearson $\chi^2 = 0.804$, df = 1, p = 0.370; Table 1). Furthermore, carnivores attacked humans in the Maasai tribal area significantly more than in the Sonjo tribal area (Pearson $\chi^2 = 51.301$, df = 1, p < 0.0001). Most human attacks occurred while people were herding livestock rather than while performing other activities, and most of these human attacks occurred during the wet season, with no significant difference between the two tribes (activity; Pearson $\chi^2 = 1.232$, df = 1, p = 0.267; season; Pearson $\chi^2 = 0.246$, df = 1, p = 0.620; Table 1).

TABLE 1 Numbers of attacks on humans in relation to the attack time, the activity that the victim was involved in, and the season

	Attack time		Activity		Season	
Tribe	Day	Night	Herding livestock	Other activities	Dry	Wet
Maasai	66	5	54	17	15	56
%	93	7	76.1	23.9	21.1	78.9
Sonjo	20	3	20	3	6	17
%	87	13	87	13	26.1	73.9

*__Other activities__ such as fetching water and searching for firewood and/or medicine

More males were attacked than females, and the number of attacked individuals in the Maasai tribal area did not differ significantly from those in the Sonjo tribal area (Pearson $\chi^2 = 0.027$, df = 1, p = 0.87; Table 2). More youths than children or adults were attacked by wild carnivores, and the attack rates of different age groups differed between the two areas (Pearson $\chi^2 = 6.63$, df = 2, p = 0.036; Table 2). More people were injured when attacked by wild carnivores than killed, and these frequencies differed significantly between the two areas (Pearson $\chi^2 = 51.44$, df = 1, p < 0.0001; Table 2).

TABLE 2 Human attacks according to gender, age group and victim fate

	Gender		Age group			Victim fate	
	Male	Female	Children	Youth	Adult	Injured	Killed
Maasai	64	7	0	58	12	59	12
%	90.1	9.9	0	82.9	17.1	83.1	16.9
Sonjo	21	2	2	14	8	20	3
%	91.3	8.7	8.3	58.3	33.4	87	13

A binary logistic regression analysis was performed to test the variation in the reported human-attacks in the two areas, with one dependent variable being the response (yes, no) and five independent variables (attack time, tribe, victim activity, attack season, and where attack occurred) being used (Wald $\chi^2 = 229.6$, df = 5, $p < 0.0001$, Nagelkerke $r^2 = 0.961$). Almost all variables (attack time; B = 8.499, Wald $\chi^2 = 9.260$, df = 1, p = 0.002; tribe, B = -14.971, Wald $\chi^2 = 8.933$, df = 1, p = 0.003; victim activity; B = 3.232, Wald $\chi^2 = 7.712$, df = 1, p = 0.005) were significant in explaining the variation on human attack incidences. Attack season was almost statistically significant (B = -5.579, Wald $\chi^2 = 3.638$, df = 1, p = 0.056). Finally, the variable "where attack occurred" was not statistically significant in explaining the variation in human-attack incidences.

b) Wild carnivores

Overall, lions (*Panthera leo*) caused most of the human attacks, followed by leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*). However, leopard attacks were more common in the Sonjo tribe than in the Maasai tribe (Table 3). The attack rates by the three wild carnivores (lions, leopards, hyenas) differed significantly between the two tribes (Pearson $\chi^2 = 11.04$, df = 2, p = 0.004; Table 3). The attack rates by lions and leopards differed significantly between the two tribes ($p < 0.0001$), while the attack rates by hyenas did not differ significantly between the two tribes (p = 0.3173; Table 3). Although both tribes claimed that the attack rates are decreasing, a significantly higher frequency of Maasai claimed that they were stable or increasing (Pearson $\chi^2 = 9.86$, df = 2, p = 0.007; Table 3).

TABLE 3 Attack trends and predators responsible for human attacks in the Maasai and Sonjo tribes

	Responsible carnivore			Attack trend		
Tribe	Lion	Leopard	Spotted hyena	Increasing	Stable	Decreasing
Maasai	55	9	7	11	12	48
%	77.5	12.7	9.8	15.5	16.9	67.6
Sonjo	2	17	4	0	0	23
%	8.7	73.9	17.4	0	0	100

c) Retaliatory killing of wild carnivores

Most of those carnivores reported to attack and/or kill humans escaped afterwards; however, the difference was not statistically significant between the two tribes (Pearson $\chi^2 = 0.36$, df = 1, p = 0.55). In both the Maasai and the Sonjo tribes, respondents were not very eager to kill carnivores once they threatened and/or killed humans in their area, although the number of "yes" responses between the two tribes differed significantly (Pearson $\chi^2 = 24.33$, df = 3, $p < 0.0001$; Table 4). Retaliatory killing of lions was most common among the Maasai, while retaliatory killing of hyenas was most common among the Sonjo (Table 4) (lions Pearson $\chi^2 = 31.25$, df = 1, $p < 0.0001$, hyenas Pearson $\chi^2 = 6.46$, df = 1, p = 0.01). Factors associated with these retaliatory killings were as follows: both lions and hyenas feeding on a carcass, lions being fearless of humans, hyenas being frequently seen, hyena's tendency to run and look back. The reason for killing hyenas was significantly different between the two tribes (Pearson $\chi^2 = 11.4$, df = 2, p = 0.003; Table 4), while for lions, the difference in reasons was not significant (Pearson $\chi^2 = 1.64$, df = 1, p = 0.201; Table 4).

TABLE 4 Retaliatory killing and reasons behind the killing

Tribe	Killing responses -Lion		Killing responses-Spotted Hyena		Reason for killing-Lion		Reasons for killing-Spotted hyena		
	Yes	No	Yes	No	Feeding on carcass	Fearless	Seen frequently	Run & look back	Feeding on carcass
Maasai	33	57	33	57	3	30	15	10	8
%	36.7	63.3	36.7	63.3	9.1	90.9	45.5	30.3	24.2
Sonjo	3	87	50	40	1	2	15	5	30
%	3.3	96.7	55.6	44.4	25	75	30	10	60

***Fearless** – never run when they see humans

DISCUSSION

This study reveals incidences of human attacks that have never been reported in the eastern Serengeti and provides insights into how such attacks occur and the characteristics of these attacks, including the time, season, people prone to these attacks, and the fate of these carnivores after attacking humans. Proximity to the park (Maasai) showed a higher rate of human attack than living further away (Sonjo) due to a higher number of carnivores coming from Serengeti National Park. Understanding the circumstances surrounding human attacks will provide insight into how to reduce such attacks. Awareness of how to reduce human-carnivore encounters and how to behave when such encounters occur will help the communities co-existing with carnivores avoid attacks that lead to serious injuries and/or loss of life. When attacks on humans are reduced, it fosters a harmonic coexistence between people and predators. Lions, leopards and spotted hyenas were the main predators responsible for human attacks. Most of these attacks occurred in the wet season during the daytime while people were herding their livestock as opposed to doing other activities. Herding livestock is the responsibility of young males according to these tribes' order of duties, and young males were in fact more susceptible to these attacks, as they sometimes pass through the risky habitats preferred by predators when searching for green pasture.

Carnivore attacks on humans

As found by Packer et al., (2005), human attacks occurred most frequently on males in both tribes because men are likely to do more outdoor activities, are more eager to kill carnivores and walk at night. More human attacks occurred in the Maasai community than in the Sonjo community most likely because the Maasai live closer to the Serengeti, which has a higher number of carnivores. Once human attacks occur, it is common for villagers to kill the responsible carnivore. In our study, those carnivores were normally lions, leopards and hyenas. When human attacks occur, they receive great attention and bring fear to the community (Røskaft et al. 2003, Thirgood et al. 2005, Nyhus 2010). There is a long history of wild carnivores attacking humans (Thirgood et al. 2005, Inskip and Zimmermann 2009). Attacks on humans typically occur in landscapes where humans and carnivores interact. As a result, promoting coexistence between humans and carnivores is the best approach to solving this problem, otherwise extinction will be the likely fate for many carnivore species around the world (Brantingham 1998, Woodroffe et al. 2005, Nyhus 2010).

