DISTRIBUTION AND HABITAT CONNECTIVITY OF LARGE CARNIVORES IN SUB-SAHARAN AFRICA AND HUMAN-CARNIVORE CONFLICTS IN WESTERN ETHIOPIA

By

FIKIRTE GEBRESENBET ERDA

Bachelor of Education in Biology
Jimma University
Jimma, Ethiopia
2005

Master of Science in Dryland Biodiversity
Addis Ababa University
Addis Ababa, Ethiopia
2008

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
July, 2018

DISTRIBUTION AND HABITAT CONNECTIVITY OF

LARGE CARNIVORES IN SUB-SAHARAN AFRICA

AND HUMAN-CARNIVORE CONFLICTS IN

WESTERN ETHIOPIA

Dissertation Approved:

Dr. Monica Papeş

Dissertation Adviser

Dr. Karen McBee

Dr. Jacqueline M. Vadjunec

Dr. Tim O'Connell

ACKNOWLEDGEMENTS

First and foremost, I would like to thank God for helping me with this project from beginning to end and guiding me through all the ups and downs with His grace.

This dissertation is a product of many people I have been extremely fortunate to ever cross paths with, and I am thankful to each of them for contributing to my journey at one step or another.

A special thank you to my advisor, Monica Papeş, who is the epitome of an advisor. Mona, I consider myself lucky to have been part of your lab. Because of your knowledgeable guidance and unrelenting mentorship, I have come out of this PhD program a better scientist than when I started. I would also like to extend my thanks to my committee members, Karen McBee, Jacqueline M. Vadjunec, and Tim O'connell, who have given me all the support I needed during my time at OSU. This work was made possible by the financial support of Schlumberger Foundation. Thank you for your generosity.

Many have inspired me to become a wildlife conservationist, and I sure cannot mention all, but I would be remiss if I left out Hans Bauer, who is a great mentor and a best friend for life. I am deeply indebted to Kahsay Gebretensae, Mesfin Tekle, Tilahun Teshome, Bemnet Regassa, Gatluak Gatok, Mulubrhan Hagos, Siraj Hussien, Mamo Gebremedhin, Henok Tamiru, and Mihret Teamir for their help in data collection.

I thank Dr. Feng, Jaffe, Sgt Walker, Panday, Iulian, Ally and Erika for being the best lab mates. Thank you all for all the intellectual (and non-intellectual) discussions, and the episodes of procrastinations. Xiao, thank you for all the R help. Cassondra: this may shock you, but you are the best company for misery, thank you! I am also grateful to have had my Anbessaw friends in Stillwater, Oklahoma. A special thanks from the group goes to Tsigereda Kebede, who cooked me delicious dishes, provided comments on parts of my dissertation, and stepped in as a baby-sitter whenever necessary. Thanks also to the OKC Genete Tsige Church community, as well as all my friends across the US and Ethiopia for their support and prayer throughout the different stages of my studies.

Last but definitely not least, I would like to thank my family. Abaye and Emaye, you sacrificed a lot for us, your children, and all our accomplishments are the fruit of all your prayers, hard work and encouragement. You were by no means society’s giants, but you carried us on your shoulders so high and strong that we stand taller and prouder with each passing day than we could ever imagine. Fa, thank you for always being there -- I will always cherish your endless love and support, your insightful edits, and your all- never-ending lectures of a big brother. Enuye, my favorite sister, you are better than the best sister that anyone could wish for! Thanks for the edits, the encouraging phone calls, and the visits.

Ade and Emnet: no words can capture what you two mean to me. Ad, thank you for all the support, understanding and unconditional love. Emnet: you were the best distraction in my grad school years. Thank you both for making me the happiest woman on earth.

Name: FIKIRTE GEBRESENBET ERDA

Date of Degree: JULY, 2018

Title of Study: DISTRIBUTION AND HABITAT CONNECTIVITY OF LARGE CARNIVORES IN SUB-SAHARAN AFRICA AND HUMAN-CARNIVORE CONFLICTS IN WESTERN ETHIOPIA

Major Field: INTEGRATIVE BIOLOGY

Abstract

Large carnivores are threatened with habitat fragmentation, prey depletion, and human-carnivore conflicts. Africa has an intact guild of large carnivores but data on their distribution and status are scare. Since large carnivores exist in low densities across large home ranges, traditional mammal survey techniques are impractical. I used a predictive modeling approach to estimate the potential distribution and connectivity between suitable patches for African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and lion (*P. leo*) across sub-Saharan Africa. Ecological niche modeling in Maxent algorithm generated potential distributions of the four carnivores by identifying environmentally suitable conditions. All Maxent models had good predictive capabilities (AUC > 0.80, and testing omission error <0.01). Removing unsuitable land cover types and high human population density from the Maxent outputs maintained majority (>88%) of the Maxent prediction. African wild dogs had the most fragmented and isolated patches, while leopards had the most intact patches. Western and central Africa appeared more fragmented, which might have been the natural state of these regions. Least-cost connectivity analysis identified 747 corridors, which could be prioritized based on different criteria. To investigate human-carnivore conflicts, I designed two local scale studies in Kafa Biosphere Reserve (KBR) and Gambella National Park (GNP), in western Ethiopia. Attitudes of local people were assessed towards lions and leopards in KBR and towards lions in GNP. Data were collected using household surveys (KBR and GNP), focus group discussions (KBR only), key informant interviews, and opportunistic informal discussions (GNP only). In Kafa, lions cause more economic damage than leopards, but lions are tolerated because they are respected in the Kafa culture. Although leopards are not given the same respect as lions, they also do not face indiscriminate killing in KBR. The data from GNP revealed that theft and disease are the leading causes of livestock loss, although respondents blame lions to be the main cause of depredation. Economic loss by lions is higher in Kafa than Gambella, but the culture of tolerance in KBR allows for the survival of lions. Participatory conservation approach, guided by Arnstein's ladder of participation, might foster tolerance in GNP.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

DISSERTATION OVERVIEW

Despite crucial social and technological innovations, human population growth and increasing consumption continue to exert pressures on ecological systems, posing extinction risks of different scales. Hardin (1968) captured this dilemma in his 'Tragedy of the commons'- as individuals try to maximize their personal gain from a given resource, the demand overcomes the supply and an additional unit of resource use by one individual harms other users by depleting the resource more and further limiting what can be used in common. Protected areas are partly responses to offset such overuse, while at the same time catering for the aesthetic and leisure demands from the public (Phillips 2004). The perception of protected areas as means of experiencing nature closely imposed the European dichotomy on nature and people in most parts of the world (Strathern 1980).

Conservation practices and Protected Area management can have different foci, i.e. improving human livelihoods or protecting biodiversity and the landscape, belonging to one side of the 'People vs Parks' debate (Wilkie et al. 2006). Nature-centered conservation practices exclude people from protected areas. National Parks are one example of such 'fortress conservation' model, which exclude human habitation and use (Büscher 2016). This approach conceives local people as only utilizers, thus destroyers, of nature, and intends to withdraw vital resources from people's basic sustenance through the creation of uninhabited parks (Colchester 2004). However, such exclusionary practices have documented negative outcomes (Agrawal and Ostrom 2001, McLean and StrÆDe 2003)..

Harrison (2011) reports no significant impact on wild fauna through traditional hunting compared to non-hunting areas, and Nepstad et al. (2006) argue that uninhabited parks do not perform significantly better than inhabited ones. Additionally, adopting this mode of protection risks focusing on areas that are large and undisturbed (or in pristine condition), relegating other areas with a possibility of recovery (Schwartzman et al. 2000).

The ethical dilemma to be surpassed in establishing a people-free park is what to prioritize, sustenance needs of the poor or intrinsic values of nature. Protagonists of this mode of conservation prioritize the latter, even in the face of serious food shortage and poverty (Rolston 1998). This however is challenged by other environmental ethics professionals, primarily as the choice between 'people v. nature' disregards the values and hard choices local people make on an everyday interaction with the (degraded) landscape they subsist on (Siurua 2006). The ethical choices made at the local community level are ignored and the value system of the West or the national elite is imposed in the creation of uninhabited National Parks.

Although widely used, the fortress model has failed to meet its objectives due to poverty, population growth, urbanization, and low political will (Terborgh 2000, Terborgh and Schaik 2002, Mora and Sale 2011). Another cause for this failure is the alienation of local people from economic and social benefits derived from the protected areas, and not involving them in the process of protected area management (Brechin et al. 2002, Adams et al. 2004). Without considering pressures from below within a context of development processes and poverty alleviation attempts, such fortress conservation attempts would risk ignoring the political agency of the poor local communities (Schwartzman et al. 2000). This realization that top-down imposition of values and nature conservation strategies will not lead to the desired goal without the cooperation of the local communities, pushed for bottom-up approaches in the last couple of decades.

The people-centered approaches strive to find a strategy that meets both the people and nature needs, while involving indigenous people and local communities in the management of protected areas. Salafsky (2011) argues that projects that try to integrate development and nature conservation will eventually lead to the selection of one of the goals or risk failing at both, and proposes the use of development as a strategy to meet conservation ends as the better option. In this option, development approaches and desired outcomes are chosen and prioritized based on the added benefit to conservation goals. Here the commending weight is given to conservation, and development is instrumentally used towards better meeting that end (Salafsky 2011).

An example of protected area following the people-centered approaches is Biosphere Reserves, which emerged from UNESCO's Man and the Biosphere (MAB) program (UNESCO and UNEP 1974). The main objective of these reserves is conservation and monitoring of biodiversity, environmental education, and local capacity building (Batisse 1982). All Biosphere Reserves are required to have three zones with specific conservation functions; core zone(s) (strictly protected ecosystems which must be legally protected under national law), buffer zone (surrounds the core zone(s) and allow wide-ranging ecological practices of research, environmental education, and biodiversity monitoring), and transition zones (combines conservation and ecologically sustainable productive activities) (Ishwaran et al. 2008, UNESCO 2017).

Adopting bottom-up approaches for conservation opens the door to integrate communities in conservation while attaining development goals. Local communities must not be defined as resource users only, they are political actors too. When deprived of their agency in a formal setting to conserve nature, locals have been documented to resist in the everyday activities (Scott 1986) by using loopholes like killing large mammals in self-defense or to protect crops in East Africa (Gibson 1999) and using fire to eradicate locust swarms in Madagascar (Kull 2004). Creating alliances with local communities reduces resistance while at the same time helping the local community offset the local costs of conservation (Schwartzman et al. 2000). Involving locals from planning to implementation stages will also legitimize conservation actions and create a sense of ownership among local people, guaranteeing a better conservation of resources (Danielsen et al. 2007). In this dissertation, I compare and contrast two case studies from Kafa Biosphere Reserve and Gambella National Park in southwestern Ethiopia.

Conservation becomes even more challenging (due to policy differences, issues of national security, and territorial sovereignty) when species or ecosystems transcend protected area, regional, or national boundaries. To conserve transboundary species or ecosystems, different kinds of transboundary initiatives have been established by conservation organizations including; Transboundary Natural Resource Management Area, Transboundary Conservation and Development Area, Transboundary Protected Area, and Parks for Peace (Braack et al. 2006). The one criterion they all have in common is that the areas they encompass are shared by two or more countries.

Transboundary conservation strategies are particularly essential for species with wide home ranges and ecosystems that transcend protected area and national boundaries. Such transnational conservation strategies have been proposed for species like the Andean condor (Lambertucci et al. 2014) and wolves (Falcucci et al. 2013). Examples of transboundary conservation areas include: the Yellowstone to Yukon (Y2Y) region, 1.3 million km^2, spanning five North American states (Washington, Oregon, Idaho, Montana and Wyoming), two Canadian provinces (British Columbia and Alberta), and two Canadian territories (Yukon and Northwest Territories) (Chester 2015), the Great Limpopo Transfrontier Park , 99,800 km^2(Mozambique, South Africa, Zimbabwe) (Wolmer 2003), the Turtle Islands Heritage Protected Areas in the Sulu Sea (Malaysia, Republic of the Philippines), La Ámistad (Costa Rica, Panama), and the High Tatras/Tatrzanski National Parks (Slovakia, Poland) (Braack et al. 2006). In my second dissertation chapter, I identified suitable areas for Africa’s large carnivores, majority of which are transnational patches. In addition to the patches, I have also identified corridors that connect potential suitable patches. These two analyses could contribute towards the creation of transboundary protected areas in sub-Saharan Africa for the protection of large carnivores.

Carnivora is the fifth largest mammalian order with more than 280 species (Wozencraft 2005) and is represented in every major land cover on Earth, from the Sahara Desert to Antarctica (Hunter 2011)). Based on their mass, carnivores that weigh > 21.5 kg are commonly regarded as large carnivores because they feed on prey that is > 45% of their own mass (Carbone et al. 1999). Large carnivores can have direct or indirect influences on community structure and biodiversity (Steneck 2005). Direct effects are as simple as feeding on prey and reducing prey numbers, while indirectly, by feeding on prey, carnivores may exert selective pressures and support the evolution of less vulnerable prey types (Gittleman et al. 2001). Therefore, large carnivores are always limited in number compared to their prey, as is the case in Eltonian food pyramids (Shipman and Walker 1989). Large carnivores are particularly susceptible to habitat fragmentation and human-carnivore conflicts because they occupy large home ranges and occur in low population densities (Ripple et al. 2014). Currently, most large carnivore populations occur across geographical boundaries of multiple countries, especially in many small African countries (Trouwborst 2015).

Although large carnivores are a critical element of ecosystems, they have experienced some of the biggest range contractions and population declines (Ripple et al. 2014, Di Minin et al. 2016) of any mammalian group. Africa harbors taxonomically diverse and functionally intact carnivore guilds (Dalerum et al. 2009) that present unique opportunities for ecological studies and exceptional challenges for their conservation. Conserving intact guilds of carnivores is of higher priority than only focusing on single species of large carnivores (Woodroffe and Ginsberg 2005); however, that needs a well-rounded understanding of the carnivores' ecology.

Sympatric large carnivore species in Africa include the African lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*) (Vanak et al. 2013), all of which are threatened and have decreasing population trends (Durant et al. 2015, Bauer et al. 2016, Stein et al. 2016, Woodroffe and Sillero-Zubiri 2012). Human-carnivore conflicts and habitat loss and fragmentation are the common threats faced by large carnivores. Survey and assessment of large carnivore populations in the wild is expensive and time-consuming. The International Union for Conservation of Nature (IUCN) has generated distribution maps and identified major threats to carnivores based on expert opinions. In this dissertation, I use existing data to approximate information that would otherwise be extremely difficult to obtain. My dissertation chapters assessed habitat suitability, fragmentation, and human perception and the role of cultures for large carnivore conservation in sub-Saharan Africa.

The objective of the first chapter of my dissertation was to identify suitable regions for prioritizing large carnivore conservation areas in sub-Saharan Africa. For this, I ran ecological niche models to predict the potential distribution of African wild dog, cheetah, leopard, and lion in sub-Saharan Africa. These models used climate and elevation layers and the carnivore occurrence points from multiple sources from 1950 onwards. I further refined the ecological niche models with two variables that affect carnivore populations, human population density and land cover. Leopards had the largest suitable area prediction, showing that majority of the environmental conditions allow them to exist in most parts of sub-Saharan Africa. The African wild dog, on the other hand, had the lowest area prediction, and the highest number of small and isolated patches. Most of the suitable patches are found in southern and eastern Africa for all four species. Central and western Africa had fewer patches for the carnivores, except leopards which had a more or less uniform distribution throughout the study area. West Africa contained the most number of small and isolated patches. To identify potential corridors, I connected the suitable patches using a least cost connectivity network analysis. The cost in this analysis refers to the resistance the animal faces when dispersing through a landscape (matrix) using a certain route. I selected the best corridors based on patch size, path (corridor) length, overlap with a protected area, and transboundary-ness. Other criteria of prioritization can be used to identify other potential corridors.

The objectives of the second and third chapters were to understand the level of human-carnivore conflicts in west Ethiopia and to examine if culture has any role in fostering tolerance of carnivore attacks. Human-carnivore conflicts are one of the leading causes of carnivore population decline and range contraction (Macdonald 2016). The need for large geographic range in carnivores and the growing human need for land are the opposing factors that mostly bring people and carnivores into conflict.

Large carnivores present actual or perceived threats to humans or livestock, to which humans may react by indiscriminate retaliatory or preemptive killings (Treves and Karanth 2003). Thus, one important step in studying human-carnivore conflicts is understanding human attitudes, behaviors, and perceptions towards carnivores, which are a sum total of humans' complex social and cultural settings (Dickman et al. 2013). Some of the factors that shape perception of carnivores include the amount of livestock loss due to depredation, level of wealth (Dickman et al. 2013), education (Lagendijk and Gusset 2008), and culture (Gebresenbet et al. 2017).

I used household surveys, focus group discussions, and key informant interviews to collect data. The study areas for the second and third chapters were Kafa Biosphere Reserve and Gambella National Park, respectively. Kafa Biosphere Reserve is located in southwestern Ethiopia and is among the last stands of Afromontane evergreen forest ecosystems in the world with an area of 760,144 ha and altitudes ranging from 500 to 3350 m above sea level (UNESCO-MBA Biosphere Reserves Directory 2010). This reserve represents an important carbon store of the country (DeVries et al. 2012) and is divided into three zones: the core, buffer, and transition zones, with the core area having the least contact with humans (Kafa Biosphere Reserve 2013). With a size of 457,500 ha, Gambella National Park is located in western Ethiopia, and is generally a lowland region with elevation of 400 m to 768 m above sea level. Expansion of large-scale mechanized agriculture (Gebresenbet 2016) and poaching (Amare 2015) are the top threats to this national park. There have been conversations about making this park a transboundary protected area system with Boma National Park in South Sudan because of transboundary migratory ecosystem (HoARECN 2013, Amare 2015).

In the second chapter, I quantified the economic impact of lions and leopards on local communities from 2009 to 2013 in two districts in Kafa that harbor the carnivores. The results show that although lions cause more attacks than leopards in Kafa, they are better tolerated due to the local culture that highly respects lions. In the third chapter, I assessed the impact of lion depredation in and around Gambella National Park. Although disease and theft are the top causes of livestock loss in Gambella, local respondents blamed lions as the leading cause of livestock loss. This study demonstrated that the amount of loss alone cannot be enough to understand the level of human-carnivore conflicts.