More young adults were attacked than children or elders. Young people are responsible for herding livestock far from their home and sometimes look after livestock in risky areas (bushes and forests), which increases the risk of attack by wild carnivores. Once a herder notices the presence of a carnivore while herding livestock, they defend their livestock and/or try to scare away the carnivores. This behaviour further increases the chance of being attacked. Most of the attacks occurred during the wet season perhaps because the grasses are taller, making it harder to detect carnivores. In most incidences, carnivores tended to escape after attacking people. Due to the present human population increase, land use changes and retaliatory killings, the number of wild carnivores has declined in recent years (Mbise et al. 2018). As a result, the reported number of human attacks in the Maasai and the Sonjo communities has decreased compared to that in earlier years.

Responsible wild carnivores and retaliatory killings

Lions, leopards and hyenas were the only carnivore species reported to cause human attacks. More of these human attack incidences occurred in the Maasai area than in the Sonjo area due to a higher number of wild carnivores in the former area because of its proximity to the SNP. Predators attacking humans is a rare phenomenon, and the reasons behind most of these attacks may be due to a depleted prey base, an inability to hunt, old age, or behaviour learned from their parents (Packer et al. 2005, Ikanda 2009, Nyhus 2010). For instance, in a recent lion attack that occurred in 2016 at Ololosokwan village, one of our respondents claimed that the lion who attacked him in the pasture while he was looking for a lost sheep was an old male. However, it was the stealthy behaviour of leopards that was responsible for more human attacks in the Sonjo tribe compared to lions and hyenas. Additionally, on Sonjo land, forests are common and represent ideal leopard habitat. During the dry season, herders usually move their livestock long distances in search of pasture, which increases the risk of attack.

Spotted hyenas were at higher risk of being poisoned following an attack on people. Kissui (2008) found the same for communities living around Tarangire National Park, Tanzania. Lion killings were also common because they do not fear people and appear during the day time (Kissui 2008). This motivates locals to smear poison on carcasses, which ultimately kills lions and hyenas. The higher frequencies of retaliatory killing in the Sonjo tribe may contribute to a higher rate of carnivore decline in this area. The Maasai tribe, on the other hand, has a long history of coexistence with carnivores compared to the Sonjo tribe, although currently, their culture has started changing dramatically, which may threaten local carnivore populations. The Sonjo used arrows coated with a poison sap from the bark of the Mroda tree *(Acokanthera spp.)* (*Anonymous, 2016*). To protect wild carnivore populations, there is an urgent need to find mechanisms for coexistence between local communities and carnivores as suggested by other studies (Rasmussen 1999). Illegal killing of carnivores can be either direct or indirect. For instance, leopards commonly suspend their kill on a tree, and locals take advantage of this by sneaking towards the carrion and putting poison on it, thus indirectly killing it. Using dogs to chase and directly kill leopards is sometimes risky because leopards habitually climb trees and can attack when approached.

Efforts against the use of lethal control have so far been successful due to the ecological and economic benefits of wild carnivores (Treves and Karanth 2003). However, there remains a great need to assess lethal methods that communities use to kill carnivores. Some killing techniques have serious effects on the carnivore population and the food web in general (Masenga et al. 2013, RCP 2018). For instance, poisoning may target a specific carnivore species but result in the deaths of other untargeted animals such as vultures and other birds of prey (RCP 2018). In conclusion, all three hypotheses are supported by our findings. Most reported human attacks occurred in the Maasai tribal area, and these attacks were more frequent while people were herding livestock than while doing other daily activities. However, retaliatory killings were most common in the Sonjo tribal area. We recommend more effort to promote coexistence between carnivores and humans in this area, and zoning would be one of the alternatives to separate human activities from the preferred habitat of wild carnivores. Based on past incidences, more awareness of avoiding these human attacks should particularly be encouraged in herders.

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Paper III

Manuscript

Paper III

Can conservation incentives promote people's willingness to coexist with large carnivores in the eastern Serengeti ecosystem?

by

Mbise, F. P., Wanda, J. S., Jackson, C., Fyumagwa, R. D., Lyamuya, R. D., Skjærvø, G. R., & Røskaft, E.

Can conservation incentives promote willingness to coexist with large carnivores in the eastern Serengeti ecosystem?

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Running head: Incentives to promote coexistence with large carnivores

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ABSTRACT

Communities living adjacent to protected areas tend to express more willingness to coexist with large carnivores in their areas when they receive tangible benefits. Our aim was to explore people's willingness to coexist with large carnivores, including lions *(Panthera leo),* leopards *(Panthera pardus)*, cheetahs *(Acinonyx jubatus)*, spotted hyenas *(Crocuta crocuta)*, African wild dogs *(Lycaon pictus)* and black-backed jackals *(Canis mesomelas schmidti)*. We used a pre-test and post-test approach by implementing a chemoprophylactic program as a conservation incentive among the Maasai and Sonjo tribes living in the eastern Serengeti, Tanzania. Chemoprophylaxis is the prevention of infectious disease by using chemical agents. The pre-test results showed that both tribes had low willingness to coexist with these large carnivores. Of the two tribes, the Sonjo tribe was less willing than the Maasai tribe. Our post-test results indicated an increase in willingness to coexist with large carnivores in their area because the livestock loss due to large carnivore depredation was significantly lower than that caused by diseases in both tribes. Therefore, this study calls for more conservation incentives to local people to promote their willingness to coexist with large carnivores in their areas.

Key words; *coexistence, depredation, diseases, large carnivores, livestock, Maasai and Sonjo tribes*

Word count: 3,747

INTRODUCTION

Coexistence between humans and carnivores is only possible (Carter and Linnell 2016) if both biological and social strategies are used wisely to curb conflict (Treves and Karanth 2003, Redpath et al. 2013) and thereby reduce carnivore mortality (Treves and Karanth 2003). According to Carter & Linnell (2016), coexistence is the "dynamic but sustainable state in which humans and large carnivores co-adapt to living in shared landscapes where human interactions with carnivores are governed by effective institutions that ensure long-term carnivore population persistence, social legitimacy, and tolerable levels of risk". Aiming for coexistence is the way forward to reduce human-carnivore conflict, which in turn will save carnivores in the future (Woodroffe et al. 2005, Dickman 2010).

Previous studies have revealed that once these conservation conflicts are managed, negative impacts on biodiversity are reduced as well (Woodroffe et al. 2005, Lagendijk and Gusset 2008, Vedeld et al. 2012, Redpath et al. 2013). The management of conflicts between people and carnivores will cultivate positive attitudes, which in turn will enhance conservation initiatives (Conover 2002). This observation also supports findings that people affected by large carnivores through human attacks and livestock depredation normally express negative attitudes and revenge by killing the carnivores using either poison and/or snares (Linnell et al. 2001, Hazzah 2006, Romañach et al. 2007, Dar et al. 2009, Abade et al. 2014).

Despite human population growth causing carnivore habitats to shrink, measures should be taken to merge both human activities and carnivore conservation (Treves and Karanth 2003). If efficient management practices are implemented, coexistence between people and predators can be enhanced (Linnell et al. 2001). Livestock depredation in rural areas is the main cause of human-carnivore conflict. Consolation programs should be implemented to help the victims realize tangible benefits from to the presence of carnivores (Breitenmoser 1998, Skonhoft 1998). It has been found that implementing conservation incentives such as a chemoprophylactic program improves coexistence between humans and large carnivores (CDPNews 2003). Chemoprophylaxis is the prevention of infectious disease by using chemical agents to boost livestock immunity (Jibbo et al. 2010). If local people are satisfied with conservation incentives, their conflicts with carnivores may be reduced.

Therefore, understanding local communities' attitudes towards carnivores is necessary in conservation planning. When attitudes are positive towards large carnivores, people are more willing to coexist with these animals, which contributes to their conservation (Hazzah 2006). For instance, African lion populations are declining due to the negative attitudes of local communities living in proximity to these species and the resulting actions (Dickman 2017). Thus, promoting and motivating local communities to increase their willingness to coexist with large carnivores will enhance their conservation initiative (Dickman et al. 2014).