Overall, my dissertation found that African wild dogs, lions, and cheetahs have a more patchy distribution than leopards. As elaborated in my first chapter's discussion, Africa's large carnivores are declining in number and contracting in range. Together with steps taken to find solutions, surveys should be conducted to identify unknown populations, and manage possible connectivity between sub-populations. My findings of potential connectivity between suitable patches provide the opportunity of including free-ranging populations of large carnivores in conservation plans of populations within protected areas, while maintaining gene flow between nearby populations. The large carnivore distribution maps can be used to survey new areas, which can lead to setting regional, national, and transboundary conservation priority areas. Fine scale studies must be conducted to understand the effects of intraguild competition on overlapping large carnivore populations. My second and third chapters have shown that local people may respond differently towards carnivore attacks, based on their attitude and culture towards the specific carnivore. Therefore, it is important to understand all underlying factors before proposing solutions and designing community education curricula. My findings described in the human-carnivore conflict chapters are of interest to academics, policy makers and locals alike. Future research should build on and expand these insights to further the understanding of human-carnivore conflicts, and test the robustness of the generalizability of mitigation approaches.

References

Adams, W. M., R. Aveling, D. Brockington, B. Dickson, J. Elliott, J. Hutton, D. Roe, B. Vira, and W. Wolmer. 2004. Biodiversity conservation and the eradication of poverty. Science **306**:1146–1149.

Agrawal, A., and E. Ostrom. 2001. Collective action, property rights, and decentralization in resource use in India and Nepal. *Politics & Society* **29**:485–514.

Amare, A. 2015. Wildlife resources of Ethiopia: Opportunities, challenges and future directions: From ecotourism perspective: A review paper. *Natural Resources* **6**:405–422.

Batisse, M. 1982. The Biosphere Reserve: A tool for environmental conservation and management. *Environmental Conservation* **9**:101–111.

Bauer, H., C. Packer, P. F. Funston, P. Henschel, and K. Nowell. 2016. *Panthera leo* (errata version published in 2017). The IUCN Red List of Threatened Species 2016: e.T15951A115130419. IUCN.

Braack, L., T. Sandwith, D. Peddle, and T. Petermann. 2006. Security considerations in the planning and management of transboundary conservation areas. IUCN, Gland, Switzerland and Cambridge, UK.

Brechin, S. R., P. R. Wilshusen, C. L. Fortwangler, and P. C. West. 2002. Beyond the square wheel: toward a more comprehensive understanding of biodiversity conservation as social and political process. *Society &Natural Resources* **15**:41–64.

Büscher, B. 2016. Reassessing fortress conservation? New media and the politics of distinction in Kruger National Park. *Annals of the American Association of Geographers* **106**:114-129.

Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**:286.

Chester, C. C. 2015. Yellowstone to Yukon: Transborder conservation across a vast international landscape. *Environmental Science & Policy* **49**:75–84.

Colchester, M. 2004. Conservation policy and indigenous peoples. *Environmental Science & Policy* **7**:145–153.

Dalerum, F., E. Z. Cameron, K. Kunkel, and M. J. Somers. 2009. Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. *Biology Letters* **5**:35–38.

Danielsen, F., M. M. Mendoza, A. Tagtag, P. A. Alviola, D. S. Balete, A. E. Jensen, M. Enghoff, and M. K. Poulsen. 2007. Increasing Conservation Management Action by Involving Local People in Natural Resource Monitoring. AMBIO: *A Journal of the Human Environment* **36**:566-570.

DeVries, B., V. Avitabile, L. Kooistra, and M. Herold. 2012. Monitoring the impact of REDD+ implementation in the UNESCO Kafa Biosphere Reserve, Ethiopia *in* IEEE International Geoscience and Remote Sensing Symposium (IGARSS 2012), Munich, Germany.

Di Minin, E., R. Slotow, L. T. B. Hunter, F. Montesino Pouzols, T. Toivonen, P. H. Verburg, N. Leader-Williams, L. Petracca, and A. Moilanen. 2016. Global priorities for national carnivore conservation under land use change. *Scientific Reports* **6**:23814.

Dickman, A., S. Marchini, and M. Manfredo. 2013. The human dimension in addressing conflict with large carnivores *in* D. W. Macdonald and K. J. Willis, editors. *Key topics in conservation biology*. John Wiley & Sons, Ltd, London.

Durant, S., N. Mitchell, A. Ipavec, and R. Groom. 2015. *Acinonyx jubatus*. The IUCN Red List of Threatened Species 2015: e.T219A50649567. IUCN.

Falcucci, A., L. Maiorano, G. Tempio, L. Boitani, and P. Ciucci. 2013. Modeling the potential distribution for a range-expanding species: Wolf recolonization of the Alpine range. *Biological Conservation* **158**:63–72.

Gebresenbet, F. 2016. Land acquisitions, the politics of dispossession, and state-remaking in Gambella, western Ethiopia. *Africa Spectrum* **51**:5–28.

Gebresenbet, F., B. Baraki, G. Yirga, C. Sillero-Zubiri, and H. Bauer. 2017. A culture of tolerance: coexisting with large carnivores in the Kafa Highlands, Ethiopia. *Oryx*: 1–10. doi: https://doi.org/10.1017/S0030605316001356.

Gibson, C. C. 1999. *Politicians and poachers: the political economy of wildlife policy in Africa*. Cambridge University Press, Cambridge.

Gittleman, J. L., S. M. Funk, D. W. Macdonald, and R. K. Wayne. 2001. Why "carnivore conservation"? Pages 1–7 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. *Carnivore Conservation*. Cambridge University Press, Cambridge.

Hardin, G. 1968. The Tragedy of the Commons. *Science* **162**:1243–1248.

Harrison, R. D. 2011. Emptying the forest: hunting and the extirpation of wildlife from tropical nature reserves. *BioScience* **61**:919–924.

HoARECN. 2013. Launch of the biodiversity management programme.

Hunter, L. 2011. *Carnivores of the world*. Princeton University Press, Princeton, New Jersy.

Ishwaran, N., A. Persic, and N. H. Tri. 2008. Concept and practice: the case of UNESCO biosphere reserves. *International Journal of Environment and Sustainable Development* **7**:118–131.

Kafa Biosphere Reserve. 2013. Zoning.

Kull, C. A. 2004. *Isle of fire: the political ecology of landscape burning in Madagascar*. University of Chicago Press, London.

Lagendijk, D. D. G., and M. Gusset. 2008. Human–carnivore coexistence on communal land bordering the Greater Kruger Area, South Africa. *Environmental Management* **42**:971–976.

Lambertucci, S. A., P. A. E. Alarcón, F. Hiraldo, J. A. Sanchez-Zapata, G. Blanco, and J. A. Donázar. 2014. Apex scavenger movements call for transboundary conservation policies. *Biological Conservation* **170**:145–150.

Macdonald, D. W. 2016. Animal behaviour and its role in carnivore conservation: examples of seven deadly threats. *Animal Behaviour* **120**:197–209.

McLean, J., and S. StrÆDe. 2003. Conservation, relocation, and the paradigms of park and people management - a case study of Padampur villages and the Royal Chitwan National Park, Nepal. *Society & Natural Resources* **16**:509–526.

Mora, C., and P. F. Sale. 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Marine ecology progress series* **434**:251–266.

Nepstad, D., S. Schwartzman, B. Bamberger, M. Santilli, D. Ray, P. Schlesinger, P. Lefebvre, A. Alencar, E. Prinz, and G. Fiske. 2006. Inhibition of Amazon deforestation and fire by parks and indigenous lands. *Conservation Biology* **20**:65–73.

Phillips, A. 2004. The history of the international system of protected area management categories. *Parks* **14**:4-14.

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

Rolston, H. 1998. Saving nature, feeding people, and the foundations of ethics. *Environmental Values* **7**:349–357.

Salafsky, N. 2011. Integrating development with conservation: a means to a conservation end, or a mean end to conservation? *Biological Conservation* **144**:973–978.

Schwartzman, S., A. Moreira, and D. Nepstad. 2000. Rethinking tropical forest conservation: Perils in Parks. *Conservation Biology* **14**:1351–1357.

Scott, J. 1986. Everyday forms of peasant resistance. *The Journal of Peasant Studies* **13**:5–35.

Shipman, P., and A. Walker. 1989. The costs of becoming a predator. *Journal of Human Evolution* **18**:373–392.

Siurua, H. 2006. Nature above people: Rolston and "fortress" conservation in the South. *Ethics and the Environment* **11**:71–96.

Stein, A. B., V. Athreya, P. Gerngross, G. Balme, P. Henschel, U. Karanth, D. Miquelle, S. Rostro-Garcia, J. F. Kamler, A. Laguardia, I. Khorozyan, and A. Ghoddousi. 2016. *Panthera pardus* (errata version published in 2016). The IUCN Red List of Threatened Species 2016: e.T15954A102421779. IUCN.

Steneck, R. S. 2005. An ecological context for the role of large carnivores in conserving biodiversity. Pages 9–33 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. *Large carnivores and the conservation of biodiversity.* Island Press, Washington DC, USA.

Strathern, M. 1980. No nature, no culture: the Hagen case. Pages 174–222 *in* M. MacCormack and M. Strathern, editors. *Nature, culture and gender*. Cambridge University Press, Cambridge, UK.

Terborgh, J. 2000. The Fate of Tropical Forests: a Matter of Stewardship. *Conservation Biology* **14**:1358–1361.

Terborgh, J., and C. V. Schaik. 2002. Why the world needs parks. Pages 3–14 *in* J. Terborgh, C. V. Schaik, L. Davenport, and M. Rao, editors. *Making parks work: Strategies for preserving tropical nature*. Island Press, Washington, DC.

Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17**:1491–1499.

Trouwborst, A. 2015. Global large carnivore conservation and international law. *Biodiversity and Conservation* **24**:1567–1588.

UNESCO-MBA Biosphere Reserves Directory. 2010. Biosphere reserve information, Ethiopia, Kafa.

UNESCO. 2017. Biosphere Reserves – Learning sites for sustainable development.

UNESCO, and UNEP. 1974. Report of the task force on criteria and guidelines for the choice and establishment of Biosphere Reserves. UNESCO-MAB Report Series, Paris.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* **94**:2619–2631.

Phillips, A. 2004. The history of the international system of protected area management categories. *Parks* **14**:4-14.

Wilkie, D. S., G. A. Morelli, J. Demmer, M. Starkey, P. Telfer, and M. Steil. 2006. Parks and people: assessing the human welfare effects of establishing protected areas for biodiversity conservation. *Conservation Biology* **20**:247-249.

Wolmer, W. 2003. Transboundary Conservation: The politics of ecological integrity in the Great Limpopo Transfrontier Park. *Journal of Southern African Studies* **29**:261–278.

Woodroffe, R., and J. Ginsberg. 2005. King of the beasts? Evidence for guild redundancy among large mammalian carnivores. Pages 154–175 *in* R. JC, R. KH, S. RS, and B. J, editors. *Large carnivores and the conservation of biodiversity*. Island Press, Washington, USA.

Woodroffe, R., and C. Sillero-Zubiri. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species 2012: e.T12436A16711116.

Wozencraft, W. C. 2005. Order carnivora. Pages 532–628 *in* D. E. Wilson and D. M. Reeder, editors. *Mammal species of the world: a taxonomic and geographic reference*. The Johns Hopkins University Press, Baltimore, MD.

CHAPTER II

LARGE CARNIVORE DISTRIBUTION AND CONNECTIVITY IN SUB-SAHARAN AFRICA

Gebresenbet F, Bauer H, and Papeş M (201x). Large carnivore distribution and connectivity in sub-Saharan Africa. (Target journal: Diversity and distribution)

Abstract

Africa's large carnivore guild includes four threatened species: African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and African lion (*Panthera leo*). Habitat fragmentation and conflict with humans are two of the leading factors threatening these carnivores. We ran ecological niche models in Maxent to identify the environmentally suitable conditions for the carnivores in eastern and southern Africa, and projected it to sub-Saharan Africa. The model outputs were further filtered using human population density and land cover layers. Least-cost connectivity analyses were conducted on the filtered models using friction layers created by combining human population density, land cover, and prey species richness (created from IUCN distribution maps). The resulting routes (corridors) were prioritized based on path cost, sizes of patches that they connect, path length, overlap with Protected Areas, and transboundary-ness. All models had high performance (AUC $\geq$ 0.80 and omission error $\geq$0.01). Our results show that greater sizes of suitable habitat patches are located in southern and eastern Africa, indicating that the habitat in western and central Africa might have been naturally more fragmented, even without present human impact. This study identified potential large carnivore distributions and possible corridors, and further prioritized corridors that may be financially cheaper to establish. However, surveys,

studies on the movement (dispersal) patterns, and intraguild interactions of the large carnivores must be conducted at finer scales to validate and make use of our landscape level analysis.

Keywords: lion, cheetah, African wild dog, leopard, large carnivores, distribution, corridor, sub-Saharan Africa, ecological niche modeling, Maxent

Introduction

Large carnivores, as apex predators, always occur at relatively low densities but play important roles in structuring ecosystems (Ripple et al. 2014). Declines of large carnivore populations trigger changes within ecological communities (Estes et al. 2011, Ripple et al. 2014). Despite their low numbers, large carnivores occupy large geographical ranges. This makes large carnivores suitable as a proxy for conservation in the absence of resources to characterize habitat preferences for all species in a landscape. Large carnivores can be used to facilitate ecosystem conservation and restoration, to symbolize conservation, to identify conservation priority areas, and to do site-based conservation planning (Ray 2005) by serving as umbrella species, keystone species, flagship species, indicator species, and vulnerable species (Gittleman et al. 2001). Despite the irreplaceable ecological role they have, most carnivores are facing population and geographical range declines (Ripple et al. 2014).

Increasing demand for land to meet the pressure of larger human population and increasing consumption patterns causes an increase in land degradation and wildlife habitat fragmentation. Habitat fragmentation decreases the ecological suitability of patches by decreasing patch size and increasing patch isolation (Fahrig 2003), thus impacting connectivity and gene flow. Large carnivores are particularly susceptible to human encroachment and edge effects (Woodroffe 2000, Cardillo et al. 2004, Ripple et al. 2014) because of their inherently low population density. Large carnivore populations are declining globally (Ripple et al. 2014) and this is particularly true in areas where habitat fragmentation and degradation occur due to land use practices. One such area is sub-Saharan Africa, where there is high demand for land due to human population growth

(Laurance et al. 2014, O'Connell et al. 2017), and land leases to commercial farms as part of the global land rush (Schoneveld 2014, Gebresenbet 2016).

Despite loss and fragmentation of carnivore distributions, there remain multiple regions in sub-Saharan Africa that support the full complement of their native predators in a guild of large carnivores (Cozzi et al. 2012). These regions provide a unique opportunity to explore the ecology and conservation of these large carnivore species. African large carnivores are: African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), African lion (*Panthera leo*), and the hyaenidae (striped hyaena (*Hyaena hyaena*), spotted hyaena (*Crocuta crocuta*), and brown hyaena (*Parahyaena brunnea*)). This study focuses on the first four species because the IUCN Red List listed these four carnivores as threatened species. The African wild dog is *endangered* (Woodroffe and Sillero-Zubiri 2012), the cheetah and leopard are *vulnerable* (Durant et al. 2015, Stein et al. 2016), and the lion is *critically endangered* in West Africa and *vulnerable* in other parts of Africa (Bauer et al. 2016). Due to the combined and ongoing threats of habitat fragmentation and conflicts with humans, the cheetah population has been declining continuously, resulting in the recommendation that its IUCN status be upgraded to endangered (Durant et al. 2017). Large carnivores require large home ranges, which mostly extend over political boundaries of a single country. This is true for the four large carnivores we use in this study (Trouwborst 2015), which can potentially add the additional challenge of differing governance systems to existing challenges of large carnivore conservation.

Intraguild relationships are important components of carnivore co-existence, conservation, and management. These interactions are dependent on local ecological conditions and can influence carnivores in different ways. African wild dog and cheetah, the subordinate carnivores, are under constant threats of interference, competition, and intraguild killings from their top competitor, lion (Vanak et al. 2013). Negative relationships have been recorded between densities of lions and cheetahs and lions and African wild dogs (Laurenson 1994, Creel and Creel 1996, Carbone et al. 2005). Population declines of subordinate carnivores can result from reduced nutrition due to kleptoparasitism, high mortality of cubs, high mortality of adults due to intraguild killing, and avoidance of high prey density areas (Creel and Creel 1996, Durant 1998, Linnell and Strand 2000, Webster et al. 2012).

Delineating distributions, identifying conservation priority areas, and maintaining landscape connectivity are important elements of large carnivore conservation in Africa. Although much research has been done on African wild dogs, both Woodroffe et al. (1997) and Woodroffe et al. (2004) pointed out gaps in knowledge of African wild dogs' distribution and suggested that surveys be conducted. Identifying distributions, particularly outside of protected areas, and mapping fragmented populations were also two of the research priorities identified for felids by Nowell and Jackson (1996). Durant et al. (2017) acknowledges the extensive effort required to survey cheetah populations in unprotected areas and poorly managed protected areas. Current ranges are the result of the carnivores' habitat preference, evolutionary history, colonization ability, and sensitivity to human caused environmental changes (Macdonald and Kays 2005). However, finding quantitative data on factors like evolutionary history, carnivore movements, and carnivore genetic structure is challenging. Two economical ways of providing information to guide extensive surveys and designing potentially functional corridors are ecological niche modeling and patch connectivity analysis.

Ecological niche modeling is an approach that identifies conditions suitable for the survival of a species based on known geographical locations of the species and environmental variables within those locations (Araújo and Peterson 2012). Identifying the geographical distribution of large carnivores and the variables determining those patterns are among the most important pieces of the large carnivore conservation conundrum in sub-Saharan Africa. The aims of this study are to estimate sub-Saharan distributions and evaluate the landscape connectivity for African wild dogs, cheetahs, leopards, and African lions. To accomplish these goals, we ran climate based ecological niche models. We also quantified patch connectivity by using resistance surfaces that reflect biological responses of the carnivores. Predictions of our models will help scientists and managers to prioritize conservation areas and manage existing patches in a better way.

Methods

Species' occurrence points and environmental variables

We compiled a total of 1175 carnivore presence records (154 African wild dogs, 211 cheetahs, 424 lions, and 386 leopards) from multiple resources, including our own and colleagues' fieldwork, published literature, specimens in the Oklahoma State University Collection of Vertebrates, and online databases such as GBIF, VertNet, and iNaturalist (Supplementary Material I). For our environmental variables we used the 19 global bioclim layers from WorldClim 1.4 (Hijmans et al. 2005), representing mean annual, seasonal, and extreme temperature and precipitation for 1950 to 2000, at a resolution of 2.5 arc minutes (~ 4.5 km) and an elevation layer GTOPO30 (USGS 1999) resampled to 4.5 km from the original resolution of 1 km. All bioclim variables and elevation were clipped to a geographic extent of 500 km around the minimum convex polygon containing all carnivore records (Fig. 1). This region was used to train the ecological niche models for the four carnivore species (see *Ecological Niche Modeling of carnivores* below). We removed highly correlated variables (≥ 0.7) from the full dataset of 19 bioclim variables using Pearson correlation, following Dormann et al. (2013). This reduced the environmental dataset to six bioclim variables: mean diurnal range, isothermality, annual precipitation, precipitation of driest month, precipitation seasonality (coefficient of variation), and precipitation of coldest three months.

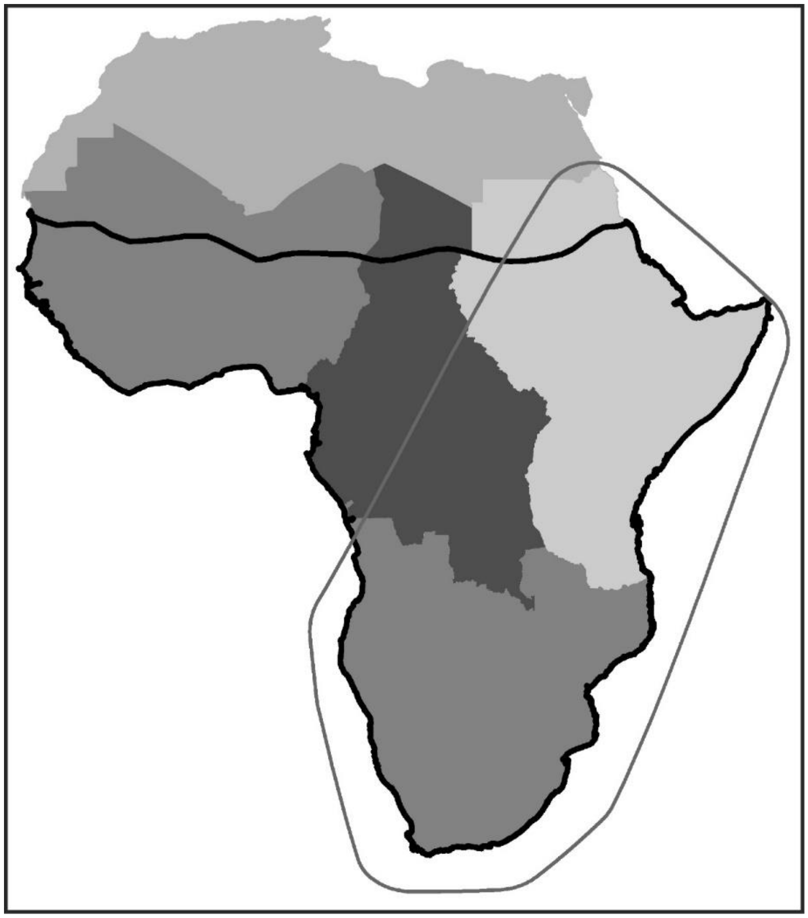

Fig 1. Map of the study area, sub-Saharan Africa (in contour). The grey polygon outline represents the geographic extent of training region used for ecological niche modeling of four carnivore species (African wild dog, cheetah, leopard, and lion). Models were projected to the continental extent to estimate potential distributions.

Ecological niche modeling of carnivore species

We used Maxent (v. 3.3.3 k), a maximum entropy algorithm in which environmental conditions associated with species' presences are contrasted with environmental conditions from background (pseudoabsences) locations across the training region to estimate the environmental suitability for the species (Phillips et al. 2004). For all four species we trained the models at the extent of the 500 km buffer around known presences and used the cross-validation approach, with five model replicates and 20% of occurrences set aside to test the performance of models obtained. The models were then projected to sub-Saharan Africa (study area hereafter). We averaged the five replicates to create a single model prediction for each species. To evaluate our models, we used the test occurrence data to calculate the area under the curve (AUC) of the receiver operating characteristic (ROC) plot. Its value ranges from 0.5 (random model) to 1 (perfect presence-absence discrimination) (Fielding and Bell 1997), and models with AUC >0.7 are considered reliable (Swets 1988).

Maxent produced models with relative probabilities of the carnivores' distribution, after evaluating the association between the carnivores and the environmental variables, by using known occurrences and pseudo-absences (location data extracted from the background pixel, in which the carnivore is not known to occur) (Elith et al. 2006, Phillips et al. 2006).

We converted the Maxent continuous probability of suitability predictions to binary maps based on the lowest training presence threshold, representing the Maxent probability value at which all occurrences used to train the models (by species) were predicted present (Pearson et al. 2007). Locations with values greater than or equal to the threshold value were considered suitable for the species studied, whereas values less than the thresholds were considered environmentally unsuitable for the species.

Since the environmental variables used in the carnivore models represented temperature and precipitation trends for 1950–2000, we further refined the binary suitability maps using the gridded population of the world v. 4 (CIESIN 2016) for the year 2015 at a resolution of 1 km, and a global land cover layer for 2015 (ESA 2017) at a resolution of 300 meters, both of which are variables that influence large carnivore distribution. To this end, we created binary maps of human population density and land cover using common thresholds from the literature to separate suitable and unsuitable conditions (population density; land cover) for the species. Specifically, Woodroffe (2000) and Riggio et al. (2013) were used for deciding the human population density thresholds: 6.3 people/km^2 for African wild dogs, 16.5 people/km^2 for cheetahs, 958 people/km^2 for leopards, and 26 people/km^2 for lions. We relied on multiple sources to reclassify the land cover map in suitable and unsuitable categories for each species (Supplementary Material II). We overlapped sequentially our binary suitability maps (4.5 km resolution) for each species with human population density and land cover maps, preserving the finer resolution of the land cover. As a result, the final potential suitability maps for the four carnivore species studied had a spatial resolution of 300 m. We then compared the IUCN range maps (extant and possibly extant) of the carnivores in sub-Saharan Africa to our predictions of suitable areas (based on climate suitability, human density, and land cover information). We also evaluated the overlap between maps of protected areas in sub-Saharan Africa and our predicted suitable areas. All analyses, except the ecological niche models, were done in ESRI ArcGIS10.4.

Connectivity analysis

We aggregated the presence pixels of the potential distribution maps into regions based on the median home range size for each carnivore species. The home range sizes of the carnivores were determined from literature (Supplementary Material III), by calculating the median of values reported. After aggregation we kept regions that had 60% or more of their area predicted suitable with the combined climatic, human population density, and land cover variables and discarded those <60% (With 2002). Lastly, we identified patches of regions (home range size) that were contiguous (i.e., shared borders, in at least one of the four cardinal directions).

The patches identified through aggregating suitable home ranges for the carnivore species were used in a connectivity analysis to find optimal least cost corridors linking these patches. We applied the graph theory approach to connect adjacent nodes (patches) using links (the lines of movement). A graph represents a set of nodes (patches of habitat in a landscape) and edges (connectivity between nodes) (Minor and Urban 2008). In our analysis, the landscape is viewed as a set of potentially suitable habitat patches, and the patches were connected with lines of potential movement (dispersal) created by avoiding high ecological costs for the specific carnivore. The costs that the carnivores incur when traveling through each pixel between any two patches was estimated with a friction layer. Thus, the friction layer represents the permeability of the matrix (i.e., the landscape) to movement of species in which the suitable patches are found. We used land cover, human density, and prey species richness maps to quantify permeability of the matrix for each carnivore species. The land cover and human density maps were the same as the ones used to refine the Maxent potential distribution predictions. For prey species richness, we downloaded the IUCN ranges of 93 prey species consumed by the carnivores (Supplementary Material IV) and stacked the ranges to create a map of number of prey species per pixel. To classify the prey species richness maps into unsuitable, low, medium, and high suitability categories, we used quantiles as cut points. To classify the human population density map into the four suitability categories, we multiplied the human population density thresholds for each carnivore species (see previous section) by factors of 0.25 or 1. The African wild dog and cheetah had lower human population density thresholds, therefore we used a multiplication factor of 1 for each suitability class. However, for lion and leopard we used a multiplication factor of 0.25 because they have higher human population density thresholds.

To create the friction layer for each species, the suitability classes were given numerical values of 1 (high suitability), 10 (medium suitability), 100 (low suitability), and 1000 (unsuitable), thus coding increasing cost of moving through the matrix. The total cost for each carnivore to moving across the landscape was obtained by adding the suitability values for all three maps (human population density, land cover, prey species richness). The resulting friction layer (at 300 m resolution) had 13 classes for lions, leopards, and cheetahs, and 11 classes for African wild dogs (due to a lack of medium suitable land cover for this species; see Supplementary Material II). For example, the lowest friction class was represented by pixels with values of 1 in each of the three maps (land cover, human density, prey species richness), whereas the second lowest friction class contained pixels with combinations of values of 1, 1, and 10 in the three maps.

We ran Cost Connectivity tool in ArcGIS 10.4 to identify the least-cost routes that connected the suitable patches (aggregated home ranges) for each carnivore species, based on calculations of costs that the carnivores will incur whilst taking a specific route through the matrix (represented by the friction layer). We also measured the length of each path that connected patches edge-to-edge and we tested for correlation between path length and path cost.

Of all paths identified with the cost connectivity analysis, we selected the best 25% corridors (paths) for each carnivore based on the path cost. We divided the sum of the area of the connected patches by the absolute value of their difference. If the quotient value was undefined, then the connected patches were of equal size, and lower quotient values indicated that a large area is connected with a small patch. However, if values of the ratio are larger, then the patches are similar in size (Supplementary material V). From the top 25% least cost corridors, we selected the best ones based on size of connected patches (using the above calculation (large ratio)), overlap with a protected area, length of the corridor, and if the corridor is transboundary or not. Therefore the identified corridors are those that: 1) connect two medium sized patches, 2) are short and have an overlap with protected areas, and 3) fall within one country only. Paths that connected patches with protected areas would be more likely to become corridors, requiring protection only for the part of path found outside of protected area. We also evaluated if these potential corridors are transboundary or not, to infer political (or governance) ease to establish these corridors.

Results

Ecological niche models of carnivores

The climate based Maxent ecological niche models (Fig 2) had high accuracy and good predictive capability, as measured with AUC (> 0.8) and testing omission error (<0.12) metrics (Table 1).

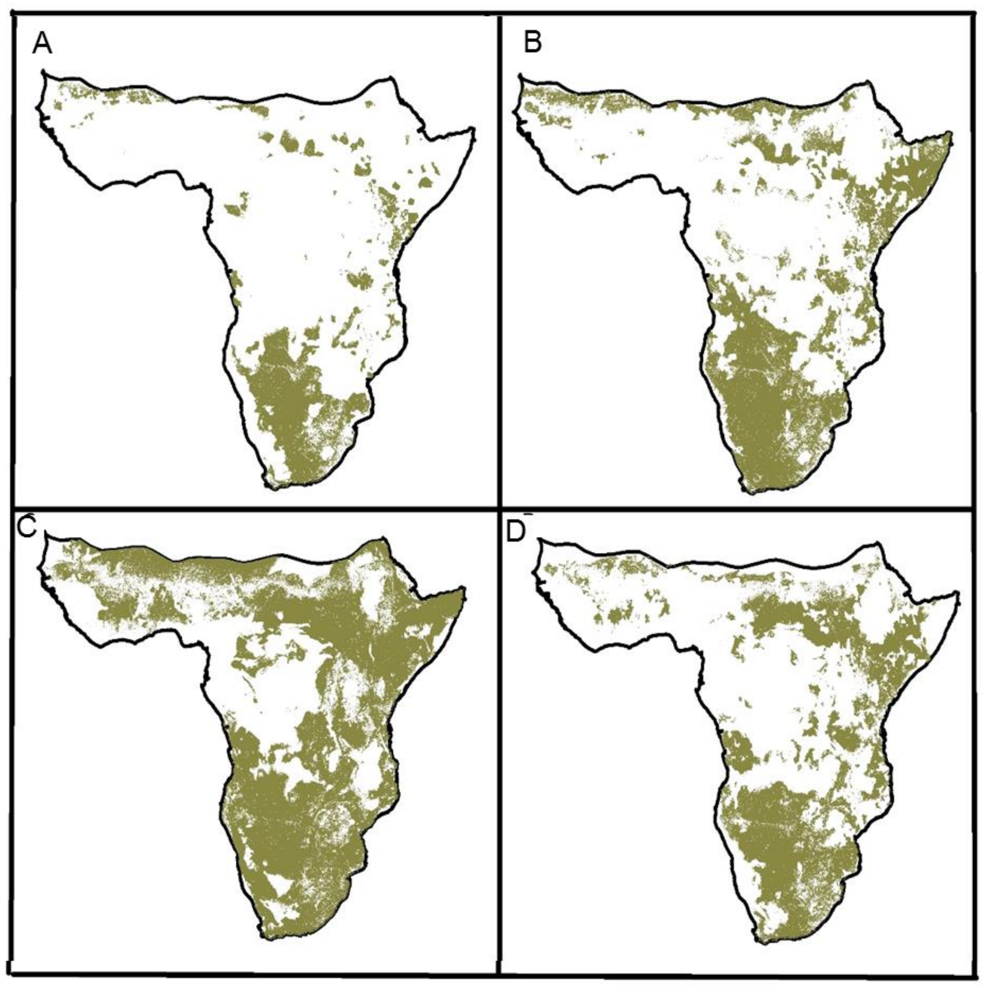

Fig. 2: Climate based potential distributions of African wild dog (A), cheetah (B), leopard (C) and lion (D) in sub-Saharan Africa, estimated with Maxent ecological niche models.

Three sets of variables contributed more than 50% to the model accuracy gain for each species (Table 1).

Table 1: Accuracy metrics of Maxent ecological niche models and contribution of variables to model accuracy for the four carnivore species studied.

Species	Testing AUC	Testing omission error	Annual precipitation (Bio 12)	Precipitation of driest month (Bio 14)	Isothermality (Bio 3)	Digital Elevation Model (GTOPO30)	Precipitation seasonality (Bio 15)	Precipitation of coldest quarter (Bio 19)	Mean diurnal range (Bio 2)
Wild dog	0.8367	0.0923	58.4	3.7	26.9	4	1.3	5	0.8
Cheetah	0.8449	0.0148	29.8	17.2	12.5	22.7	9	4.9	4
Leopard	0.8086	0.0526	38.9	19.4	10.4	14.6	4.7	3.1	9
Lion	0.8675	0.021	49.2	18.5	6.9	11.5	9.2	2.4	2.2

The potential distributions based on Maxent models were reduced in extent by as much as 11% (for cheetah) and as little as 2.9% (for leopard) when refined with land cover and human population density maps. Half or more of the extant and possibly extant IUCN ranges overlapped with the refined potential distributions for all four carnivores (Table 2).

Our models predicted high overlaps between the subordinate carnivores, African wild dog and cheetah, and the top predator lion. The overlap between African wild dog and lion was 79.69% of African wild dog predicted suitable range and between cheetah and lion was 65.65% of cheetah predicted suitable range.

Connectivity analysis

Regionally, eastern and southern Africa contained the majority of the corridors for all carnivores except leopards. For leopards, western Africa had the highest number of potential corridors (Table 3). Central Africa had the lowest proportions of all potential corridors for all species.

The majority of the top 25% least cost corridors for the four carnivores are located in eastern and southeastern sub-Saharan Africa. Different sets of criteria can be applied to select the best corridors. Our criteria (patch size, overlap with a protected area, corridor length and transboundary-ness), resulted in six best corridors for the three carnivores (two each), except lions. The best corridor for African wild dog is located in Zambia and is 25.62 km long with only about 2.16 km existing outside of a protected area. This corridor connects patch sizes of 14,950 km^2 and 19,500 km^2. The best corridor for the cheetah is 91.17 km long and is transboundary between Democratic Republic of Congo and South Sudan with about 24 km of its length occurring outside of a protected area on the Sudanese side. The best corridor for the leopard is located in Democratic Republic of Congo, stretching across 30.62 km of land, out of which about 28.21 km is located inside a protected area. We have provided the list of the top 25% corridors and the calculations we conducted to select the best ones (Supplementary Material VI).