The overall aim of this study was to test whether people's willingness to coexist with large carnivores would change after the implementation of a chemoprophylactic program. In testing, we had two hypotheses: (1) Livestock diseases are the main contributing factor to livestock loss and cause more deaths than carnivore depredation among the livestock of the Maasai and Sonjo tribes, and (2) therefore, the implementation of a chemoprophylactic program would be of paramount importance to these communities because it would reduce livestock losses, which would be expected to improve tolerance towards large carnivores.

MATERIAL AND METHODS

Study area

Our study was conducted in the Eastern Serengeti ecosystem, Tanzania, and all surveyed villages were located in the Loliondo Game Controlled Area (LGCA). The Maasai tribe lives inside the LGCA, and the Sonjo tribe lives on the eastern border of this area. Administratively, the LGCA is under the Ngorongoro District Council (MNRT 2013) and covers approximately 4500 km^2 (Lyamuya et al. 2016). The LGCA is bordered by Serengeti National Park to the west, Ngorongoro Conservation Area to the south, Kenya to the north, and Lake Natron to the east (Masenga and Mentzel 2005, Lyamuya et al. 2016). The LGCA has a rich diversity of ungulate species, including wildebeest (*Connochaetes taurinus),* zebra (*Equus burchelli)*, impala (*Aepyceros melampus*), Grant's gazelle (*Nanger granti)*, and Thomson's gazelle *(Eudorcas thomsonii*), which occur sympatrically with humans. The famous Serengeti-Mara wildebeest migration passes through parts of the LGCA. The area has all five large carnivore species: lions *(Panthera leo),* leopards *(Panthera pardus)*, cheetahs *(Acinonyx jubatus)*, spotted hyenas *(Crocuta crocuta)*, and African wild dogs *(Lycaon pictus)* (Maddox 2003, Holdo et al. 2010). The Maasai and the Sonjo tribes experience significant livestock losses to large carnivores and diseases (Lyamuya et al. 2016). We collected data from six villages: three Maasai tribes (Ololosokwan, Soitsambu and Oloipiri) and three Sonjo tribes (Yasimdito, Samunge and Sale) (Fig. 1). The Maasai tribe are pastoralists, while the Sonjo tribe are agro-pastoralists (Masenga and Mentzel 2005).

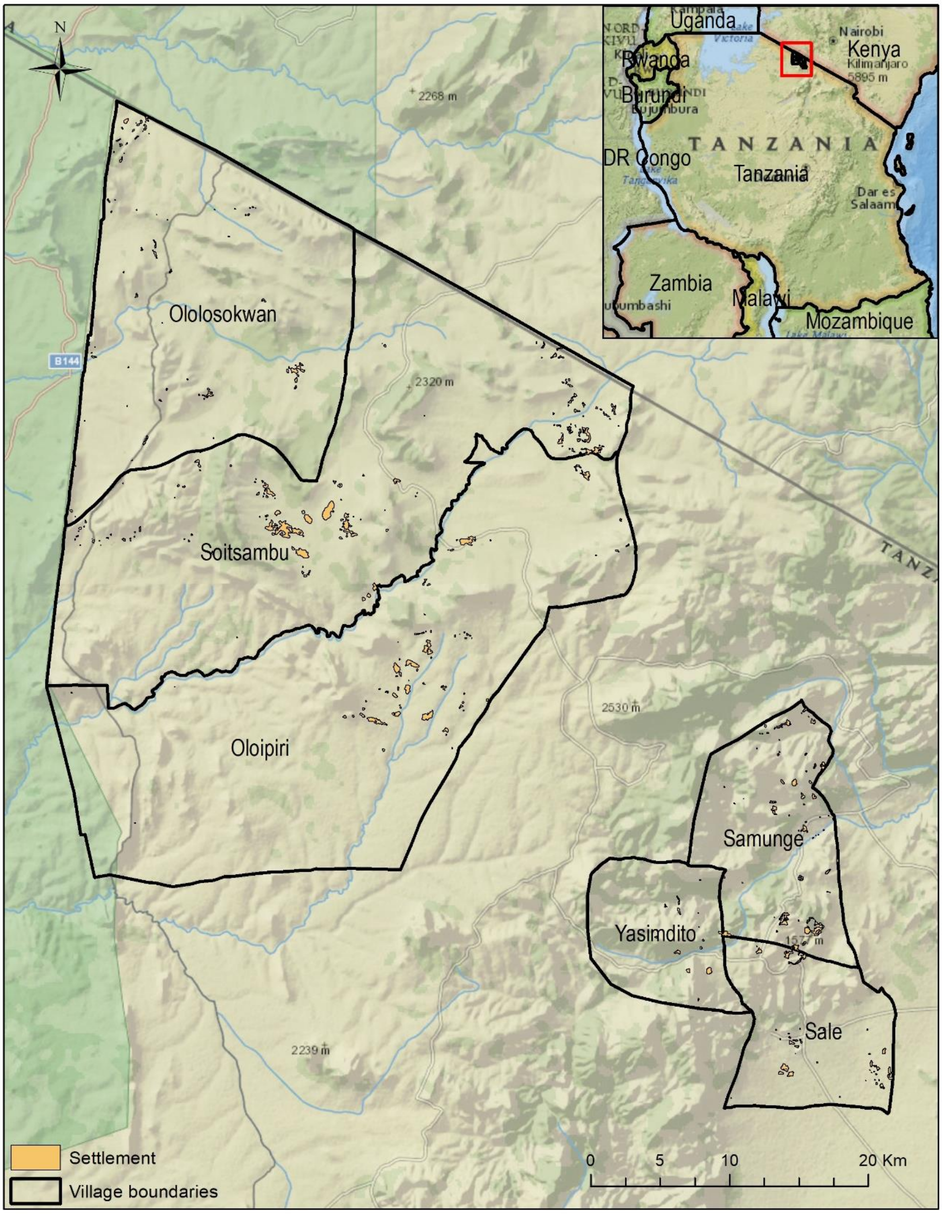

Figure 1: Map showing the study villages of Ololosokwan, Soitsambu, Oloipiri, Samunge, Sale, and Yasimdito in the Eastern Serengeti ecosystem.

Data collection

Data were collected in September 2016 and again in February 2017 using a pre-test and post-test questionnaire survey. In September 2016, the survey of people's willingness to coexist with large carnivores was carried out as the pre-test with the aim of gathering responses from the Maasai and Sonjo tribes before the conservation incentive (chemoprophylactic program) was introduced. The people's willingness to coexist with large carnivores was assessed in an open way to determine whether the responses were positive, neutral or negative. The question asked was "Will conservation incentives be helpful to motivate your willingness to coexist with large carnivores?" The question assessed the respondents' willingness to coexist with large carnivores in their area based on whether they agreed that conservation incentives promote willingness to overlook livestock loss due to depredation by large carnivores (positive), whether the respondents disagreed on the issue (negative) and whether the respondents had no opinion regarding the two ideas (neutral). To avoid influencing the respondents' answers, we did not mention what incentive would come next. In conjunction with this question, we also recorded the reported number of livestock losses for the last two years (2015 and 2016) caused by large carnivores and diseases.

Common diseases in the area were coenurosis, East Coast fever (ECF), Contagious Bovine Pleuropneumonia (CBPP), and anthrax. However, in the chemoprophylactic program we targeted helminths infestation and tick-borne haemoparasites especially ECF. ECF is caused by *Theileria parva* from infected ticks (*Rhipicephalus appendiculatus*). ECF affects lymph nodes first and then spreads to the red blood cells, resulting in severe lung edema and finally death (Kivaria 2007, Gilioli et al. 2009). Coenurosis is a common neurological disease for both goats and sheep caused by tapeworms of the genus *Taenia multiceps*. The cyst is transmitted when infected domestic animals and large carnivores contaminate pastures with their feces. The infective *Coenurus cerebralis* cysts are then swallowed by sheep and goats (Scala and Varcasia 2006, Sharma and Chauhan 2006). CBPP is transmitted by infective aerosol inhalation of *Mycoplasma mycoides mycoides* (Scott 2014, Almaw et al. 2016). Anthrax is a zoonotic disease caused by the *Bacillus anthracis* bacterium, which can be transmitted to humans through the consumption of infected carcasses or by handling infected animal products. The bacterium has no animal reservoir but is an environmental bacterium that exists in spore form in the environment and in vegetative form in infected animals, and the disease affects all warm-blooded animals, both wild and domestic (Smith et al. 1999, Hugh-Jones 2014).