Table 2: Areas of the ecological niche models and the refined suitable patches and their overlaps with IUCN ranges and protected areas

Species	Maxent projected suitable area (Km^2)	Refined patch area (Km^2)	% area change between Maxent projection & refined patches	IUCN and patch overlap area (Km^2)	% IUCN range that fell in the refined patches	% refined patch that fell inside IUCN range	PA and Refined patch overlap (Km^2)	% refined patch that fell inside PAs
Wild dog	3,194,895.95	2,984,892.57	6.57	619,631.49	50.63	20.76	613,224.89	20.54
Cheetah	6,330,655.16	5,614,019.05	11.32	2,114,404.02	62.97	37.66	979,341.47	17.44
Leopard	10,819,901.22	10,497,949.90	2.98	4,050,096.01	63.47	38.58	2,027,083.01	19.31
Lion	6,350,000.69	5,998,534.09	5.54	1,287,896.88	65.29	21.47	1,312,683.38	21.88

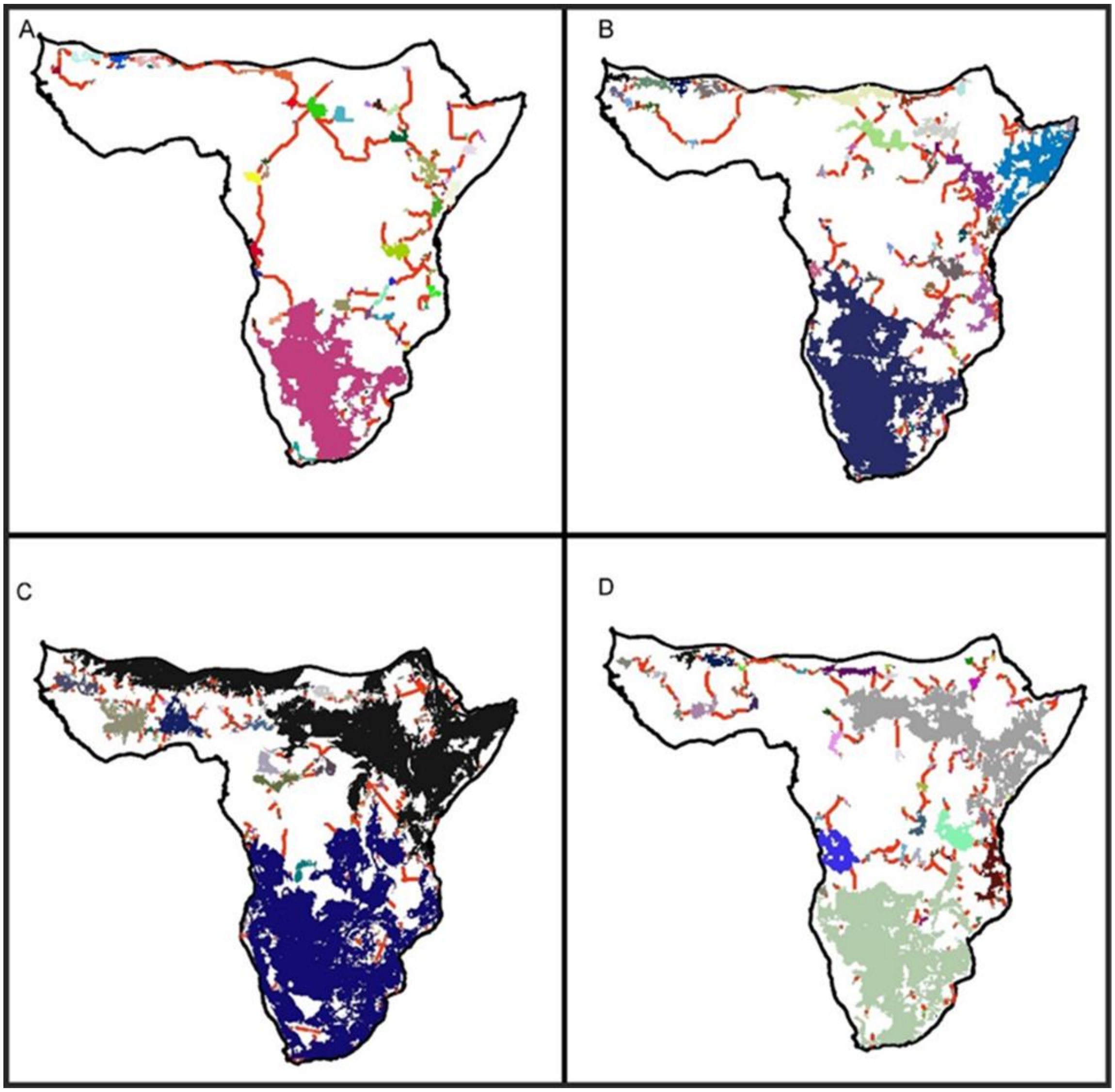

Fig. 3: Corridors (least cost paths) for four carnivore species (in red), identified by cost connectivity analyses integrating climatic suitability, human density, land cover, and home range information. The different colors represent aggregated contiguous home ranges for African wild dog (A), cheetah (B), leopard (C) and lion (D). Only the best 25% corridors are shown, selected based on path cost.

The criteria for selecting the best corridors can be modified according to existing conditions in specific areas using Supplementary Material VI.

Table 3: The share of least cost optimal paths per region and carnivore species

	% South	% West	% East	% Central
Total no. of corridors	20.80	24.80	38.13	16.27
Lion	20.99	21.55	38.12	19.34
Leopard	16.21	34.83	32.07	16.90
Cheetah	22.41	15.52	45.40	16.67
African wild dog	30.48	18.10	42.86	8.57

We observed a trend in which the least cost optimal paths were also shorter in length for African wild dogs and cheetahs (Pearson's correlation of 0.69 and 0.85, respectively; *P* <0.001 for both), while the relationship appeared weaker for lions (Pearson's correlation of 0.58; *P*< 0.001), and the weakest for leopards (Pearson's correlation = 0.3, *P* <0.001) (Fig. 4).

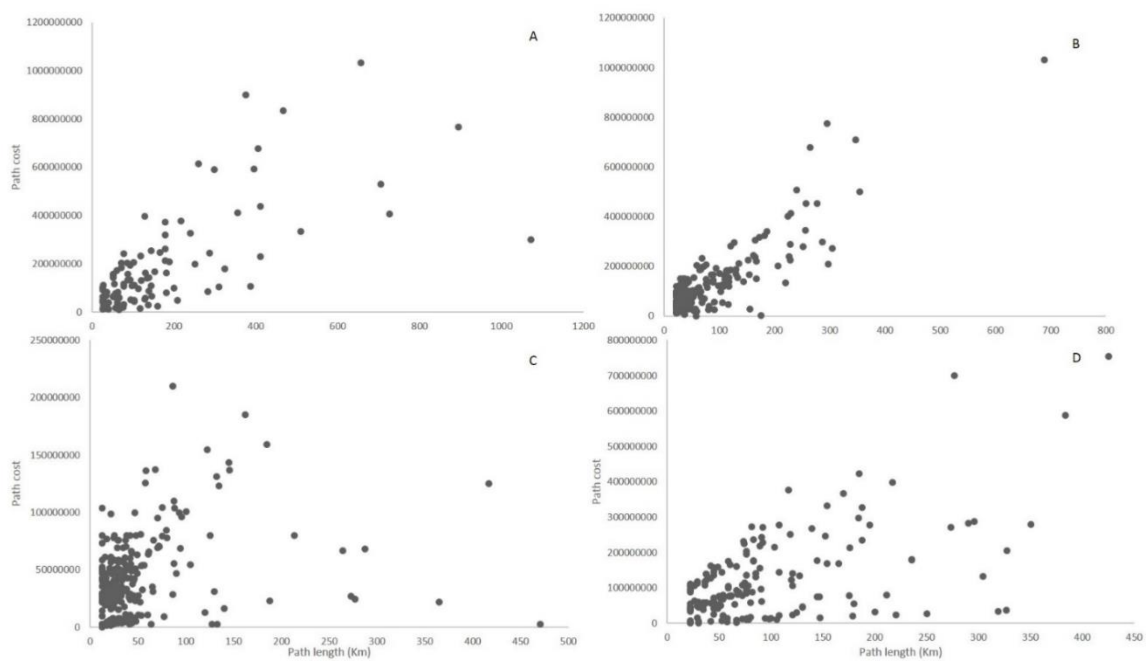

Fig. 4: Correlation of path cost and length for African wild dog (A), cheetah (B), leopard (C) and lion (D).

Discussion

Scientists have been studying different aspects of large carnivores for more than a century (Pocock 1909, Adams 1916, Pocock 1917). While comparing the felids, Nowell and Jackson (1996) ranked cheetahs and leopards to be highly studied (100-200 publications) while lions were considered very highly studied (200+ publications). Woodroffe et al. (1997) compiled more than 300 publications about African wild dogs. From January 1996 to May 2018, we found 548 cheetah, 466 lion, and 530 leopard articles from SCI journals in Web of Science. We also found 100 SCI publications about African wild dog between January 1997 and May 2018. These extensive amounts of research show the wealth of information on different aspects of these carnivore species. Ray et al. (2005) ranked lions as the most studied of all the African large carnivores while cheetah, African wild dog, and leopard ranked third, fourth, and sixth respectively. Although African wild dog has been the focus of many studies, both Woodroffe et al. (1997) and Woodroffe et al. (2004) have pointed out gaps in knowledge of African wild dogs' distribution and suggested that surveys be conducted in some range countries including Angola, Cameroon, Central African Republic, Ethiopia, Mozambique and Sudan. Identifying cat distributions, particularly outside of protected areas, and mapping fragmented cat populations were also two of the research priorities identified by Nowell and Jackson (1996). However, reliable data are missing for some parts of Africa regarding lion populations (Bauer et al. 2015).

Large carnivore populations' are declining globally (Ripple et al. 2014) and this is particularly the case in areas experiencing habitat fragmentation and human population expansion. In sub-Saharan Africa, demand for land is high due to human population growth (Laurance et al. 2014, O'Connell et al. 2017). Sub-Saharan Africa harbours an intact guild of large carnivores (Cozzi et al. 2012) providing a unique opportunity to explore the ecology and conservation of large carnivores. To conserve and manage these species, one must first know the distribution patterns across the landscape. Distribution models entail simplification, but they also provide information about the general environmental constraints that deter the expansion of species ranges. The distribution models that we created for African wild dog, cheetah, leopard, and African lion resulted in spatial predictions of environmental suitability. These models can serve a crucial purpose as starting points of prioritizing large carnivore conservation areas.

Our ecological niche models had high levels of statistical significance; i.e. AUC $\geq$ 0.8 and omission error $\geq$0.01, for all carnivores. AUC values indicate that if we sampled random pairs of points from the presence and absence sites, our prediction would be higher for the presence $\geq$ 80% of the time. The omission error values indicate that less than 1% of the known presences are incorrectly predicted absent by our models.

Geographical distributions of large carnivores depend on four factors and their dynamic interactions: 1) if local environmental conditions allow the carnivore populations to exist; 2) if the inter-/intra-specific interactions and biological processes allow the carnivores to thrive; 3) if the carnivores can find an accessible location to disperse, given their dispersal abilities; and 4) if the carnivores are evolutionarily capable of adapting to new conditions (Soberón and Peterson 2005). In this paper, we incorporated the first three factors directly or indirectly by inferring to the model outputs and biological knowledge of the carnivores.

Most of the climatically suitable space projected by our ecological niche models is not lost when refined by land cover and human population density, suggesting that our Maxent outputs were conservative. This was unexpected, because habitat loss and human-carnivore conflicts are two of the dire threats on carnivores (Durant et al. 2015, Bauer et al. 2016, Macdonald 2016, Stein et al. 2016, Woodroffe and Sillero-Zubiri 2012). This result suggests that present situations might be close to the 'natural pattern', and conservation efforts might not increase large carnivore populations, regardless of amount of effort and resources invested.

Our ecological niche models, based on environmental constraints, depicted certain common patterns, which potentially could be the result of essential natural or anthropogenic predictors that affect large carnivores. Southern Africa harboured the largest unfragmented suitable predicted areas for all four carnivores, followed by eastern Africa. Central Africa has some large suitable patches for leopards and lions, while western Africa had the smallest amounts and sizes of suitable patches for all carnivores but leopards. Several authors have attributed regional differences and particularly west African fragmentation to recent population declines (Packer et al. 2013, Bauer et al. 2015, Brugière et al. 2015), but our work indicates that there were important natural regional differences to begin with. The extreme fragmentation of today is only partly a result of people, and partly by nature.

Leopards had the highest prediction of suitable habitat in terms of coverage of the study area (54.72% of sub-Saharan Africa), which is expected, since leopards occur in almost all habitat types, have a broad and flexible diet, kill smaller competitors (according to data compiled by Nowell and Jackson (1996)), and are able to exist close to people (Kuhn 2014, Odden et al. 2014).

African wild dog is the most threatened of our study species (Ray et al. 2005), with only about 6000 individuals remaining in the wild and with extirpation from 25 of 39 its historical range countries (Woodroffe et al. 2004). This canid has the lowest suitable area prediction in our models, 16.16% of sub-Saharan Africa, which was reduced to 15.1% when refined by land cover and human population density. In addition to this, most of the patches predicted suitable are small and isolated. For example, 36 out of the 123 individual patches are 650 km^2, which is the home range size of African wild dogs used in this study. Small and isolated groups of African wild dogs are particularly susceptible to population decline (Woodroffe et al. 1997), and are very slow to recover from such declines (Carbone et al. 1997). Therefore, priority should be given to surveying the suitable areas that extend beyond protected areas and are interconnected with other suitable patches.

Cheetah populations have declined significantly over the past few decades and latest estimates put the known resident ranges in Africa (including north of Sahara) at 2,976,963 km^2 (Durant et al. 2017). Our models predicted highest suitable areas in southern (61 patches covering 3,433,000 km^2) and eastern (91 patches covering 1,509,000 km^2) Africa, with relatively higher fragmentation in eastern Africa.

Interspecific and intraspecific interactions are among the factors that influence the geographical distribution of organisms (Soberón and Peterson 2005). Our model outputs provide information on environmental suitability. We refined the model outputs with biotic interactions represented by known ranges of prey species in the connectivity analysis. Adding biological knowledge on elements like the intraguild interaction, competition, ways of co-existence in a landscape, and movement within the landscape will improve the usability of our models.

The high overlap between predicted suitable ranges of our subordinate carnivores, African wild dog and cheetah, and their top competitor, the lion, should not lead to the assumption that long-term reproduction and survival of the subordinate carnivores are unlikely in these patches. Different ways of co-existence have been reported including; minimizing temporal overlap and interference competition (Hayward and Slotow 2009), inhabiting the lowest resource availability areas (Vanak et al. 2013), and reactively responding to risks of competition from top competitors (Broekhuis et al. 2013). Intraguild interactions are dependent on multiple factors, thus shared areas must be studied to draw site-specific conclusions.

Protected areas are important for conservation of large carnivores. For example, Riggio et al. (2013) and Durant et al. (2017) estimated about 56 and 23% of lion and cheetah ranges, respectively, to occur inside protected areas. However, most protected areas in Africa have suffered severe wildlife declines (Craigie et al. 2010), and are unable to provide the space needed for supporting viable populations of large carnivores (van der Meer et al. 2014). Therefore, large carnivore conservation strategies must include efforts to connect (and conserve) populations that are free ranging.

Land use changes could convert what was once suitable habitat for the carnivores to smaller, isolated patches bordered by unsuitable areas. Habitat fragmentation results in isolated populations of large carnivores, posing risks of inbreeding depression and loss of genetic diversity. As the isolated patches get smaller, the effect worsens. Cheetah and African wild dog are examples of species experiencing such genetic variability loss (Merola 1994, Campana et al. 2016). This amplifies the need for connecting isolated populations of large carnivores. Reducing edge effects and maintaining connectivity are important components of having viable large carnivore populations (Durant et al. 2017). To deal with physically and politically fragmented landscapes, conservation actions need to extend beyond the borders of formally recognized protected areas and also embrace transboundary conservation.

The 747 least cost paths identified based on the smallest possible resistances from human population density, land cover, and prey species richness can potentially serve to connect different subpopulation across sub-Saharan landscapes upon proper planning. Except for leopards, the carnivores have the same pattern in terms of number of corridors regionally. Southern Africa has the lowest number of corridors because of the relatively lower fragmentation. Southern Africa has 97 patches that represented 40.49% of the total leopard suitable patches, of which a single patch constituted 98.13% of the southern suitable area. Western Africa had 165 patches (13.21% of the total suitable leopard patches) and the largest patch accounted for 53.9% of the total western suitable area.

For the African wild dog and cheetah, the least cost paths were significantly correlated with short path lengths. Shorter corridors that pass through protected areas are financially cheaper to establish. However, decisions should be accompanied by studies at finer scales to avoid linking populations with potential sink areas.

Transboundary conservation should be an element of connectivity planning. In considering transboundary conservation schemes, some regions and countries appear pivotal in terms of connectivity. For example, Zambia borders eight countries, dedicates about 40% of its land for wildlife purposes, and incorporates three transboundary conservation areas (Watson et al. 2015).

Dispersal, although one of the most important biological processes, is a least understood biological process (Bowler and Benton 2005), creating a gap in management and conservation of carnivore metapopulations. Our analysis showed that suitable patches for carnivores in eastern and southern sub-Saharan Africa might have better connectivity than central and western patches. Multiple factors affect carnivore movement patterns and intraguild interactions, hence the relationship between these biological elements should be examined at finer scales. Our broad results represent large carnivore potential distributions at the landscape scale, and can be used as first steps to conduct surveys and validate them via fieldwork at finer scales. Our results can also be used to establish functional corridors.

References

Adams, C. C. 1916. Distribution and abundance of African elephants and lions. *Geographical Review* **1**:158–159.

Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**:1527–1539.

Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. T. B. Hunter, D. W. Macdonald, and C. Packer. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences* **112**:14894–14899.

Bauer, H., C. Packer, P. F. Funston, P. Henschel, and K. Nowell. 2016. *Panthera leo* (errata version published in 2017). The IUCN Red List of Threatened Species 2016: e.T15951A115130419. IUCN.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80**:205–225.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology* **82**:1098–1105.

Brugière, D., B. Chardonnet, and P. Scholte. 2015. Large-scale extinction of large carnivores (Lion *Panthera leo*, Cheetah *Acinonyx jubatus* and Wild Dog *Lycaon pictus*) in protected areas of West and Central Africa. *Tropical Conservation Science* **8**:513–527.

Campana, M. G., L. D. Parker, M. T. R. Hawkins, H. S. Young, K. M. Helgen, M. Szykman Gunther, R. Woodroffe, J. E. Maldonado, and R. C. Fleischer. 2016. Genome sequence, population history, and pelage genetics of the endangered African wild dog (*Lycaon pictus*). *BMC Genomics* **17**:1013.

Carbone, C., J. T. Du Toit, and I. J. Gordon. 1997. Feeding success in African wild dogs: Does kleptoparasitism by spotted hyenas influence hunting group size? *Journal of Animal Ecology* **66**:318–326.

Carbone, C., L. Frame, G. Frame, J. Malcolm, J. Fanshawe, C. FitzGibbon, G. Schaller, I. J. Gordon, J. M. Rowcliffe, and J. T. Toit. 2005. Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology* **266**:153–161.

Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. 2004. Human population density and extinction risk in the world's carnivores. *PLOS Biology* **2**:e197.

CIESIN. 2016. **-** Center for International Earth Science Information Network **-** Columbia University. *Gridded population of the world*, *Version 4 (GPWv4): Population density*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY.

Cozzi, G., F. Broekhuis, J. W. McNutt, L. A. Turnbull, D. W. Macdonald, and B. Schmid. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology* **93**:2590–2599.

Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology* **10**:526–538.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**:27–46.

Durant, S., N. Mitchell, A. Ipavec, and R. Groom. 2015. *Acinonyx jubatus*. The IUCN Red List of Threatened Species 2015: e.T219A50649567. IUCN.

Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology* **67**:370–386.

Durant, S. M., N. Mitchell, R. Groom, N. Pettorelli, A. Ipavec, A. P. Jacobson, R. Woodroffe, M. Böhm, L. T. B. Hunter, M. S. Becker, F. Broekhuis, S. Bashir, L. Andresen, O. Aschenborn, M. Beddiaf, F. Belbachir, A. Belbachir-Bazi, A. Berbash, I. Brandao de Matos Machado, C. Breitenmoser, M. Chege, D. Cilliers, H. Davies-Mostert, A. J. Dickman, F. Ezekiel, M. S. Farhadinia, P. Funston, P. Henschel, J. Horgan, H. H. de Iongh, H. Jowkar, R. Klein, P. A. Lindsey, L. Marker, K. Marnewick, J. Melzheimer, J. Merkle, J. M'soka, M. Msuha, H. O'Neill, M. Parker, G. Purchase, S. Sahailou, Y. Saidu, A. Samna, A. Schmidt-Küntzel, E. Selebatso, E. A. Sogbohossou, A. Soultan, E. Stone, E. van der Meer, R. van Vuuren, M. Wykstra, and K. Young-Overton. 2017. The global decline of cheetah *Acinonyx jubatus* and what it means for conservation. *Proceedings of the National Academy of Sciences* **114**:528–533.

Elith, J., C. H. Graham, R. P. Anderson, Dud, xed, M. k, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, C. O. Jacob Mc, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, Sober, xf, J. n, S. Williams, M. S. Wisz, N. E. Zimmermann, and M. Araujo. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**:129–151.

ESA. 2017. Annual global land cover map at 300 m European Space Agency, UCLouvain, Belgium.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B.

Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. *Science* **333**:301–306.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**:487–515.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38.

Gebresenbet, F. 2016. Land acquisitions, the politics of dispossession, and state-remaking in Gambella, western Ethiopia. *Africa Spectrum* **51**:5–28.

Gittleman, J. L., S. M. Funk, D. W. Macdonald, and R. K. Wayne. 2001. *Why "carnivore conservation"?* Pages 1–7 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore Conservation. Cambridge University Press, Cambridge.

Hayward, M. W., and R. Slotow. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research* **39**:109–125.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**:1965–1978.

Kuhn, B. F. 2014. A preliminary assessment of the carnivore community outside Johannesburg, South Africa. *South African Journal of Wildlife Research* **44**:95–98.

Laurance, W. F., J. Sayer, and K. G. Cassman. 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution* **29**:107–116.

Laurenson, M. K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of Zoology* **234**:387–408.

Linnell, J. D. C., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions* **6**:169–176.

Macdonald, D. W. and R. Kays. 2005. *Walker's carnivores of the world*. Pages 1-67. The John Hopkins University Press, Baltimore, Maryland.

Macdonald, D. W. 2016. Animal behaviour and its role in carnivore conservation: examples of seven deadly threats. *Animal Behaviour* **120**:197–209.

Merola, M. 1994. A reassessment of homozygosity and the case for inbreeding depression in the cheetah, *Acinonyx jubatus*: implications for conservation. *Conservation Biology* **8**:961–971.

Minor, E. S., and D. L. Urban. 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology* **22**:297–307.

Nowell, K., and P. Jackson. 1996. Wild cats: status survey and conservation action plan. IUCN/SSC Cat Specialist Group, IUCN, Gland.

O'Connell, M. J., O. Nasirwa, M. Carter, K. H. Farmer, M. Appleton, J. Arinaitwe, P. Bhanderi, G. Chimwaza, J. Copsey, J. Dodoo, A. Duthie, M. Gachanja, N. Hunter, B. Karanja, H. M. Komu, V. Kosgei, A. Kuria, C. Magero, M. Manten, P. Mugo, E. Müller, J. Mulonga, L. Niskanen, J. Nzilani, M. Otieno, N. Owen, J. Owuor, S. Paterson, S. Regnaut, R. Rono, J. Ruhiu, J. Theuri Njoka, L. Waruingi, B. Waswala Olewe, and E. Wilson. 2017. Capacity building for conservation: problems and potential solutions for sub-Saharan Africa. *Oryx*:1–11.

Odden, M., V. Athreya, S. Rattan, and J. D. C. Linnell. 2014. Adaptable neighbours: movement patterns of gps-collared leopards in human dominated landscapes in India. *PLOS ONE* **9**:e112044.

Packer, C., A. Loveridge, S. Canney, T. Caro, S. T. Garnett, M. Pfeifer, K. K. Zander, A. Swanson, D. MacNulty, G. Balme, H. Bauer, C. M. Begg, K. S. Begg, S. Bhalla, C. Bissett, T. Bodasing, H. Brink, A. Burger, A. C. Burton, B. Clegg, S. Dell, A. Delsink, T. Dickerson, S. M. Dloniak, D. Druce, L. Frank, P. Funston, N. Gichohi, R. Groom, C.

Hanekom, B. Heath, L. Hunter, H. H. DeIongh, C. J. Joubert, S. M. Kasiki, B. Kissui, W. Knocker, B. Leathem, P. A. Lindsey, S. D. Maclennan, J. W. McNutt, S. M. Miller, S. Naylor, P. Nel, C. Ng'weno, K. Nicholls, J. O. Ogutu, E. Okot-Omoya, B. D. Patterson, A. Plumptre, J. Salerno, K. Skinner, R. Slotow, E. A. Sogbohossou, K. J. Stratford, C. Winterbach, H. Winterbach, and S. Polasky. 2013. Conserving large carnivores: dollars and fence. *Ecology Letters* **16**:635–641.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**:102–117.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**:231–259.

Phillips, S. J., M. Dudik, and R. E. Schapire. 2004. *A maximum entropy approach to species distribution modeling*. Page 83 Proceedings of the twenty-first international conference on Machine learning. ACM, Banff, Alberta, Canada.

Pocock, R. I. 1909. *On the skulls of Leopards*. Proceedings of the Zoological Society of London **1909**:204–209.

Pocock, R. I. 1917. VII. On the external characters of the Felidæ. *Annals and Magazine of Natural History* **19**:113–136.

Ray, J. 2005. Large carnivorous animals as tools for conserving biodiversity: assumptions and uncertainties. *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. *Large carnivores and the conservation of biodiversity.* Island Press, Washington DC, USA.

Ray, J. C., L. Hunter, and J. Zigouris. 2005. *Setting conservation and research priorities for larger African carnivores*. WCS Working Paper No. 24., Wildlife Conservation Society, New York.

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

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. *Science* **343**:1241484-1–11 . https://doi.org/10.1126/science.1241484

Schoneveld, G. C. 2014. The geographic and sectoral patterns of large-scale farmland investments in sub-Saharan Africa. *Food Policy* **48**:34–50.

Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental Ecological Niches and species' distributional areas. *Biodiversity Informatics* **2**:1–10.

Stein, A. B., V. Athreya, P. Gerngross, G. Balme, P. Henschel, U. Karanth, D. Miquelle, S. Rostro-Garcia, J. F. Kamler, A. Laguardia, I. Khorozyan, and A. Ghoddousi. 2016. *Panthera pardus* (errata version published in 2016). The IUCN Red List of Threatened Species 2016: e.T15954A102421779. IUCN.

Swets, J. 1988. Measuring the accuracy of diagnostic systems. Science **240**:1285–1293.

Trouwborst, A. 2015. Global large carnivore conservation and international law. *Biodiversity and Conservation* **24**:1567–1588.

USGS. 1999. *A global digital elevation model - GTOP030*. Report 123–99.

van der Meer, E., H. Fritz, P. Blinston, and G. S. A. Rasmussen. 2014. Ecological trap in the buffer zone of a protected area: effects of indirect anthropogenic mortality on the African wild dog *Lycaon pictus*. *Oryx* **48**:285–293.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* **94**:2619–2631.

Watson, F. G. R., M. S. Becker, J. Milanzi, and M. Nyirenda. 2015. Human encroachment into protected area networks in Zambia: implications for large carnivore conservation. *Regional Environmental Change* **15**:415–429.

Webster, H., J. W. McNutt, and K. McComb. 2012. African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors. *Ethology* **118**:147–156.

With, K. A. 2002. *Using percolation theory to assess landscape connetivity and effects of habitat fragmentation* Pages 105–130 *in* K. J. Gutzwiller, editor. Applying landsape ecology in biological conservation Springer, New York.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* **3**:165–173.

Woodroffe, R., J. Ginsberg, D. W. Macdonald, and I. S. C. S. Group. 1997. The African wild dog - status survey and conservation action plan. IUCN, Gland, Switzerland.

Woodroffe, R., J. W. McNutt, and M. G. L. Mills. 2004. African wild dog, *Lycaon pictus*. Pages 174–183 *in* C. Sillero-Zubiri and D. W. Macdonald, editors. Canids: foxes, wolves, jackals and dogs: status survey and conservation action plan. IUCN, Gland, Switzerland.

Woodroffe, R., and C. Sillero-Zubiri. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species 2012: e.T12436A16711116.

CHAPTER III

A CULTURE OF TOLERANCE: LARGE CARNIVORE COEXISTANCE IN THE KAFA HIGHLANDS, ETHIOPIA

The following chapter appears as published in *Oryx*:

Gebresenbet F, Baraki B, Yirga G, Sillero-Zubiri C, and Bauer H (2017). A culture of tolerance: Coexisting with large carnivores in the Kafa Highlands, Ethiopia. *Oryx*, 1-10. https://doi.org/10.1017/S0030605316001356

Abstract

We assessed losses of livestock to lions *Panthera leo* and leopards *Panthera pardus* in the Adiyo and Gimbo districts in Kafa Biosphere Reserve, Ethiopia. We quantified the economic impact, conducted household and group interviews, and explored potential solutions with local people. During 2009-2013 there were 350 and 62 attacks by lions and leopards, respectively. Households that suffered attacks on their livestock lost a mean of USD 287 and USD 310 in 2012 and 2013, respectively. Although lion attacks are more frequent than leopard attacks, our qualitative data indicate that tolerance for the former is higher because lions are more respected in the local culture. We describe how depredation is culturally mitigated and how retaliatory killing is avoided. Given people's tolerance towards them, carnivores may persist in their highland refugium, opening an arena for conservation that is not strictly linked to protected areas or to classical economics.

Keywords: Attitude, behaviour, depredation, Ethiopia, interview, leopard, lion, *Panthera leo*

Introduction

Wildlife is in crisis globally, mainly as a result of the increasing human population and consequent consumption (Baillie et al., 2010). Carnivores are particularly affected because of their spatial and dietary requirements, leading to low density and high conflict with human interests (Ripple et al., 2014). Carnivores appear to be recovering in developed countries (Chapron et al., 2014) but in Africa carnivore populations are largely declining (Woodroffe & Sillero-Zubiri, 2012; Bauer et al., 2015). Where carnivores and people coexist, competition for resources is likely to lead to attacks by carnivores on people or livestock, which often motivates retaliatory or indiscriminate killing (Hazzah et al., 2014). Whether that motivation leads to action depends on various factors, tolerance being an important one. Tolerance has been defined by some as an attitude (Manfredo & Dayer, 2004; Treves, 2012) but many scholars define it as a behaviour (Bruskotter & Fulton, 2012, Bruskotter et al., 2015). We adopt the definition of tolerance as behaviour because tolerating carnivore attacks is a behavioural result of an individual's attitude, given that the individual has the opportunity to act in a certain way (Manfredo et al., 2003; Ajzen & Fishbein, 2005).

Literature on this topic often uses the term human–wildlife conflict, even though this term can be misleading; the conflicts are often between people with different views on the impacts of wildlife (Redpath et al., 2015; Fisher, 2016). Conflicts are the result of complex social and ecological interactions that vary in space and over time (Treves et al., 2006; Ale et al., 2007; Dickman et al., 2011; Schuette et al., 2013). The outcome of conflict is determined by perceptions, norms, attitudes and intentions (Marchini & Macdonald, 2012) but most literature focuses on costs and benefits for local people (Dickman et al., 2011).

Literature from southern Africa generally suggests that depredation and retaliation are directly related, by inferring that people kill carnivores to maximize livestock-related profits (Marker et al., 2003; Hemson et al., 2009). In South Africa there is low tolerance for depredation, and reserves with lions are fenced (Packer et al., 2013). Retaliatory killing is explained by rational choice theorists on the basis that humans are self-centred beings focused on maximizing their immediate outcomes (Ostrom, 1998). Literature from East Africa partially follows this paradigm, but other work describes how people and wildlife are integrated in landscapes, and determinants of coexistence are not only economic but also cultural (Romañach et al., 2007; Hazzah et al., 2009, 2014; Goldman et al., 2010a; Blackburn et al., 2016). As a result, retaliatory killing occurs only if depredation exceeds tolerance, whereby tolerance is culturally determined and may vary in space and over time. In this context, carnivore conservation hinges on mitigation to reduce losses or compensation to buy tolerance for losses, or both (Ogada et al., 2003; Kissui, 2008; Dickman et al., 2011; Lichtenfeld et al., 2015; Bauer et al., 2017).

In West, Central and the Horn of Africa the significance of livestock goes beyond its economic productivity and contributes to livelihoods in the broadest sense within their cultural community (Moritz, 2013). Sogbohossou et al. (2011) and Tumenta et al. (2013) give examples of the economic approach to conflict management in Benin and Cameroon, respectively. However, Bauer et al. (2010) noted that the most common mitigation measure practised throughout West and Central Africa is the use of magic, a combination of traditional cultural and religious practices (e.g. incantations by a professional marabout, the use of amulets or the practice of voodoo). In Ethiopia research has shown that spotted hyaenas *Crocuta crocuta* depend on church forests for daytime cover and adapt their diet during Christian fasting periods, adding a religious dimension to the economic and cultural aspects of coexistence (Yirga et al., 2012). Yirga et al. (2013, 2014) also reported high tolerance and close coexistence, and Baynes-Rock (2015) described how spotted hyaenas in the eastern Ethiopian town of Harar have become part of the community. However, little is known about lions in Ethiopia (Gebresenbet et al., 2009).

We investigated conflict with large carnivores, especially lions and leopards, in the moist montane forest ecosystem of Kafa Biosphere Reserve (hereafter the Reserve), in the south-west of Ethiopia. The habitat occupied by lions within the Reserve is unusual; anecdotal information suggests that they were extirpated from the savannahs at lower altitudes, and the montane coffee and bamboo forests at c. 3,000 m in the margins of their former distribution have now become their core refugium (NABU, 2016). Considerable local and international interest in the conservation of this biosphere has led to the creation of a fund that aims to promote coexistence and address depredation.

We studied conflicts with lions and leopards in two districts, using both quantitative (household survey) and qualitative approaches (focus group discussion; Krueger & Casey, 2000; Williams, 2003; Krosnick & Presser, 2010). Incorporating the focus group discussions helped to include the voices of various social groups (mainly adult females and college students), which otherwise might not have been captured. A case study of a particular depredation incident added further insight into local coping mechanisms that would not have been uncovered through quantitative research. Our objective was to assess the economic impact of predation on livestock and to understand local perceptions and attitudes to large carnivores. We analysed the results in the context of local cultural and religious practice and used qualitative information to explain why depredation does not lead to retaliatory killings, and to explore elements of culture and religion that influence the complex relationship between predation on livestock, attitudes and behaviour.

Study area

The Reserve was established in 2010, covering 7,500 km^2, of which 47% is forest (Dresen, 2011), at an altitude of 400–3,100 m (Pratihast et al., 2014). It harbours moist montane forest habitats, with trees of wild coffee *Coffea arabica* that are naturally part of the ecosystem, and wetland and aquatic habitats. The abundance of coffee trees makes the area economically important both locally and nationally. The area is recognized by UNESCO as a Biosphere Reserve and is protected under regional by-laws, but it is not gazetted as a protected area at federal level. Although it hosts c. 21% of the country's rich mammalian diversity and is an important conservation area, it is threatened by habitat destruction (Berhan, 2008; IBC, 2009). The forest cover is high but the density of prey is low. Wildlife includes large carnivores, including leopards and lions, but it is unclear if they are resident throughout the year, or how far eastwards they range. The size of the forest has declined as a result of human encroachment (Berhan, 2008). Lions are now observed regularly in only two of the seven districts in the Reserve (Gimbo and Adiyo), and these were selected as the study area (Fig. 1). Adiyo is a highland district, whereas Gimbo has highland and lowland; the mean altitude is 1,747 m but lions are primarily found at c. 2,700 m.

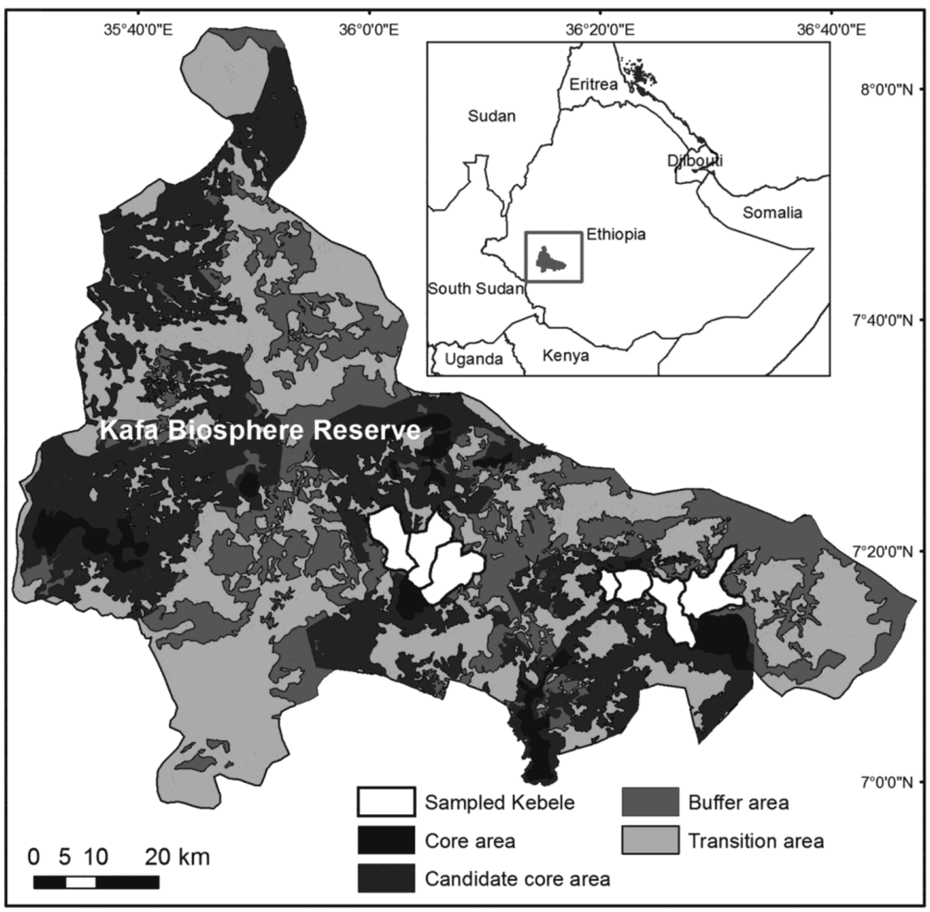

Fig. 1 Locations of subdistricts in Kafa Biosphere Reserve, south-west Ethiopia, in which household surveys and focus group discussions were conducted.