After four months (February 2017), a post-test survey was carried out at the same time that chemoprophylaxis was given to the livestock of our previous respondents. The chemoprophylactic program exercise was administered by a Tanzania Wildlife Research Institute (TAWIRI) veterinary officer. We administered two sets of drugs: (1) oxytetracycline hydrochloride 20%, a long acting antibiotic against a wide range of gram-positive and gram-negative bacteria and other microorganisms, such as *Mycoplasma pneumoniae*, *Coxiella burnetti* and *Plasmodium spp.*; and (2) albendazole 10%, a broad spectrum anthelminthic for the prophylaxis and treatment of immature and mature infectious gastrointestinal nematodes, lung worms, tape worms and trematodes.

During February, due to drought, some respondents moved their livestock to other villages, so our sample size dropped from 180 to 120 respondents. We asked the same question about their willingness to coexist with large carnivores if they received conservation incentives that was asked previously. In the Maasai and Sonjo tribes, only men have a right of say, so we had more male participants than female s (Table 1) (Mbise et al. 2018). Therefore, it is a challenge to acquire an equal number of males and females, and doing so requires additional time in the field (Mbise et al. 2018). Age categories were split into three groups (youth = 18 – 35 years, adult = 36 – 49 years, and elderly = above 50 years). Most of the respondents belonged to the adult group (Table 1). Most of the respondents had a primary education (Table 1), and all the respondents were either from the Maasai or Sonjo tribes (Table 1).

Data analyses

We used SPSS version 24 for the data analyses (IBM 2016), which included multinomial logistic regression, paired samples t-tests, one-way ANOVA tests and chi-square tests. Multinomial logistic regression was used to determine the predictor variable that explained most of the variation in people's willingness to coexist with large carnivores. Paired t-tests were used to assess potential changes in people's willingness to coexist with large carnivores in both tribes. A one-way ANOVA test was used to explain the differences in livestock losses due to diseases and depredation. The chi-square test was used to explain disease frequency differences between the two tribes. The data were tested for normality, and the p-value was set to below 0.05.

Table 1: Demographic variables of the respondents

		N	%
Sex	Male	97	80.8
	Female	23	19.2
Age	Youth	39	32.5
	Adult	49	40.8
	Elderly	32	26.7
Education	Informal	35	29.2
	Primary	71	59.2
	Secondary	14	11.6
Tribe	Maasai	60	50.0
	Sonjo	60	50.0

RESULTS

People's willingness to coexist with large carnivores before implementing the conservation incentive

We used a multinomial logistic regression analysis to test the variation in the people's willingness to coexist with large carnivores before implementing the chemoprophylactic program (positive, neutral, and negative) as a dependent variable towards three independent variables (tribe, age and education). The test was statistically significant (Pearson $\chi^2 = 23.896$, df = 10, p = 0.008, Nagelkerke $r^2 = 0.237$). However, tribe was the only predictor variable explaining this variation in the people's willingness to coexist with large carnivores. Both tribes had lower willingness to coexist with large carnivores, although the Sonjo tribe was less willing than the Maasai tribe (Pearson $\chi^2 = 8.159$, df = 2, p = 0.017; Table 2).

Table 2: People's willingness to coexist with large carnivores before the chemoprophylactic program

Tribe	Positive		Neutral		Negative	
	N	%	N	%	N	%
Maasai	7	10	17	30	36	60
Sonjo	1	1.7	6	10	53	88.3

People's willingness to coexist with large carnivores after implementation of the conservation incentive

To explain the variation in the people's willingness to coexist with large carnivores after implementation of the chemoprophylactic program (positive, neutral, and negative), we tested three independent variables (tribe, age and education) using multinomial logistic regression. The test was statistically significant (Pearson $\chi 2 = 47.917$, df = 10, $p < 0.0001$, df = 10, Nagelkerke $r^2 = 0.427$). Again, tribe was the only predictor variable explaining this variation in the people's willingness to coexist with large carnivores, with the Maasai tribe's willingness being higher than that of the Sonjo tribe (Pearson $\chi^2 = 36.149$, df = 2, $p < 0.0001$; Table 3). The willingness to coexist with large carnivores increased in both tribes after the conservation incentive was implemented (Maasai: Paired samples t-test, $t = 7.812$, df = 59, $p < 0.0001$; Sonjo: Paired samples t-test, $t = 15.108$, df = 59, $p < 0.0001$) (Tables 2 & 3).

Table 3: People's willingness to coexist with large carnivores after the chemoprophylactic program

Tribe	Positive		Neutral		Negative	
	N	%	N	%	N	%
Maasai	55	91.7	5	8.3	0	0
Sonjo	33	55	4	6.7	23	38.3

Major factors contributing to livestock losses

Our results revealed that the number of livestock losses due to large carnivore depredation was significantly lower than the number caused by diseases in both tribes (Maasai: $t = -5.373$, df = 3 and 59, $p < 0.0001$; Sonjo: $t = -7.820$, df = 3 and 59, $p < 0.0001$) (Table 4). Goats and sheep were significantly more prone to diseases than cattle in both tribes ($F = 34.89$, df = 1 and 118, $p < 0.0001$) and ($F = 25.79$, df = 1 and 118, $p < 0.0001$), respectively. Additionally, predators killed significantly more goats and sheep than cattle ($F = 9.47$, df = 1 and 118, $p = 0.003$), ($F = 9.16$, df = 1 and 118, $p = 0.009$), and ($F = 20.59$, df = 1 and 118, $p < 0.0001$), respectively (Table 4).

Table 4: Comparison of livestock losses related to diseases and carnivore depredation in the Maasai and Sonjo tribes.

Tribe		Cattle loss-diseases	Goat loss-diseases	Sheep loss-diseases	Depredated cattle	Depredated goats	Depredated sheep
Maasai	Mean	12.7	25.8	20.7	2.5	3.2	14.7
	Std.	15.4	21.1	16.5	1.9	2.5	13
Sonjo	Mean	5.9	10.4	6.7	1.6	1.5	1.6
	Std.	5.7	8.8	6.6	1	0.8	2.7

East Coast Fever and Contagious Bovine Pleuropneumonia were the most common diseases causing cattle loss in the Maasai and the Sonjo tribes, respectively; however, the difference between the two tribes was not statistically significant (Pearson $\chi^2 = 1.427$, df = 2, $p = 0.49$; Table 5). Goats and sheep were more affected by coenurosis than by anthrax, and East Coast Fever, with no differences between the two tribes (Pearson $\chi^2 = 0.962$, df = 2, $p = 0.81$; Table 5).

Table 5: Cattle, goat and sheep losses due to different diseases

	Diseases-cattle			Diseases-goats		Diseases-sheep		
Tribe	Anthrax	CBPP	ECF	Coenurosis	Anthrax	Coenurosis	Anthrax	ECF
Maasai	5	18	25	46	13	29	13	15
%	10.4	37.5	52.1	78	22	50.9	22.8	26.3
Sonjo	4	8	8	37	14	20	13	10
%	20	40	40	72.5	27.5	46.5	30.2	23.3

DISCUSSION

This study's findings give insight into what can be done for communities living in the same landscape as large carnivores, as is the case in the eastern Serengeti ecosystem, by providing cost-effective and tangible benefits to the local people who bear most of the conservation costs. This applies strongly in developing countries, especially in Africa, where many governments do not have the full potential to compensate people for the loss of their livestock to predators. In the Maasai and Sonjo tribes in the eastern Serengeti ecosystem, disease was more likely to cause livestock loss than depredation by carnivores. Exploring alternatives for promoting willingness to tolerate depredation, treating livestock against disease presents one of the option for producing harmonic coexistence between people and predators, especially in these two tribes. However, this alternative option must be implemented with caution as in a long-term will increase the livestock number which ultimately decreases wild prey, increases the rate of depredation, conflict, and retaliation.

People's willingness to coexist with large carnivores before and after the implementation of a conservation incentive

This study revealed that the Maasai tribe was more willing to coexist with large carnivores than the Sonjo tribe if their livestock were treated against diseases, which represent a much greater cause of livestock loss than large carnivore depredation. The Sonjo tribe members were more rigid in their attitude toward coexist with large carnivores in their area, even after receiving a conservation incentive. According to previous studies by Bencin et al. (2016) and Hazzah et al. (2017), for the better conservation of carnivore species, efforts should be dedicated to influencing human behavior to realize and appreciate the benefits (ecologically and economically) of large carnivores. Currently, financial compensation after livestock depredation loss is not necessarily an effective and sustainable tool for carnivore conservation (CDPNews 2003, Naughton-Treves et al. 2003).

To explore alternatives, this study tested people's willingness to coexist with large carnivores before and after the implementation of a chemoprophylactic program, which serves as an alternative conservation incentive. The program was positively received because the Maasai and Sonjo communities lose more livestock to diseases than depredation. Many respondents indicated that they were willing to lose livestock to depredation because the rates of depredation are low. Disease-related livestock loss was three times higher for the Maasai tribe and five times for the Sonjo tribe than depredation; therefore, getting a sustainable program to treat livestock against diseases will promote willingness for coexisting with large carnivores.

Most communities living adjacent to or inside-protected areas are less willing to coexist with large carnivores (Spira 2014). Policy makers and researchers have a challenging of addressing a long history of conflict (Kideghesho et al. 2007). If communities realize a tangible benefit, direct or indirect, due to the presence of carnivores, the probability of sustainable coexistence will be improved (Newmark et al. 1993, Bencin et al. 2016). When conservation incentives are provided to such communities, they enhance positive behavior and perceptions towards carnivores in the vicinity (Smith 2005, Lagendijk and Gusset 2008).

These communities bear the costs of carnivore conservation, and thus, in the long term, a sense of ownership is cultivated when tangible benefits are realized, which ultimately tends to reduce the existing human-carnivore conflict (Newmark et al. 1993, Kidegesho 2008). Tangible benefits tend to improve the tolerance level of the costs of large carnivores (Lagendijk and Gusset 2008). For the coexistence of people and carnivores, it is imperative to minimize existing human-carnivore conflicts, such as livestock depredation (Newmark et al. 1993, Nyahongo and Røskaft 2012, Lyamuya et al. 2014, Mbise et al. 2018).

Major factors contributing to livestock losses

In many savannah ecosystems, pastoralists live together with large carnivores, and the main threat of livestock loss is diseases, followed by depredation (Nyahongo and Røskaft 2012). When large carnivores co-occur with livestock in the same landscape the likelihood of livestock depredation is higher (Spira 2014, Mbise et al. 2018). Loss from diseases and depredation negatively impacts the livelihoods of the communities experiencing such problems (Gifford-Gonzalez 2000, Nyahongo and Røskaft 2012). The effective control of diseases with multi-host pathogens is complex (Lembo et al. 2008); however, if communities with livestock are given proper awareness of disease control and prevention, they can minimize the disease severity in their areas.

In the tropics, the prevalence of diseases that affect livestock is the major cause of income loss. Most of the pastoral communities depend on livestock for their survival (Gifford-Gonzalez 2000). Different measures are available to treat livestock, such as chemoprophylaxis, which boosts immunity against diseases (Jibbo et al. 2010). However, in developing countries, due to a lack of disease awareness, livestock are untreated with disease prevention measures (Nyahongo and Røskaft 2012). Most communities have a large number of livestock with suboptimal health. Large livestock herds are a sign of wealth and prestige in both the Maasai and the Sonjo communities (Hodgson 2011). Thus, there is a need for increased awareness of the benefits of selling a few animals to buy drugs to treat the rest, as many pastoralists have no formal education to inform important life decisions.

Additionally, awareness of diseases is very important for these communities because some diseases that affect livestock are relatively simple to prevent and control if the community is well educated. For instance, during our chemoprophylactic program, we found that many sheep and goats were dying because of coenurosis disease. If these communities implement veterinary guidelines such as deworming domestic dogs and providing chemoprophylaxis for livestock, the long-existing problem of livestock loss due to diseases will decline. Furthermore, a compliment was given to the chemoprophylactic program for the healthy progress of all the livestock that received chemoprophylaxis. Most of the livestock were in poor condition due to drought and thus were susceptible to diseases.

Both hypotheses were supported by our findings. First, disease is responsible for more livestock losses than carnivore depredation; therefore, treating livestock against diseases will improve tolerance of depredation loss. Second, people's willingness to coexist with large carnivores increased after the implementation of the chemoprophylactic program. We conclude that harmonic coexistence between humans and large carnivores goes hand in hand with providing tangible benefits to the communities living with these species. Treating the livestock of these two tribes against diseases will provide tangible benefits that will justify the costs incurred from living with large carnivores in their areas. However, precautions should be taken as treating livestock against disease will increase the number of livestock in the area, which is a current source of habitat destruction and human-carnivore conflict.

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Paper IV

Manuscript

Paper IV

Do carnivore surveys match reports of carnivore presence by pastoralists? A case of the eastern Serengeti ecosystem

by

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Do carnivore surveys match reports of carnivore presence by pastoralists? A case of the eastern Serengeti ecosystem

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ABSTRACT

Human-carnivore encounters are common where humans and wild carnivores share the same landscape. The frequency of such encounters gives insight on carnivore density and might correlate with human-carnivore conflict incidences. Conflict between carnivores and pastoralist communities may influence the accuracy of reported carnivore presence from local livestock owners. We interviewed livestock owners in the eastern Serengeti ecosystem and recorded reported carnivore presence and relative abundance. We then conducted a carnivore survey to assess the potentially variability of reported carnivore presence and that recorded during the surveys. The call-in surveys attracted 9 lions (*Panthera leo*), 88 spotted hyenas (*Crocuta crocuta*) and 47 black-backed jackals (*Canis mesomelas schmidti*) to 12 sites which were resurveyed three times (36 call-ins in total). Reported encounters with lions, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas, African wild dogs (*Lycaon pictus*) and jackals were higher closer to the Serengeti National Park (SNP). Data from carnivore surveys and what people reported in the same area were positively correlated. The results indicate that local reports of encounters with wild carnivores were reliable indicators of their presence in the area. Combining observational data through surveys with data reported by local people in areas where humans and wild carnivores coexist likely complement each other.

Key words: *call-in survey, coexistence, distance, encounter, observation, Serengeti, wild carnivores*

Word count: 3,817

INTRODUCTION

Human-carnivore interactions in African savannas are a common phenomenon (Lagendijk and Gusset 2008, Lindsey et al. 2013, Lyamuya et al. 2014b, Spira 2014). Local people living with wild carnivores can interact with these species on a daily basis, and the frequency of encounters is often a function of the distance to adjacent protected areas (Lagendijk and Gusset 2008, Carter et al. 2012, Lindsey et al. 2017). However, it has been argued that local people's perception of carnivore occurrence might differ from the actual presence of the species due to biases in observability, lack of knowledge or socio-cultural prejudice towards certain species (Purchase et al. 2007, Rodriguez 2007, Karanth et al. 2011, Anand and Radhakrishna 2017). If data on carnivore occurrence are collected by questionnaire surveys, this might provide a cost-efficient first step toward estimating occurrence without having to implement often costly and time-consuming monitoring.