Methods

Ethical clearance was obtained from the Human Subjects Research Institutional Review Board of Oklahoma State University. Local research permits were acquired from the Kafa Zone Regional Administration office and the district and subdistrict level administration offices. The Zone and the two districts provided formal letters of introduction. All participants were given a printed descriptive summary of the research (if participants were illiterate the document was read to them). Prior informed consent was obtained orally from all participants. Data were collected during February–April 2014 using household surveys with semi-structured questionnaires (quantitative) and focus group discussions (qualitative). The quantitative survey data provided an estimate of the economic impacts of depredation, and the qualitative data from the focus group discussions helped in understanding local attitudes towards lions and leopards. In general, data collection focused on attitudes of local people towards lions and leopards, tolerance of livestock losses, retaliatory actions, conflict mitigation techniques, changes in conflict intensity, and the cultural connotation of livestock depredation. Attitude was defined as how a person evaluates a certain object or entity, and behaviour as the action performed by the person on that entity (Ajzen & Fishbein, 1977).

The household survey was conducted in seven subdistricts (or *kebeles*; the lowest administrative level in Ethiopia), where 30 household heads were selected randomly from the list of households provided by each subdistrict administration office. When a household head was not present the household head of the right-side neighbour was surveyed instead. We conducted 210 questionnaires in total, each lasting c. 1 hour. The questionnaire was in two parts. The first comprised 36 open and closed questions, and the second comprised 36 statements, which were scored on a Likert scale (Albaum, 1997) from 1 (strongly agree) to 5 (strongly disagree). The survey assessed five issues: demographics, general knowledge about lions and leopards, conflicts, attitudes, and behaviours. Questions that assessed demographics were used to group respondents based on their social and economic status. Information collected included gender, educational level, occupation and number of livestock owned. The second set of questions assessed the general knowledge of respondents about the carnivores, including their population status in the Reserve, their diet, frequency of sightings, legal protection and hunting in the Reserve. The third set of questions gathered information on human–carnivore conflicts, and included questions about attacks on people and livestock, grazing distance, presumed reason for depredation, and retaliatory killings. Questions to assess attitude asked how the respondents felt about the carnivores, how they felt if they had encountered a lion or a leopard, whether they wanted the carnivores to be extirpated from their communities, how they felt about compensation payments, whether they thought they had a moral obligation to conserve lions and leopards for future generations, and how they perceived cultural practice in the Kafa context to conserve lions and leopards. The fifth set of questions assessed the behaviour of respondents, focusing on their behavioural intentions in the event of livestock depredation, their likely behavioural intentions in the event of future attacks, depredation preventive techniques, and whether respondents respected regulations for conserving carnivores. Before preparing the final version of the questionnaire we conducted test interviews in Bonga, the Zone capital, which is adjacent to the study area, to ensure that all questions were clear.

We calculated the frequencies of response to the 10 statements about attitude scored on the Likert scale. A correlation test showed a high correlation between scores for similar questions for lions and leopards, and therefore we separated the questions pertaining to lions and leopards. We conducted a reliability analysis in *SPSS v. 20.0* (IBM, Armonk, USA) to test the measure of internal consistency, based on Cronbach's α. We also calculated the mean of the responses and presented them as a composite attitude scale, assigning the following values to responses: 5, strongly agree; 4, agree; 3, neutral; 2, disagree; 1, strongly disagree. We multiplied the number of respondents for each response with its assigned value, summed these values, and divided the sum by the total number of respondents (210). Before calculating the weighted mean and running the reliability analysis we reversed the scores of two questions (7 and 8; Table 2) to make them comparable to the other questions.

Three focus group discussions were conducted, with elderly leaders, adult females and college students. There were 10 participants in each group, and the discussions took place during a traditional coffee ceremony, a social setting preferred by the participants. The elderly and female focus groups were selected based on guidance from zonal and subdistrict administration offices, the Reserve's local project coordinator, and Reserve rangers who were trained as interviewers and used as translators. The college students were selected based on communication with the Bonga College of Teacher Education, the only such college in Kafa Zone. Each focus group discussion lasted c. 2 hours. All three discussions focused on the following themes: comparison of past and current human–carnivore conflicts, experiences of livestock loss and culturally acceptable retaliatory actions, conflict prevention techniques, support from the local administration to reduce conflicts, and the distribution of carnivores.

At the outset we asked 30 randomly selected people how they would define rich, moderately well off, and poor households; they agreed that the criteria were ownership of livestock, land and houses. Respondents then indicated thresholds for all three criteria to define categories of wealth, which were subsequently used in the analysis. Numbers of the various types of livestock were converted to Tropical Livestock Units (Njuki et al., 2011). Livestock prices for years prior to 2014 were calculated using mean prices from various markets in Kafa Zone in 2014. We used the consumer price index (Index Mundi, 2014) and the rate of inflation (Trading Economics, 2014) for a specific year to adjust for inflation by taking the ratio of that year's index and the index for 2014. This ratio matches the ratio of livestock prices for the same years, and thus livestock prices for past years could be computed (Appelbaum, 2004).

The quantitative data analysis mainly involved descriptive analysis. We used Spearman's rank correlation to investigate if there was an association between loss of livestock to carnivore attacks and how respondents said they would react to future attacks (a behavioural intention we henceforth refer to as presumed action). We ranked the responses from low (1) to high (3 for leopards, 4 for lions) based on the severity of the respondents' presumed action: 1, doing nothing because it is a course of nature; 2, conducting a traditional begging ritual so lions would stop their attacks on livestock; 3, reporting to local officials; and 4, retaliating by killing the carnivores. The analysis for leopards included only 1, 3 and 4. We also used Spearman's rank correlation to investigate the association between livestock loss and respondents' attitudes towards having a carnivore-free place to live. We asked if respondents would want lions and leopards to be extirpated from their environment, and ranked responses from strong disagreement (5) to strong agreement (1). Livestock losses as a result of attacks by leopards and lions were 0–3.23 and 0–20.05 Tropical Livestock Units per household, respectively.

To analyse the qualitative data from the focus group discussions we used discourse analysis, which is the process of understanding issues by identifying similarities and differences (Jørgensen & Phillips, 2002; Doody et al., 2013). We used participants' language (how they described and framed issues, together with their body language) regarding their knowledge about, attitude and behaviour towards lions and leopards to identify patterns and commonalities within and among the three groups.

Results

We surveyed 210 households, 13 headed by women and 197 headed by men; 67% of respondents were > 35 years old. People who had > 13 cattle, ≥ 4 ha of land and ≥ 3 houses were considered to be rich in the local context. Those who had 8–12 cattle, 2–3.75 ha of land and two houses were of moderate wealth, and those with less were considered to be poor. The mean number of livestock per household was 9 ± SD 14.9. Grazing always occurred during the day and in the presence of a herder, and distance from home was generally low (< 1 km for c. 93% of respondents).

Knowledge about lions and leopards

Although uncommon now, lions used to be present in the highlands and lowlands of the Reserve. However, respondents stressed that lions have become progressively restricted to the higher altitudes. Focus group members from the highlands claimed that lions were unable to withstand the cold weather and the ants that are common in the forest. Leopards, on the other hand, have been known to exist at all elevations in the Reserve. All focus groups reached consensus that the community did not know where the lions were resident, when they came, which route they used, and other related information. The elderly and student focus groups claimed that the number of attacks escalated at the end of the dry season and the beginning of the rainy season.

Overview of attacks and economic losses

Circa 42% (n = 89) of the respondents knew of lion attacks on people during their lifetime. We recorded a total of 17 attacks on people, four of which were fatal (all before 2006); 12 occurred during 2009–2013. Only 1.4% (n = 3) of respondents claimed to know of leopard attacks on people, two of which happened in 1996 and one in 2000. More losses were reported for lions than leopards (Fig. 2). Rich households lost more than moderate and poor ones to both lion (48.3, 29.7 and 22.0%, respectively) and leopard (40.59, 34.7 and 24.5%, respectively) attacks. Livestock depredation claims during 2009–2013 accounted for 80% (n = 350) of reported attacks by lions and 62% (n = 62) of reported attacks by leopards (Table 1), on 73 and 20 households, respectively. Of these households, 14 incurred losses to both carnivores. Lions caused 85% of the total livestock depredation during 2009–2013. In 2012 and 2013, 38 households claimed loss of livestock worth

USD 11,259, with the damage caused by lions amounting to USD 10,841 (96%). Households that suffered livestock loss in 2012 and 2013 had mean losses of USD 287 and 310, respectively, per year. If livestock losses are considered in terms of a direct reduction in household income, these households lost c. 70 and 66% of the mean Ethiopian gross domestic product per capita (which was USD 410 and 470 in 2012 and 2013, respectively; World Bank, 2013).

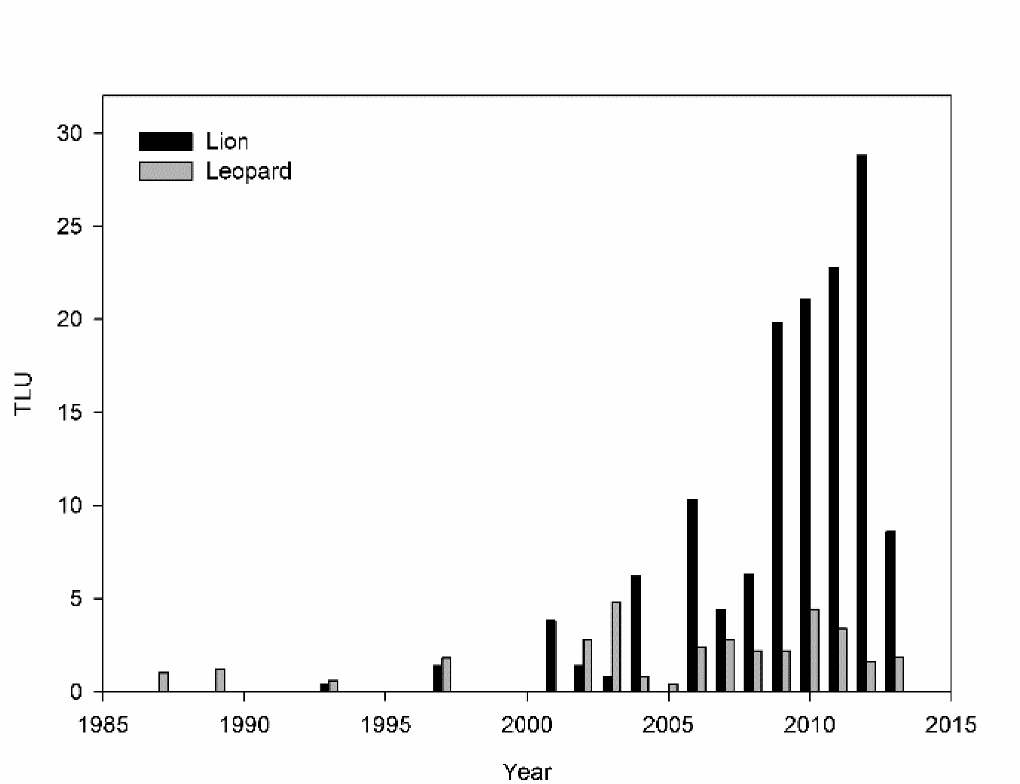

Fig. 2 Recorded Tropical Livestock Units lost as a result of attacks by lions *Panthera leo* and leopards *Panthera pardus* in Kafa Biosphere Reserve (Fig. 1).

Table 1 No. of livestock lost to lions *Panthera leo* and leopards *Panthera pardus* during 2009–2013 by 210 households in the Kafa Highlands, Ethiopia (Fig. 1).

	No. of livestock lost to lions						No. of livestock lost to leopards			
Year	Cattle	Sheep	Goats	Horses	Mules	Donkeys	Cattle	Sheep	Goats	Horses
2009	7	58	12	15	0	1	0	2	5	1
2010	13	17	3	20	0	0	1	11	9	0
2011	13	20	6	19	4	0	0	17	0	0
2012	15	63	4	20	3	1	0	0	8	0
2013	6	16	10	2	1	1	1	5	2	0

Attacks by lions in the Reserve were not restricted to grazing fields. There were reported cases of lions entering peoples' houses at night and attacking them. More than half of the survey respondents, and all focus groups, mentioned an incident that occurred in Adiyo in 2010: a lioness entered a house during the night, ate two goats and attacked the owner, who was sleeping in her bed. The woman survived after medical treatment, with scars on her face and scalp. Two-thirds (63%) of the lion attacks reportedly occurred during 18.00–06.00, and approximately half (55%) of the leopard attacks occurred during 12.00–18.00. Half of the household survey respondents thought that the main reason for these attacks was the lack of wild prey as a result of destruction of the forest. However, 26% thought that attacks happened because lions are violent in nature and habitual raiders.

During focus group discussions, the consensus was that the community tried to share the burden of losing livestock; typically, neighbours contributed money to buy a calf to help victims cope with the loss. In line with this, 76% of respondents who incurred losses informed only their neighbours, with only 26.9% reporting losses to the local administration.

Attitudes towards lions and leopards

Respondents had broadly similar, positive attitudes towards both carnivores (Table 2). Of the 10 statements about attitude, the one that was scored highest was that conserving lions/leopards is a positive cultural practice in Kafa (with a mean weighted score of 4.33 for lions and 4.32 for leopards). Cronbach's α. was 0.64 for lions and 0.63 for leopards, which suggests that 64 and 63% of the variance is reliable for the attitude data collected for lions and leopards, respectively.

Table 2 Percentage of responses to 10 statements relating to attitude towards carnivores, scored on a Likert scale, and mean responses as a composite attitude scale.

No.	Questions	Strongly agree	Agree	Neutral	Disagree	Strongly disagree	Average
1	I like seeing lions in the wild	53.81	22.38	11.9	10.48	1.43	4.17
2	I like to see leopards in the wild	50.95	20.48	14.29	13.81	0.48	4.08
3	Conserving lions is culturally a positive practice in Kafa	51.9	34.76	8.57	4.29	0.48	4.33
4	Conserving leopards is culturally a positive practice in Kafa	50.48	36.67	8.57	3.33	0.95	4.32
5	People should relocate from areas of lions' habitat	30.95	24.76	4.76	29.05	10.48	3.37
6	People should relocate from areas of leopards' habitat	31.43	22.38	6.67	29.05	10.48	3.35
7	I would like lions to disappear from my community	6.19	6.67	10	70	7.14	3.65
8	I would like leopards to disappear from my community	6.19	5.71	10	70.95	7.14	3.67
9	The presence of a lion is a sign of a healthy environment	48.1	30	8.1	9.52	4.29	4.08
10	The presence of a leopard is a sign of a healthy environment	47.62	29.05	8.57	10	4.76	4.05

A majority of respondents and the student focus group, and all participants of the female and elderly focus groups, did not refer to lions as *Dahero* (lion); they used the name *Donno*, which is a respectful way of addressing elderly and other socially respected people. When they hear others referring to lions simply as lions, they cover their ears as a way of saying ‘I cannot hear this’. This deep-rooted respect and honour for lions is maintained even at the time of attacks. During the focus group discussions with the elderly, one of the participants explained:

We do not think lions take our livestock to hurt us. As a result, we do not refer to it as an attack or killing but taking what they needed.

Leopards are not afforded the same honour and respect, although they do not face retaliatory or preventive killings. Most (91.4%) respondents claimed that fear of legal action is an additional reason for the absence of lion and leopard killings in the Reserve (86% were aware that killing lions is prohibited by law in Ethiopia).

All focus groups explained that losing livestock to lions is considered to be a sign of good luck, and of upcoming wealth, throughout the Reserve. Three of the participants in the female discussion group and four in the elderly group explained that the number of their livestock had increased significantly after losing some to lions. One of the women explained:

Before 7 years, two of our cattle were taken in one night. In the morning, my husband and I were very happy to see lion footprints because we believed our livestock were going to be fertile and we were going to be wealthy. And indeed we have been blessed since.

In the Kafa culture lions are considered to be kinder than leopards. One participant in the elderly focus group expressed:

If we encounter a lion while on the road, all we have to do is cut some leaves and put them on our head and beg the lion and bow down. It is guaranteed that it will walk away. Male lions even convince or drag lionesses with them, who otherwise might block the path and lay around for a long time. But a leopard never shows such mercy; it always attacks if confrontation happens accidentally.

The focus groups also revealed that community elders hold a ritual ceremony when lion attacks become frequent, in which they beat drums and pray that the lions will leave them and their livestock alone. Participants in the elderly focus group explained that a few years ago there had been an incident in which a lion became a problem, taking livestock every night but not eating them, just killing them and walking away. They claim that a local spiritual leader prayed and the lion died. An informant told us confidentially that people killed the lion but maintained the narrative, which illustrates the respect for the lion and the spiritual leader but also the resentment that led to retaliatory killing. The lion carcass was given a ceremonial burial; it was covered in hand-made traditional cloth before being buried in a meadow that remains fenced to this date.

Our findings indicate that although most of our respondents are afraid to go to the field or into the forest where lions and leopards are believed to live, they also like seeing these carnivores in the wild and do not want them to disappear from the Reserve (Table 2).

Behaviours and actions

There are few retaliatory killings of lions and leopards in the Reserve. Only 2.9% (n = 6) and 1.9% (n = 4) of respondents had witnessed killings of lions and leopards, respectively. Three lion killings and one leopard killing occurred during 2009–2013. Of the 93 households that suffered livestock losses during this time, only 2.1% (n = 2) responded that they wanted to kill the carnivores in retaliation (and may do so if it happens in the future). However, the majority (71%; n = 66) did not want to retaliate and replied that they would not retaliate in the future.

Correlation of economic losses with attitude and behaviour

Spearman's correlation showed a significant association between livestock loss and presumed reaction to leopard attacks ($\rho_s = 0.181$, $P < 0.01$), but that association was not significant for lion attacks ($\rho_s = -0.132$, $P = 0.056$). Spearman's correlation between wanting to see carnivores extirpated in their community and livestock loss showed a non-significant association for both leopards ($\rho_s = 0.015$, $P = 0.83$) and lions ($\rho_s = -0.108$, $P = 0.118$).

Compensation vs prevention

A minority of livestock owners who experienced carnivore attacks (17%, n = 60, for lions and 24%, n = 15, for leopards) said they would like to be compensated. The rest of the victims believed depredation was a course of nature and no one was responsible for compensating their loss. All respondents and focus groups highlighted the importance of preventive techniques. The two most preferred remedies (79% of respondents) were (1) introducing better protection schemes for livestock and (2) fencing the Reserve to keep the carnivores away from people. Better protection techniques include keeping cattle in houses or in fenced fields at night and not grazing livestock in forests. The majority of respondents and all focus groups suggested that the carnivores' habitat, particularly that of lions, should be fenced, at least during the rainy season. The focus groups explained that fire and watch dogs were commonly used for night guarding but their efficiency as a preventive technique had diminished, as the carnivores, particularly lions, attacked livestock even in the presence of fire and dogs. The elderly and student focus groups reported five incidents in which dogs were killed by lions during attacks.

Discussion

Depredation had an economic impact on the households studied, but in general the damage was not high compared to other landscapes with lions (Gifford-Gonzalez, 2000; Frank et al., 2005). The tolerance expressed by the participants is striking; tolerance for carnivore attacks varies across Africa but is relatively common in India (Karanth et al., 2013; Meena et al., 2014). Effective conservation of carnivores is difficult where tolerance is low (Sillero-Zubiri & Laurenson, 2001; Bruskotter & Wilson, 2014); in the Reserve the habitat and prey availability are suboptimal (deforestation, low prey density; Berhan, 2008) and it is probably because of the prevailing culture of tolerance that lions and leopards have survived.

By combining the overview provided by quantitative data with insights and details provided by qualitative data we were able to make a more complete analysis. We found that rational choice theory poorly explains human–lion interaction; social, political and cultural factors are at least as important as economic rationale (Inskip & Zimmermann, 2009; Bruskotter & Shelby, 2010).

Traditionally in Kafa if individuals lose livestock to lions they are happy because they believe it to be a sign that their livestock number is to increase. People's response to conflict with carnivores is culturally contextualized and complex; rational choice theory would predict retaliation but culture can be a stronger incentive and encourage the conservation of carnivores (Karanth & Chellam, 2009; Kopnina, 2015; Thomas et al., 2015). Increasing levels of depredation and external influences may erode tolerance and lead to different narratives (Ikanda & Packer, 2008; Maclennan et al., 2009) but thus far people in Kafa have proved to be tolerant, with few retaliatory killings. Attitude, whether positive or negative, to carnivores will influence behaviour towards them (Thorn et al., 2015).

Human–carnivore conflicts are increasing in many areas (Treves & Karanth, 2003). Attacks on people have been reported in Ethiopia (Gebresenbet et al., 2009) but are not a major problem in the Reserve at present. The suspected increase in human–lion interactions in the wet season could be a result of seasonal variation in prey availability (Patterson et al., 2004; Woodroffe & Frank, 2005). Although our reliability analysis suggests a less than ideal (70%) variance reliability, the qualitative responses and the frequency of responses suggest there is a positive attitude in Kafa towards lions and leopards. The highest mean ratings (Table 2) for the statement that conserving lions and leopards is a positive cultural practice in Kafa (with a mean weighted score of 4.33 for lions, and 4.32 for leopards) also support this claim. Additionally, there was a non-significant correlation between livestock loss and wanting to see carnivores extirpated in the community for both lions and leopards, supporting the claim that there is a positive attitude towards both carnivores.

Lions are more problematic than leopards in the Reserve, yet there is more tolerance towards lions than leopards. The correlation between livestock loss and respondents' presumed actions following lion attacks was not significant, supporting the claim that there is a culture of tolerance towards lions. However, attitudes to leopards were less positive, and the significant correlation between livestock loss and respondents' presumed actions following leopard attacks reveals that as households lose more livestock to leopards their behavioural intention to retaliate becomes stronger. The Reserve appears to be exceptional in this regard, as leopards generally coexist more easily with people; with their diet adaptability and secretive behaviour, leopards can often persist close to people without significantly affecting them (Hayward et al., 2006; Odden et al., 2014; Athreya et al., 2016).

Wildlife and people coexist across Ethiopia, where the biosphere reserve model fits the de facto management of protected areas that are almost all open access systems (Gebresenbet et al., 2013). In the context of widespread extreme poverty, depredation must therefore be addressed. Our results show that policy will be more effective and efficient if it looks beyond economic impacts and considers the depth and complexity of communities' relationships with large carnivores. Integrated damage mitigation (Bauer et al., 2010) may be more appropriate than segregation (e.g. fences; Packer et al., 2013) or compensation (Naughton-Treves et al., 2003; Dickman et al., 2011; Bauer et al., 2017). There are plans for a pilot consolation scheme in the Reserve (Schütze, 2014); it will not compensate directly for losses but will provide a more general subsidy for coexistence. This fits with global trends in conservation that focus on ecosystem services, monetary values and trade-offs (Goldman et al., 2010b; Anyango-Van Zwieten et al., 2015). This may improve attitudes and lead to better conservation outcomes; however, other factors are equally important (Heberlein, 2012). For example, fear, personal and social motivations and internal and external barriers to retaliatory killing (e.g. lack of skills and force of law, respectively) have been found to influence jaguar killing (Marchini & Macdonald, 2012). We add that communal coping mechanisms, beliefs in long-term positive wealth impacts and a culture of tolerance are important. The relative importance of these factors varies in space and time, adding to the complexity of conservation.

Acknowledgements

Fieldwork was supported financially by the German Nature and Biodiversity Conservation Union (NABU) and by the Wildlife Conservation Research Unit at the University of Oxford, UK. We thank all NABU staff based in Bonga, Kafa, for greatly assisting the research, Mesfin Tekle and Tilahun Teshome for sharing their ideas during the planning and implementation stages of the data collection, Kafa Biosphere Reserve rangers Siraj Hussien and Mamo Gebremedhin for assistance in collecting data and in translation whenever the Kafa language was used, Mulubrhan Hagos for facilitating communications with students from the Bonga College of Teacher Education, and all participants of the survey and focus group discussions for taking the time to answer our questions.

References

Ajzen, I. & Fishbein, M. (1977). Attitude-behaviour relations: A theoretical analysis and review of empirical research. *Psychological Bulletin*, **84(5)**, 888–918.

Ajzen, I. & Fishbein, M. (2005) The influence of attitudes on behaviour. In: *The handbook of attitudes* (Eds. D. Albarracín, B. T. Johnson & M. P. Zanna) Lawrence Erlbaum Associates, Mahwah, NJ.

Albaum, G. (1997) The Likert scale revisited: an alternate version. *Journal of the Market Research* Society, **39(2)**, 331–349.

Ale, S.B., Yonzon, P. & Thapa, K. (2007) Recovery of snow leopard *Uncia uncia* in Sagarmatha (Mount Everest) National Park, Nepal. *Oryx*, **41,** 89–92.

Anyango-Van Zwieten, N., Van Der Duim, R. & Visseren-Hamakers, I.J. (2015) Compensating for livestock killed by lions: payment for environmental services as a policy arrangement. *Environmental Conservation*, **42**, 363–372.

Appelbaum, E. B. (2004) The Consumer Price Index and inflation - Adjust numbers for inflation. *Journal of Online Mathematics and its Applications. http://www.maa.org/press/periodicals/loci/joma/ the-consumer-price-index-and-inflation-adjust-numbers-for-inflation [accessed 25 June 2014].*

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J. & Karanth, K.U. (2016) A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx*, **50**, 156–162.

Baillie, J. E. M., Griffiths, J., Turvey, S.T., Loh, J. & Collen, B. (2010) *Evolution lost: Status and trends of the world's vertebrates*. Zoological Society of London, UK.

Bauer, H., de Iongh, H. & Sogbohossou, E. (2010) Assessment and mitigation of human-lion conflict in West and Central Africa. *Mammalia*, **74**, 363–367.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W. & Packer, C. (2015a) Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, **112**, 14894–14899.

Bauer, H., Müller, L., Van Der Goes, D. & Sillero-Zubiri, C. (2015b) Financial compensation for damage to livestock by lions *Panthera leo* on community rangelands in Kenya. *Oryx*, 1-9.

Baynes-Rock, M. (2015) Ethiopian buda as hyenas: Where the social is more than human. *Folklore*, **126**, 266–282.

Berhan, L.A. (2008) Status and distribution of faunal diversity in Kafa Afromontane coffee forest. A report submitted to PPP project; Nature and Biodiversity Conservation Union (NABU), Ethiopia.

Blackburn, S., Hopcraft, J.G.C., Ogutu, J.O., Matthiopoulos, J. & Frank, L. (2016) Human–wildlife conflict, benefit sharing and the survival of lions in pastoralist community-based conservancies. *Journal of Applied Ecology*, **53**, 1195–1205.

Bruskotter, J.T. & Fulton, D.C. (2012) Will hunters steward wolves? A comment on Treves and Martin. *Society & Natural Resources*, **25**, 97–102.

Bruskotter, J.T. & Shelby, L.B. (2010) Human dimensions of large carnivore conservation and management: Introduction to the special issue. *Human Dimensions of Wildlife*, **15**, 311–314.

Bruskotter, J.T., Singh, A., Fulton, D.C. & Slagle, K. (2015) Assessing tolerance for wildlife: Clarifying relations between concepts and measures. *Human Dimensions of Wildlife*, **20**, 255–270.

Bruskotter, J.T. & Wilson, R.S. (2014) Determining where the wild things will be: Using psychological theory to find tolerance for large carnivores. *Conservation Letters*, **7**, 158–165.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D. & Boitani, L. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**, 1517–1519.

Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. (2011) A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, **108**, 13937–13944.

Doody, O., Slevin, E. & Taggart, L. (2013) Focus group interviews. Part 3: Analysis. *British Journal of Nursing*, **22**, 266–269.

Dresen, E. (2011) Forest and community analysis—Final report for the project "Climate protection and preservation of primary forests—A management model using the wild coffee forests in Ethiopia as an Example". Nature and Biodiversity Conservation Union (NABU), Berlin, Germany.

Fisher, M. (2016) Whose conflict is it anyway? Mobilizing research to save lives. *Oryx*, **50**, 377–378.

Frank, L.G., Rosie, W. & Mordecai, O.O. (2005) People and predators in Laikipia District, Kenya. In: *People and wildlife: Conflict or coexistence?* (Eds. R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 286–304. Cambridge University Press, Cambridge.

Gebresenbet, F., Bauer, H., Hunter, L. & Gebretensae, K. (2009) Proceedings of the national lion conservation workshop. Ethiopian Wildlife Conservation Authority, Addis Ababa, Ethiopia

Gebresenbet, F., Daniel, W., Bauer, H. & Haile, A. (2013) Governance: for effective and efficient conservation in Ethiopia. In*: Conservation Biology: Lessons from the Tropics*. (Eds. Navjot, S.S & Raven, P.H) Wiley-Blackwell, Oxford, UK.

Gifford-Gonzalez, D. (2000) Animal disease challenges to the emergence of pastoralism in Sub-Saharan Africa. *The African Archaeological Review*, **17**, 95–139.

Goldman, M.J., Roque De Pinho, J. & Perry, J. (2010a) Maintaining complex relations with large cats: Maasai and lions in Kenya and Tanzania. *Human Dimensions of Wildlife*, **15**, 332–346.

Goldman, R.L., Daily, G.C. & Kareiva, P. (2010b) Trade-offs in making ecosystem services and human well-being conservation priorities. In: *Trade-offs in conservation: Deciding what to save* (eds N. Leader-Williams, W. M. Adams & R.J. Smith), Wiley-Blackwell Publishing Ltd, UK.

Heberlein, T.A. (2012) Navigating environmental attitudes. *Conservation Biology*, **26**, 583–585.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. (2006) Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, **270**, 298–313.

Hazzah, L., Mulder, M.B. & Frank, L. (2009) Lions and warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biological Conservation*, **142**, 2428–2437.

Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C.T.T., Mwebi, O., Kearney, F. & Frank, L. (2014) Efficacy of Two Lion Conservation Programs in Maasailand, Kenya. *Conservation Biology*, **28**, 851–860.

Hemson, G., Maclennan, S., Mills, G., Johnson, P. & Macdonald, D. (2009) Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. *Biological Conservation*, **142**, 2718–2725.

IBC; Institute of Biodiversity Conservation (2009) Convention on Biological Diversity (CBD) – Ethiopia´s 4th Country Report. Addis Ababa, Ethiopia.

Ikanda, D. & Packer, C. (2008) Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania. *Endangered Species Research*, **9**, 67–74.

Index Mundi (2014) Ethiopia - Consumer price index. http://www.indexmundi.com/facts/ethiopia/consumer-price-index [accessed 14 Jan 2014].

Inskip, C. & Zimmermann, A. (2009) Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, **43**, 18–34.

Jørgensen, M. & Phillips, L. (2002) *Discourse analysis: as theory and method*, SAGE Publications, London.

Karanth, K.K., Naughton-Treves, L., DeFries, R. & Gopalaswamy, A.M. (2013) Living with wildlife and mitigating conflicts around three Indian Protected Areas. *Environmental Management*, **52**, 1320–1332.

Karanth, K.U. & Chellam, R. (2009) Carnivore conservation at the crossroads. *Oryx*, **43**, 1–2.

Kissui, B.M. (2008) Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation*, **11**, 422–432.

Kopnina, H. (2015) Revisiting the Lorax complex: deep ecology and biophilia in cross-cultural perspective. *Environmental Sociology*, **1**, 315–324.

Krosnick, J. A. & Presser, S. (2010) Question and questionnaire design. In: *Handbook of survey research* (eds. P. V. Marsden & J. D. Wright), pp. 263–313. Emerald Group Publishing Limited, UK.

Krueger, R.A. & Casey, M.A. (2000) *Focus Groups: A practical guide for applied research*. Sage Publications, New Delhi, India.

Lichtenfeld, L.L., Trout, C. & Kisimir, E.L. (2014) Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodiversity and Conservation*, **24**, 483–491.

Maclennan, S.D., Groom, R.J., Macdonald, D.W. & Frank, L.G. (2009) Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. *Biological Conservation*, **142**, 2419–2427.

Manfredo, M.J. & Dayer, A.A. (2004) Concepts for exploring the social aspects of human–wildlife conflict in a global context. *Human Dimensions of Wildlife*, **9**, 1–20.

Manfredo, M., Teel, T. & Bright, A. (2003) Why are public values toward wildlife changing? Human Dimensions of Wildlife, 8, 287–306.

Marchini, S. & Macdonald, D.W. (2012) Predicting ranchers' intention to kill jaguars: Case studies in Amazonia and Pantanal. *Biological Conservation*, **147**, 213–221.

Marker, L.L., Mills, M.G.L. & Macdonald, D.W. (2003) Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology*, **17**, 1290–1298.

Meena, V., Macdonald, D.W. & Montgomery, R.A. (2014) Managing success: Asiatic lion conservation, interface problems and peoples' perceptions in the Gir Protected Area. *Biological Conservation*, **174**, 120–126.

Moritz, M. (2013) Livestock transfers, risk management, and human careers in a West African pastoral system. *Human Ecology*, **41**, 205–219.

NABU (2016) Kafa Biosphere Reserve Biodiversity assessment report, (in press)

Naughton-Treves, L., Grossberg, R. & Treves, A. (2003) Paying for Tolerance: Rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, **17**, 1500–1511.

Njuki, J., Poole, J., Johnson, N., Baltenweck, I., Pali, P., Lokman, Z. & Mburu, S. (2011) *Gender, livestock and livelihood indicators*. International Livestock Research Institute (ILRI).

Odden, M., Athreya, V., Rattan, S. & Linnell, J.D.C. (2014) Adaptable neighbours: Movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS ONE*, **9**, e112044.

Ogada, M.O., Woodroffe, R., Oguge, N.O. & Frank, L.G. (2003) Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology*, **17**, 1521–1530.

Ostrom, E. (1998) A behavioural approach to the rational choice theory of collective action: Presidential Address, American Political Science Association, 1997. *American Political Science Review*, **92**, 1–22.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., DeIongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., Maclennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J.O., Okot-Omoya, E., Patterson, B.D., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H. & Polasky, S. (2013) Conserving large carnivores: dollars and fence. *Ecology Letters*, **16**, 635–641.

Patterson, B.D., Kasiki, S.M., Selempo, E. & Kays, R.W. (2004) Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighbouring Tsavo National Park, Kenya. *Biological Conservation*, **119**, 507–516.

Pratihast, A.K., DeVries, B., Avitabile, V., de Bruin, S., Kooistra, L., Tekle, M. & Herold, M. (2014) Combining satellite data and community-based observations for forest monitoring. *Forests*, **5**, 2464–2489.

Redpath, S.M., Bhatia, S. & Young, J. (2015) Tilting at wildlife: reconsidering human–wildlife conflict. *Oryx*, **49**, 222–225.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484-1 – 1241484-11.

Romañach, S.S., Lindsey, P.A. & Woodroffe, R. (2007) Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. *Oryx*, **41**, 185–195.

Schuette, P., Creel, S. & Christianson, D. (2013) Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. *Biological Conservation*, **157**, 148–154.

Schütze, K. (2014) Ethiopia's rare mountain lions. http://www.dw.de/ethiopias-rare-mountain-lions/a-17632135 [accessed 9 July 2014].

Sillero-Zubiri, C. & Laurenson, K. (2001) Interactions between carnivores and local communities: Conflict or co-existence? In: *Proceedings of a carnivore conservation symposia* (eds J. Gittleman, S. Funk, D.W. Macdonald & R.K. Wayne), pp. 282–312. Zoological Society of London, UK.

Sogbohossou, E.A., de Iongh, H.H., Sinsin, B., de Snoo, G.R. & Funston, P.J. (2011) Human–carnivore conflict around Pendjari Biosphere Reserve, northern Benin. *Oryx*, **45**, 569–578.

Thomas, R.E.W., Bruyere, B., Sundaresan, S., Bouzo, S., Welden, R. & Trimarco, J. (2015) Youth experiences with wildlife during a period of significant cultural change in Laikipia, Kenya. *Human Dimensions of Wildlife*, **20**, 133–146.

Thorn, M., Green, M., Marnewick, K. & Scott, D.M. (2015) Determinants of attitudes to carnivores: implications for mitigating human–carnivore conflict on South African farmland. *Oryx*, **49**, 270–277.

Trading Economics (2014) Ethiopia inflation rate. http://www.tradingeconomics.com/ethiopia/-inflation-cpi [accessed 25 June 2014].

Treves, A. (2012) Tolerant attitudes reflect an intent to steward: A reply to Bruskotter and Fulton. *Society & Natural Resources*, **25**, 103–104.

Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, **17**, 1491–1499.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. (2006) Co-Managing Human–Wildlife Conflicts: A Review. *Human Dimensions of Wildlife*, **11**, 383–396.

Tumenta, P.N., de Iongh, H.H., Funston, P.J. & Udo de Haes, H.A. (2013) Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx*, **47**, 237–242.

Williams, A. (2003) How to … Write and analyse a questionnaire. *Journal of Orthodontics*, **30**, 245–252.

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

Woodroffe, R. & Sillero-Zubiri, C. (2012) *Lycaon pictus*. The IUCN Red List of Threatened Species. Version 2015.2. http://www.iucnredlist.org [accessed 16 August 2015].