Habitat loss and depletion of prey availability for wild carnivores increases the chances of human-carnivore encounters (Mbau 2013, Yirga et al. 2013, Ronnenberg et al. 2017). On Maasai land, coexistence with carnivores is likely due to seasonal shifts of the people's settlements and grazing areas. In southern Kenya, lions were found in more secluded habitats when humans were nearby (Schuette et al. (2013). Mapping the habitats preferred by carnivores will be a good measure for reducing human-carnivore encounters (Abade et al. 2014). Informing local people where and when carnivore encounters might occur may help reduce encounter frequency, which will improve coexistence between humans and wild carnivores (Campbell et al. 2014). Zoning could also be a promising option to reduce the frequency of human-carnivore encounters (Breitenmoser 1998, Packer et al. 2013). Additionally, assessment of the spatial separation between carnivores' habitats and human activities may contribute to solid measures on how to reduce existing human-carnivore conflicts due to livestock depredation and attacks on humans (Shivik 2006, Mbau 2013, Packer et al. 2013).

Historically, the Maasai tribe, in northern Tanzania, were purely pastoralists, but they are increasingly switching to agro-pastoralism to provide food for sustenance (Lyamuya et al. 2014b, Masao et al. 2015) in a similar way to the neighbouring Sonjo tribe. Due to the present human population increase in Africa, land for livestock pasture is declining, which might cause conflicts with other stakeholders such as farmers, conservationists and pastoralists (Mbau 2013, Pooley et al. 2017). Land ownership is one of the factors that affects local people's tolerance towards wild carnivores (Romañach et al. 2007), and balancing resource demands between wildlife and people is challenging (Peterson et al. 2010). Anthropogenic activities near the boundaries of protected areas threaten conservation of carnivores (Shivik 2006). Wild carnivore encounter rates can guide management plans for effective measures that will promote coexistence (Smith 2005, Lagendijk and Gusset 2008, Dorresteijn et al. 2014). Carnivore encounters might be positively correlated with conflict intensity, although the phenomenon is not always true due to other factors such as terrain, habitat, and prey abundance (Carter et al. 2012). For instance, due to a decline in wild prey abundance, carnivores present in the area are more likely to prey on livestock (Karlsson and Johansson 2010, Yirga et al. 2014). Thus, different approaches are needed to inculcate human-carnivore coexistence and tolerance in this game-controlled area.

This study hypothesized that the reported encounters with spotted hyenas (*Crocuta crocuta*) and black-backed jackals (*Canis mesomelas schmidti*) by local people will match field observations from carnivore call-in surveys in twelve selected sites along a distance gradient from the Serengeti National Park (SNP) border. This study is among few studies that have correlated observations of carnivores with what local people report.

METHODS

Study area

The Maasai and the Sonjo tribes live in the eastern part of the Serengeti ecosystem in the designated reserve called the Loliondo Game Controlled Area (LGCA). The study area lies between 2°5′00″–2°2′60″S and 35°61′67″–35°37′00″E (Masenga 2011) (Fig. 1). The Maasai tribe are pastoralists, whereas the Sonjo tribe are agro-pastoralists (Lyamuya et al. 2014a, Mbise et al. 2018). The human population in this area increases at a rate of > 3% annually and is presently most populated in the small town of Wasso due to cross-border business with Kenya (Masenga and Mentzel 2005, Lyamuya et al. 2016b). This human population increase has also led to major land use changes in the areas of both tribes through farming expansion and settlements (Lyamuya et al. 2014a). However, the area is still rich in both ungulates and wild carnivores (Maddox 2003, Holdo et al. 2010), although there are signs that the wild carnivore population in particular is declining in this area (Lyamuya et al. 2016a, Lyamuya et al. 2016b, Mbise et al. 2018).

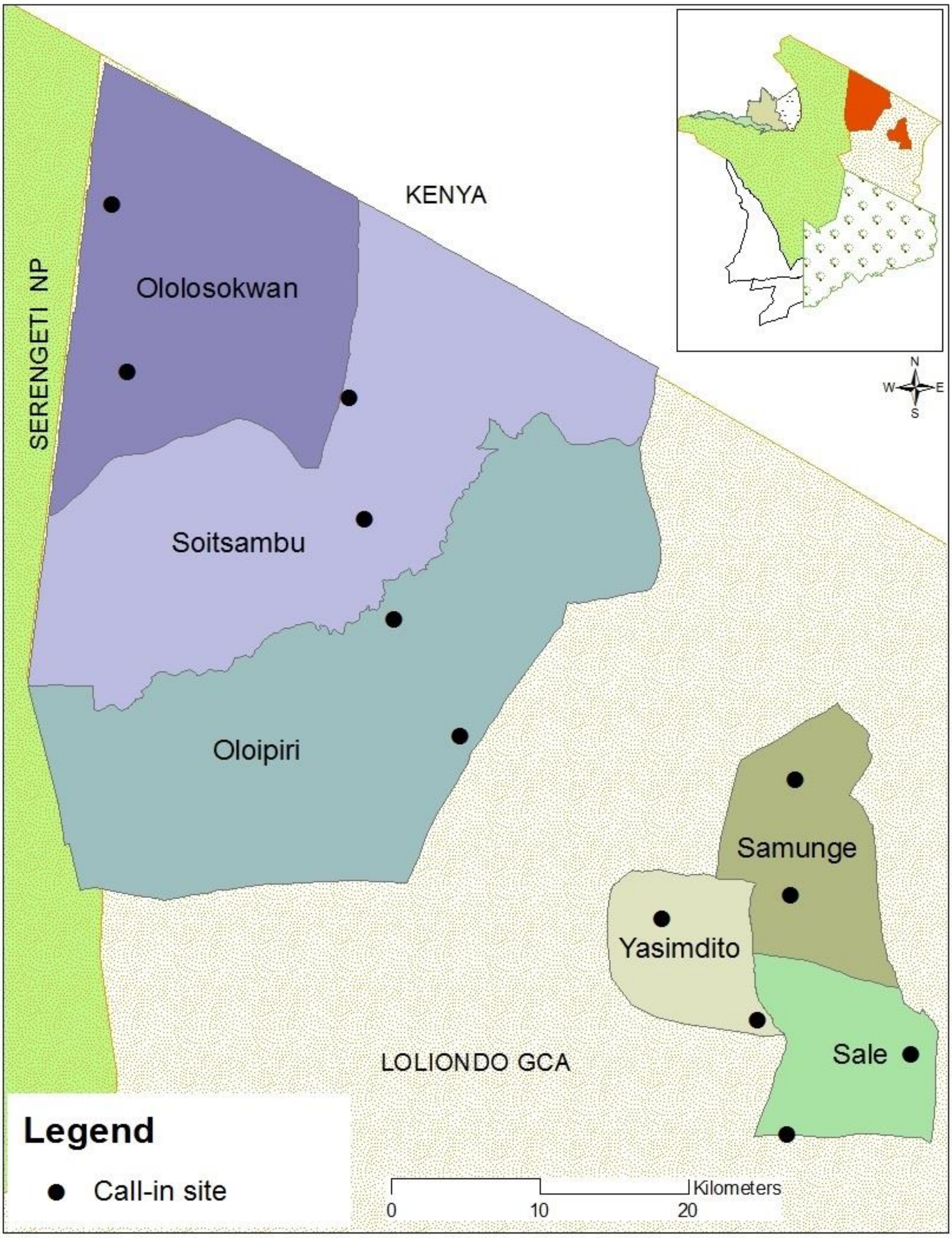

Figure 1: Map showing call-in sites (black dots) and study villages in the eastern Serengeti ecosystem. Upper right: the green area is Serengeti National Park and the red areas are the study area.

Data collection

Call-in surveys are frequently used for estimating the density of large carnivores in African savanna ecosystems (Ogutu and Dublin 1998, Mills et al. 2001, Ferreira and Funston 2010, Dacier et al. 2011, Cozzi et al. 2013, Omoya et al. 2013). Call-in techniques give reasonable estimates of carnivore species found around the call-in sites (Ogutu and Dublin 1998). Our study aimed to test the validity of what local people report about the presence of carnivore species in their areas. Therefore, we performed a correlation analysis between what we observed versus encounters that local people reported. Our call-in surveys followed protocols developed by Maddox (2003), however, the duration of each call-in was reduced from 60 to 30 minutes to avoid disturbing the villagers. The 12 call-in sites, two in each village land, were resurveyed during three sessions: two during the dry season in November 2016 and February 2017 and one during the wet season in July 2017.

Distance between the two call-in sites within one village land ranged from 7.8 to 11.4 kilometres. The distance covered by the broadcast was 2.5 - 3.0 kilometres away as calibrated by Maddox (2003). The volume of the call-ins reached a peak of 114 db. Call-in surveys were only conducted when there was little wind to minimize the effects on the detection of the sound by carnivores. We used two speakers (130 db max SPL), a Pioneer GM-D8604 amplifier, mp3 player, sound metre (model SL 328), wind speed metre (model WS 9500), binoculars (Olympus 10x25 WP II BLK), GPS (eTrex® Vista HCX), and range finder (Nikon Laser 350 G). Our instruments were different from those used by Maddox (2003) but had the same audible range when calibrated. Therefore, the difference in the protocol used are duration of call-ins and the way we selected our points compared to Maddox (2003).

Call-in surveys were performed in grassland, shrub land, wooded grassland and woodland habitats and were broadcasted using two speakers, pointed in opposite directions, and placed on the roof of a Land Cruiser. After 15 minutes, the speakers' direction was rotated 90 degrees, allowing us to cover all directions equally. The audio lasted for 15 minutes; the first 3 minutes broadcasted a wildebeest calf distress call followed by 12 minutes of hyenas and a lion squabbling over a kill. We counted all spotted hyenas and jackals that arrived within 100 m of the speakers during a period of 30 minutes. Our analysis included only two species of interest because they were common around all twelve call-in sites and were commonly attracted (Maddox 2003). Altogether, 36 call-in surveys were conducted, three in each of the twelve sites. All call-in surveys were carried out between 6:00 am and 9:00 am. Distance from village centres to call-in sites varied between 5 - 10 kilometres depending on village size.

To compare the observed numbers of the two carnivore species at the call-in sites with statements from interviewed villagers, we administered a questionnaire survey about the chances of observing spotted hyenas and jackals and other carnivore species such as lions, leopards, cheetahs, and African wild dogs on a daily, weekly, and monthly basis or rarely in relation to the respondent's gender, age group (youth = 18 – 35 years, adult = 36 – 49 years, and elderly = above 50 years) and village distance from the SNP (Table 1). The question was closed-ended: "How often do you see the following carnivore species (lions, leopards, cheetahs, spotted hyenas, African wild dogs, and jackals) around your area?" We interviewed only one respondent from each household using random sampling. We interviewed 15 respondents who were as close as possible to each call-in site, thus in each village we divided the 30 respondents in two groups according to their closeness to each of the two sites. A total of 180 respondents were interviewed for the twelve call-in sites, including six sites from the Maasai tribe and six sites from the Sonjo tribe. During the survey, we interviewed local people who were given permission by the village chairperson. Whether in the Maasai tribe or the Sonjo tribe, we mixed languages (Swahili, Maasai, and Sonjo) depending on the respondent's fluency. Before interviewing, we introduced the purpose of our survey and the content of our questions and promised all the respondents that their identities would remain anonymous.

Data analysis

We used the Statistical Package for Social Sciences (SPSS) version 24 for data analysis (IBM 2016). Spearman's rho, Chi-squared, and multinomial logistic regression tests were used. Spearman's rho tests were used to explain correlations between number of observed hyenas and jackals at a call-in site along the distance gradient from the SNP border. Additionally, Spearman's rho tested the correlation between observed and reported encounters with hyenas and jackals in relation to distance from the SNP.

Correlation analysis between the number of observed (12 call-in sites) and reported encounters with these carnivore species was based on maximum counts and median scores of reported encounters. Additionally, correlation was performed in relation to maximum counts observed for each carnivore species at each call-in site relative to the median scores of what people encountered in their areas (daily, weekly, monthly, or rarely). Chi-square tests were used to explain the reported encounters with lions, leopards, cheetahs, spotted hyenas, African wild dogs, and jackals by the interviewed persons in relation to their closeness to the SNP border. In some analyses for those species that were not attracted by call-in surveys we pooled distances in two groups (<35 km and > 35 km). As Fig. 1 shows, the first 3-villages were found in a distance below 35 km, and the other three villages were found in a distance above 35 km. Multinomial logistic regression tests were used to determine the predictor variable that explained most of the variation in the reported encounters with lions, leopards, cheetahs, spotted hyenas, African wild dogs, and jackals. In the model, we excluded education and tribe because these variables were not statistically significant in explaining the variation in observing these carnivore species.

Table 1: Demographic variables of the respondents

		N	%
Gender	Male	144	80.8
	Female	36	19.2
Age group	Youth	82	45.6
	Adult	58	32.2
	Elder	40	22.2
Education	Informal	44	24.4
	Primary	120	66.7
	Secondary	16	8.9
Tribe	Maasai	90	50.0
	Sonjo	90	50.0
Village	Ololosokwan	30	16.7
	Oloipiri	30	16.7
	Soitsambu	30	16.7
	Yasimdito	30	16.7
	Samunge	30	16.7
	Sale	30	16.7

RESULTS

Reported encounters with spotted hyenas and jackals along the distance gradient from the SNP

Reported encounters with spotted hyenas and jackals by the persons interviewed along the distance gradient from the SNP border (daily, weekly, monthly and rarely) as a dependent variable were tested with three independent variables (sex, age group and village distance from the SNP) using a multinomial logistic regression analysis (spotted hyenas; Pearson $\chi^2 = 142.6$, df = 12, $p < 0.0001$, Nagelkerke $r^2 = 0.586$; jackals; Pearson $\chi^2 = 253.3$, df = 12, $p < 0.0001$, Nagelkerke $r^2 = 0.830$). However, distance from the SNP was the only predictor variable that significantly explained the reported encounters with hyenas and jackals along the distance gradient from the SNP border (spotted hyenas; Pearson $\chi^2 = 128.4$, df = 3, $p < 0.0001$; jackals; Pearson $\chi^2 = 240.4$, df = 3, $p < 0.0001$; Table 2). Sex and age group were insignificant.

Table 2: Reported encounters with spotted hyenas and jackals along the distance gradient from the SNP

Village distance from SNP	Species	Daily		Weekly		Monthly		Rare	
		N	%	N	%	N	%	N	%
10 km	SH	17	56.7	8	26.7	5	16.7	0	0
	J	23	76.7	7	23.3	0	0	0	0
20 km	SH	21	70	3	10	6	20	0	0
	J	23	76.7	7	23.3	0	0	0	0
30 km	SH	19	63.3	10	33.3	1	3.3	0	0
	J	25	83.3	5	16.7	0	0	0	0
40 km	SH	0	0	5	16.7	11	36.7	14	46.7
	J	0	0	0	0	7	23.3	23	76.7
50 km	SH	0	0	8	26.7	17	56.7	5	16.7
	J	0	0	0	0	1	3.3	29	96.7
60 km	SH	0	0	11	36.7	8	26.7	11	36.7
	J	0	0	0	0	10	33.3	20	66.7

SH – Spotted hyena **J - Jackal**

Reported encounters with other carnivores (lions, leopards, cheetahs and African wild dogs) from the SNP (<35 km and >35 km)

The reported encounters with lions, leopards, and cheetahs from the SNP were all statistically significant (lions; Pearson $\chi^2 = 30.4$, df = 1, $p < 0.0001$; leopards; Pearson $\chi^2 = 8.6$, df = 1, $p = 0.003$; cheetahs; Pearson $\chi^2 = 22.5$, df = 1, $p < 0.0001$; Table 3). However, the reported encounters with African wild dogs was not statistically significant (Pearson $\chi^2 = 0.7$, df = 1, $p = 0.396$; Table 3). On average, the reported encounters of these carnivore species were much higher closer to the SNP border.