World Bank (2013) Country at a glance, Ethiopia. http://www.worldbank.org/en/country/ethiopia [accessed 12 June 2014].

Yirga, G., De Longh, H. H., Leirs, H., Gebrihiwot, K., Deckers, J., & Bauer, H. (2012) Adaptability of large carnivores to changing anthropogenic food sources: Diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. *Journal of Animal Ecology*, **81**, 1052–1055.

Yirga, G., Ersino, W., De Iongh, H.H., Leirs, H., Gebrehiwot, K., Deckers, J. & Bauer, H. (2013) Spotted hyena (*Crocuta crocuta*) coexisting at high density with people in Wukro district, northern Ethiopia. *Mammalian Biology*, **78**, 193–197.

Yirga, G., Imam, E., De Iongh, H.H., Leirs, H., Kiros, S., Yohannes, T.G., Teferi, M. & Bauer, H. (2014) Local spotted hyena abundance and community tolerance of depredation in human-dominated landscapes in Northern Ethiopia. *Mammalian Biology*, **79**, 325–330.

CHAPTER IV

BEYOND THE NUMBERS: HUMAN ATTITUDES AND CONFLICT WITH LIONS (*PANTHERA LEO)* IN GAMBELLA NATIONAL PARK, ETHIOPIA

The following chapter is under review process in PLOS ONE

Gebresenbet F, Bauer H, Vadjunec JM, and Papeş M (201x) Beyond the numbers, human attitudes and conflict with lions (*Panthera leo)* in Gambella National Park, Ethiopia. PLOS One

Abstract

Human-lion conflict is a threat to lions. Knowing the local attitude toward lions and the drivers of human-lion conflict is important for conflict mitigation. We assessed the attitude toward lions in and around Gambella National Park, and compared the findings with published data from Kafa Biosphere Reserve, both in western Ethiopia. We quantified via household interviews the amount of livestock loss due to depredation by lions. This study demonstrates that the amount of depredation alone is not sufficient to understand human-lion conflicts and highlights the importance of cultural differences in lion conservation. Respondents focused on lion attacks, whereas objectively disease and theft were the top factors of livestock loss. We emphasize the low cultural value of lions in the region, the growing human population, and the land-grabbing pressures as main impediments to conserving lions in Gambella region. Our recommendation is to use Arnstein's ladder of participation for conservation education to ensure a proactive involvement of locals in conservation.

Keywords: lion, depredation, conflict, conservation education, Gambella

Introduction

Conserving large carnivores is a global challenge in the face of increasing human population and associated land-use and land-cover change. Human-lion conflict, a situation in which people retaliate against lions that actually or presumably negatively affect people's livelihood or well-being, is a major cause for the reduction of lion populations throughout Africa [1-3]. Conflicts escalate as frequency of human-lion interactions increases with human population growth and encroachment into lion habitats, ultimately resulting in declines of lion populations [4]. Pastoralism and poor animal husbandry practices create further opportunities for livestock depredation by lions as humans move into or close to protected areas in search of resources [2] and lions disperse to adjacent areas in search of prey [5].

Predators, such as lions, may represent actual or perceived threats to humans or livestock [6], leading to indiscriminate retaliatory or preemptive killings of predators [7]. Human attitudes, behaviors, and perceptions towards carnivores, resulting from complex social and cultural settings, are key factors in understanding human-carnivore conflicts [8]. Local perceptions towards carnivores can be shaped by various factors, including the amount of livestock loss due to depredation, level of wealth [8] and education [9], but certainly also culture [10]. The personal experience of livestock depredation has been linked to negative attitudes toward carnivores, resulting in intentional killings to reduce their numbers [3, 11]. Not sharing conservation benefits with local people will also perpetuate the notion that lions are conserved at the cost of locals' safety and economic survival.

Management of human-lion conflicts depends on human tolerance for livestock depredation. Tolerance towards carnivores is influenced by attitudes and perceptions that are deeply rooted within cultures [12]. Positive engagement with local cultural contexts facilitates wildlife conservation [13]. Participatory approaches that include locals from planning to implementation stages ensure legitimacy of proposed solutions. However, if locals are passive participants, the participatory approach remains nominal and lacks power-sharing and partnership [14]. The classic carrot-and-stick approach, rewarding desired human behaviors and disciplining undesired ones, can be used to improve public cooperation, including managing human-wildlife conflicts [15]. Community participation and collaboration can become effective if guided through the levels of participation proposed by Arnstein [16]. These levels range from a non-participation stage (in which local populations will be educated on the importance of carnivores) to citizen power and empowerment (where locals actively participate in the conservaion process and hold the managerial decision-making capabilities) [16].

The African lion (*Panthera leo*) is listed as “Vulnerable” by the International Union for Conservation of Nature (IUCN), with about 43% range decline between 1993 and 2014 [1, 17]. Most lions today are found in protected areas [18], although this is not evident for the Ethiopian population, as data are lacking. Several studies exist on various aspects of lion conservation from different African countries [19-23]. In Ethiopia, lions are, in general, considered important socially and culturally [24], however a substantial gap remains in our knowledge of Ethiopian lions. The need to fill this gap is critical because the recorded decline in Ethiopian lion population [24] could have crucial effects on the whole African population, as southern Ethiopia is the only bridge connecting East and Central African lion populations [25].

In this study, we surveyed the attitude of people towards lions in and around Gambella National Park (GNP), in Gambella Regional State, western Ethiopia. We compared our findings from Gambella with already published data from Kafa Biosphere Reserve [10]. We followed the definitions of Ajzen and Fishbein [26] for *attitude*, an evaluation of an object by an individual, and *behavior*, an action performed by the individual; behavior is strongly influenced by attitude. Two main ethnic groups inhabit Gambella region: the Anuak (21% of total population) and the Nuer (46% of total population) [27]. Following the South Sudanese civil war in late 2013, Gambella region became home for more than 399,000 refugees and asylum seekers, as of date, from neighboring South Sudan [28]. Gambella is also one of the regions considered to have a viable lion population in Ethiopia [24], but the level of human-lion conflict and its cultural and economic dimensions have not been studied. Understanding region- and time-specific attitudes and behaviors towards carnivores is important for developing effective conservation measures [29]. To this effect, we surveyed the attitudes of people in Gambella towards lions and compared our findings with those of a published study from Kafa region, southwestern Ethiopia [10].

Methods

Study area

Gambella National Park (GNP) is located in Gambella Regional State, 850 km west of Ethiopia's capital Addis Ababa. The region has a population of 364,891 and two main ethnic groups, Anuak and Nuer. The Anuak are resident agriculturalists, fisherfolk, and hunters, and the Nuer are pastoralists and agro-pastoralists [30, 31]. The Anuak villages are located along river banks, encompassing most of the 0.5% fertile alluvial riverine land in the region [32]. Hunting is also common in Gambella region [33, 34], indicating that bushmeat is a major source of protein for locals. Resource-based conflicts are common between the Anuak and Nuer [30-32] and GNP can be perceived as a third party in the competition for resources.

GNP was established upon the recommendation by Fred Duckworth, a British hunter and game warden who was contracted by the central/imperial government to assess the situation of animal killings in the region in the 1970s [35]. Duckworth [35] suggested immediate action to protect the wildlife in the form of establishing a national park and banning hunting for a minimum of five years. Based on Duckworth's report, an internal committee from the Ethiopian Wildlife Conservation Organization (EWCO) decided to establish a reserve flanked by two hunting areas. The decision was based on the assumption that it would be difficult to institute strict conservation reserves in an area without control and with little reach of the state [35]. However, a year later, in 1974, EWCO revised its stand and established GNP. At the time of its establishment, GNP was the largest national park in Ethiopia, with an area of 5061 km^2 [35], but its size and borders were modified in 2011 following land transfers to investors for large scale mechanized commercial agriculture ('land grabs') [36]. Currently, the total area of GNP is 4575 km^2 and it borders South Sudan.

The park is generally dominated by a flat topography with elevation ranging from 400 to 768 m above sea level [37]. Although GNP has areas of higher elevation where deciduous woodland and savanna occur, its most distinct feature is the floodplain located between Baro and Gilo rivers [33]. Due to its transboundary migratory ecosystem [33, 38], there is an initiative to transform GNP into a transboundary protected area system with Boma National Park in South Sudan [39]. During the time of our data collection, the Ethiopian Wildlife and Conservation Authority (EWCA) was co-managing GNP with African Parks Network (APN), a non-profit conservation organization specializing in long-term management of protected areas in partnership with the country's government. However, APN terminated their contract with the Ethiopian government and left the country in 2016.

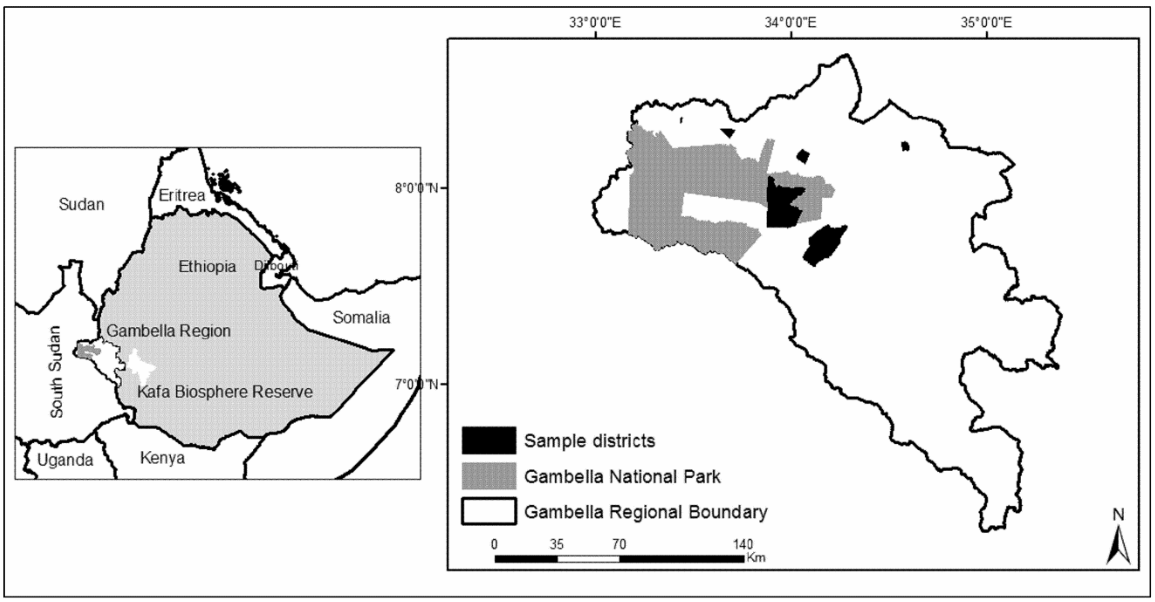

Fig. 1. Map of study area

Data collection and analysis

We conducted interviews with key-informants (i.e., government and NGO officials, experts), household surveys, and informal discussions with local people in and around GNP to assess their attitudes toward lions. Ethical clearance was obtained from the Human Subjects Research Institutional Review Board of Oklahoma State University after appropriate training. Local research permits were acquired from Gambella regional and district level administration offices. A printed descriptive summary of the research was given (or read aloud) to all participants, and informed consent was obtained orally from all participants. We trained three park scouts from GNP as data collectors, and trial interviews were conducted in Gambella town to test the data collectors and to ensure that all questions were clear. Participation to our study was voluntary (none of the participants were given money).

Our data collection focused on: estimating the level of livestock depredation attributed to lions in GNP, general knowledge of locals about carnivores, evaluating tolerance and retaliatory actions towards lions, and the general attitude and cultural value of lions in GNP. Data were collected using two techniques: key-informant interviews and household survey using questionnaires (S1 Questionnaire). The household survey data were collected from May 2015 to December 2015 while key-informant interviews were conducted April 2015 to December 2016.

Six key-informants were identified based on their work experience in and around GNP, and key-informant interviews were conducted after getting individual verbal consent. The interviews were semi-structured and were conducted in informal settings. Questions focused on the status of lions, livestock depredation by lions, retaliatory killings, and problems for conserving lions in GNP. We also obtained reports of lion attacks and lion killings in GNP.

The household surveys were conducted in five different districts within Gambella region, namely Wentwa, Puldiang, Ngenngang, Ulaw, and Puchala, and Gambella town. The first three districts were from Nuer zone, the part of Gambella region where peoples' livelihood is based on pastoralism, more so than in Ulaw and Puchala districts from Anuak zone, and the last one was the capital of the regional state. For the survey, we randomly selected 35 household heads (respondents hereafter) in each district from the list of household head names provided by each district office. If a household head was not present at the time of interview, household heads one door to the right of the selected one were interviewed. The questionnaire required about one hour to complete.

The questionnaire had four sections. The first section assessed the demographic and economic status of respondents. The second section assessed respondents' management, perception, attitude, and knowledge of lion populations in Gambella and was comprised of 15 questions using a Likert scale from 1 (strongly agree) to 5 (strongly disagree). The third section gathered information about respondents' broad knowledge about carnivores in general. In this section respondents were asked to identify carnivores and their tracks by looking at photos of six carnivores (African wild dogs, hyena, jackal, leopard, lion and serval) and four carnivore tracks (African wild dogs, hyena, leopard, and lion). The last section of the questionnaire assessed the problem of lion attacks on humans and livestock, the preventive actions that people take, reasons for lion attacks, the trend of these attacks in the past five years, and it also asked how much livestock loss is associated with disease and theft.

Additionally, we held opportunistic informal discussions with individuals or groups of people. There was no overlap between participants to the informal discussions and key-informants or household survey subjects. These discussions occurred based on self-initiated conversations from participants' side about what we were doing or by individuals approaching us with information that they thought might be of interest to us. During all informal discussions, we communicated to the participants that their responses might be reported anonymously and we obtained their verbal consent to proceed.

We converted the different types of livestock in Gambella region to Tropical Livestock Units [40] to obtain a standardized value that is comparable across stock types. We used descriptive statistics for the quantitative part of the analysis. We selected Likert scale questions that measured attitude and calculated Cronbach's α to measure the internal consistency. We used Spearman's rank correlation to test associations between desire to have lions extirpated from the region and livestock wealth and loss. We categorized responses to desire to have lions extirpated as Yes (3), Indifferent (2) and No (1). We also ran Spearman's rank correlation to test an association between educational level and people's view of the importance of conserving lions. The education levels of respondents were: illiterate, reading and writing, middle school, high school, and college diploma and above.

To compare attitude data from Gambella with those published for Kafa [10], we computed a composite attitude scale (or index) by calculating the mean of responses for identical Likert Scale questions that measured attitude. To do this, we assigned values to responses (5: strongly agree, 4: agree, 3: neutral, 2: disagree, 1: strongly disagree) and multiplied the count of respondents for each question with its assigned value, summed the values, and divided the sum by the total number of respondents. We also ran Mann Whitney U test, a non-parametric test that deals with ordinal variables with no definite distribution, [41], to measure differences in attitude between Kafa and Gambella.

Results

A total of 210 respondents participated in the survey; the majority of these respondents were males (N=147; 70%) born in Gambella region (N=196; 93.33%), where they lived their whole lives. Half of the respondents (49.5%) were from the agricultural sector, 24.3% were government employees, 11.4% were dependent, 8.6% were self-employed, and 6.2% were employees of private companies and daily laborers. Among those whose occupation was agriculture; 53.85% are pastoralists, 7.69% are agro-pastoralists and 38.46% practiced crop farming and animal husbandry. The majority of our respondents (70.5%) did not own land, and only 23.3% owned > 0.5 ha of land. Almost all (96.67%) of our respondents disclosed their annual income and the income ranged from less than or equal to 500 Ethiopian Birr (approximately 22.22 USD; 16.67% of respondents) to over 3,000 Ethiopian Birr (approximately 133.33 USD; 23.33% of respondents). These income estimates do not include earnings from informal economies and do not indicate consumption levels.

Knowledge about carnivores

Almost all respondents could identify lions (98.6%) and hyenas (97.6%) from the given set of photos. Other carnivores that were recognized by a large percentage of respondents were leopard (87.6%), jackal (68.1%), and serval (67.6%). African wild dog was the least recognized carnivore (37.6%). Accordingly, 87.6% and 85.7% of the respondents had seen a hyena and a lion, respectively, at least once in their life. A low proportion of respondents (17.6%) stated that they had seen an African wild dog. Consequently, the majority of our respondents could identify pictures of lion and hyena tracks, 70.5% and 60%, respectively, while only 3.3% were able to identify tracks of an African wild dog. Furthermore, all the key-informants (100%) agreed that the lion population is declining in GNP, although no actual data confirming this trend exist.

Lion attacks and lion killings

Our survey revealed three lion attacks on humans and 31 livestock depredation incidents on seven households altogether. All three recorded human attacks happened before 2000, and the last depredation incident occurred in 2010. A single respondent reported almost a third of the depredations (10), all in 2010. Overall, the respondents identified diseases as the most frequent factor for livestock losses (Fig. 2.a), although theft caused the highest amount of livestock loss, as measured in Tropical Livestock Units (Fig. 2.b). However, none of our respondents mentioned theft or disease as issues in the last section of the questionnaire (comments and concerns regarding livestock) or during informal discussions.

All six key-informants (100%) stated that livestock depredation by lions is a serious problem, and that this problem is more pronounced in Nuer zone due to the higher number of livestock. According to these interviewees, human-lion conflicts increase in the wet season (June to November), following the flooding of Gambella's plains and migration of the white eared kob (*Kobus kob*), an important prey item for lions, to South Sudan. When most of the plains are flooded, to escape the water, lions shift movements closer to villages, and as a result feeding on livestock increases.

Most of our respondents thought that depredations occur because livestock graze close to (and inside) lion habitats and because lions are violent in nature (Fig. 3). The majority (60.9%) of our respondents believed that depredation has decreased in the past five years, while 33.8% responded they do not know whether depredation has increased or decreased.

In addition, the majority of our respondents (90.9%) stated that lions are not hunted in and around GNP. However, in informal discussions, people in most villages mentioned that any wildlife should be killed if it is a problem animal (if it attacks people, domestic animals, or damages crops). The few respondents (9.1%) that answered 'lions are hunted in Gambella' gave the following reasons: to protect livestock from attacks (84.2%), because lions are dangerous and should be kept away from human environment (10.5%), and because cattle rustlers kill lions to use their skin to make the stolen cattle run faster (5.3%). The last reason came up often in informal discussions with respondents that said 'lions are not hunted in Gambella'. The same group of respondents mentioned frequently during informal discussions that people living in and around Metar district kill lions for their skin because lion skin is used to make jewelry in Metar and in adjacent areas in South Sudan.