Table 3: Reported encounters with lions, leopards, cheetahs and African wild dogs from the SNP

	Distance from SNP	Lions		Cheetahs		Leopards		African wild dogs	
		N	%	N	%	N	%	N	%
Monthly	<35 km	26	28.9	20	22.2	36	40	26	28.9
	>35 km	0	0	0	0	18	20	21	23.3
Rarely	<35 km	64	71.1	70	77.8	54	60	64	71.1
	>35 km	90	100	90	100	72	80	69	76.7

Observations of spotted hyenas and jackals

In total, 9 lions, 88 hyenas and 47 jackals were attracted at the twelve call-in sites during the three repetitions of call-in surveys. There was a statistically significant negative correlation between number of observed spotted hyenas at call-in sites and the distance from the SNP border (Spearman's rho = -0.532, n = 36, p = 0.001; Fig. 2). However, habitat and season did not explain any of the variation in hyena numbers relative to distance from the SNP border (Spearman's rho = 0.200, n = 36, p = 0.242; Spearman's rho = -0.027, n = 36, p = 0.876 respectively). Similarly, there was a statistically significant negative correlation between number of jackals at call-in sites and distance from the SNP border (Spearman's rho = -0.735, n = 36, p < 0.0001; Fig. 2). Habitat and season were not statistically significant in explaining the variation in jackal numbers relative to distance from the SNP border (Spearman's rho = -0.011, n = 36, p = 0.948; Spearman's rho = 0.022, n = 36, p = 0.898, respectively).

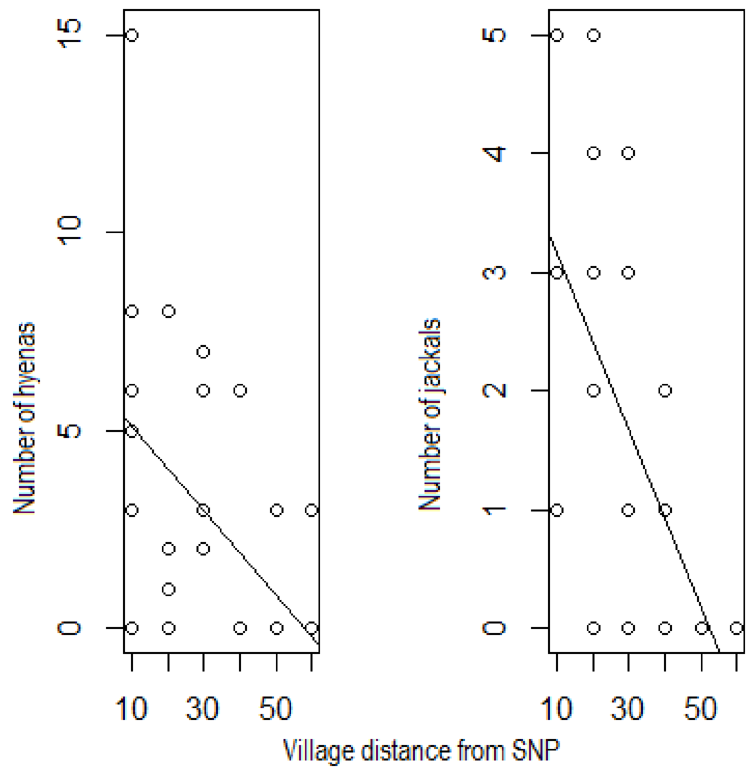

Figure 2: Spotted hyena and jackal numbers at call-in sites along the distance gradient (in kilometres) along the distance gradient from the SNP

Correlation between field observations and reported encounters with spotted hyenas and jackals in relation to distance from the SNP

There was a statistically significant positive correlation between number of observed spotted hyenas at call-in sites and reported encounters with these species relative to distance from the SNP border (Spearman's rho = 0.732, n = 12, $p = 0.007$). Furthermore, there was a statistically significant positive correlation between number of observed jackals at call-in sites and reported encounters with these species relative to distance from the SNP border (Spearman's rho = 0.963, n = 12, $p < 0.0001$).

DISCUSSION

Hyena and jackal observations at call-in sites match what people reported on their encounters for the same areas. We can therefore conclude that people were reporting encounters with other carnivore species such as lions, leopards, cheetahs, and African wild dogs honestly. The chances of encountering African wild dogs were similar in both areas (<35 km and >35 km). The reported encounters with lions, leopards, cheetahs, hyenas, and jackals from the SNP were highest closer to the SNP. However, one village at 30 km from the park boundary showed a deviating trend as the reported encounter rates with lions, leopards, cheetahs, and African wild dogs were much higher than those reported closer to the park. Although this observation needs further research, one possible explanation might be that this village has a favourable habitats for carnivores.

At call-in sites, we observed a significant negative correlation between spotted hyena and jackal numbers and distance from the SNP. On average, the closer to the park, the higher the observed numbers of these carnivore species. However, habitat and seasonal variables were not important indicators in explaining variation in hyena and jackal observations along the distance gradient from the SNP. A study by Cozzi et al., (2013) in northern Botswana found that hyenas were evenly distributed independent of habitat and season. However, Ogutu and Dublin (1998) in the Maasai Mara National Reserve, Kenya, found that carnivore response tends to vary seasonally with the presence/absence of migratory prey. Additionally, village distance from the SNP was the only predictor variable that significantly explained the reported encounters with hyenas and jackals along the distance gradient from the SNP border.

While some people might be biased or untruthful during interviews, with a sufficient sample size (Delice 2010), it would be rare for all to be biased or untruthful; hence, such a bias is highly controlled by increasing respondents' sample size. In the case of this study, sample size was satisfactory for minimizing bias and we were able to correlate information with field observations for two of the carnivore species. The reported encounters with hyenas and jackals were significantly correlated with field observations in the Maasai and Sonjo tribal lands. Lions, leopards, cheetahs, and African wild dogs can be encountered in the area, although we focused on comparing the two common species that were attracted by call-in surveys with the respondents' reported encounters with these species in their area. Nine individual lions were attracted only once at Ololosokwan village (10 km), which was the closest village to the SNP.

Anthropogenic activities adjacent to protected areas negatively affect wildlife populations in their intact habitats (Shivik 2006, Markovchick-Nicholls et al. 2008). A study from Taveta district adjacent to Tsavo National Park in Kenya found that due to human population increase, land use and land cover changes are largely caused by agricultural expansion (Mbau 2013). Similarly, the Maasai and Sonjo tribal lands are now in high demand for farming activities because the Maasai are switching to agro-pastoralism and the population increase of the Sonjo tribe requires more farming area to be cleared at the expense of forests and wild carnivores' pristine habitats. Major threats to wild carnivore populations are conflicts with people living adjacent to protected areas (Woodroffe and Ginsberg 1998). People's hostility toward carnivores in areas outside the SNP that are not well protected is greatly increasing, which threatens the conservation of these species. The areas outside SNP are becoming a sink for wild carnivore populations due to hunting and retaliatory killings (mostly by poisoning) (Masenga et al. 2013). For instance, in Queen Elizabeth Conservation Area (QECA), Uganda, Omoya and Plumptre (2011) found that most retaliatory killings of hyenas and other carnivore species were caused by poison (*carbofuran and other agro-vet chemicals*). Similarly, currently in Tanzania most retaliatory killings of carnivores species is mainly caused by poison in areas outside protected areas (Masenga et al. 2013, RCP 2018).

Wild carnivores play an important role in ecosystem dynamics, ecosystem health and economics for local people living with these keystone species (Treves and Karanth 2003, Cozzi et al. 2013). As hypothesized, the reported encounters with spotted hyenas and jackals by local people matched the numbers observed at call-in sites near twelve selected sites along the distance gradient from the SNP border. We conclude that if what people report is taken seriously and verified by employing interdisciplinary techniques, this verification will help managers develop plausible conservation strategies for carnivores, especially in human-dominated landscapes.

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods

1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher

1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*

1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*

2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania

2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy

2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world:adaptions to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river

2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*

2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (Rissa tridactyla)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills

2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (***Giraffa camelopardalis tippelskirchi***) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for endusers.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (Lycaon pictus) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of Tanytarsus van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxixity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on Arabidopsis thaliana
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae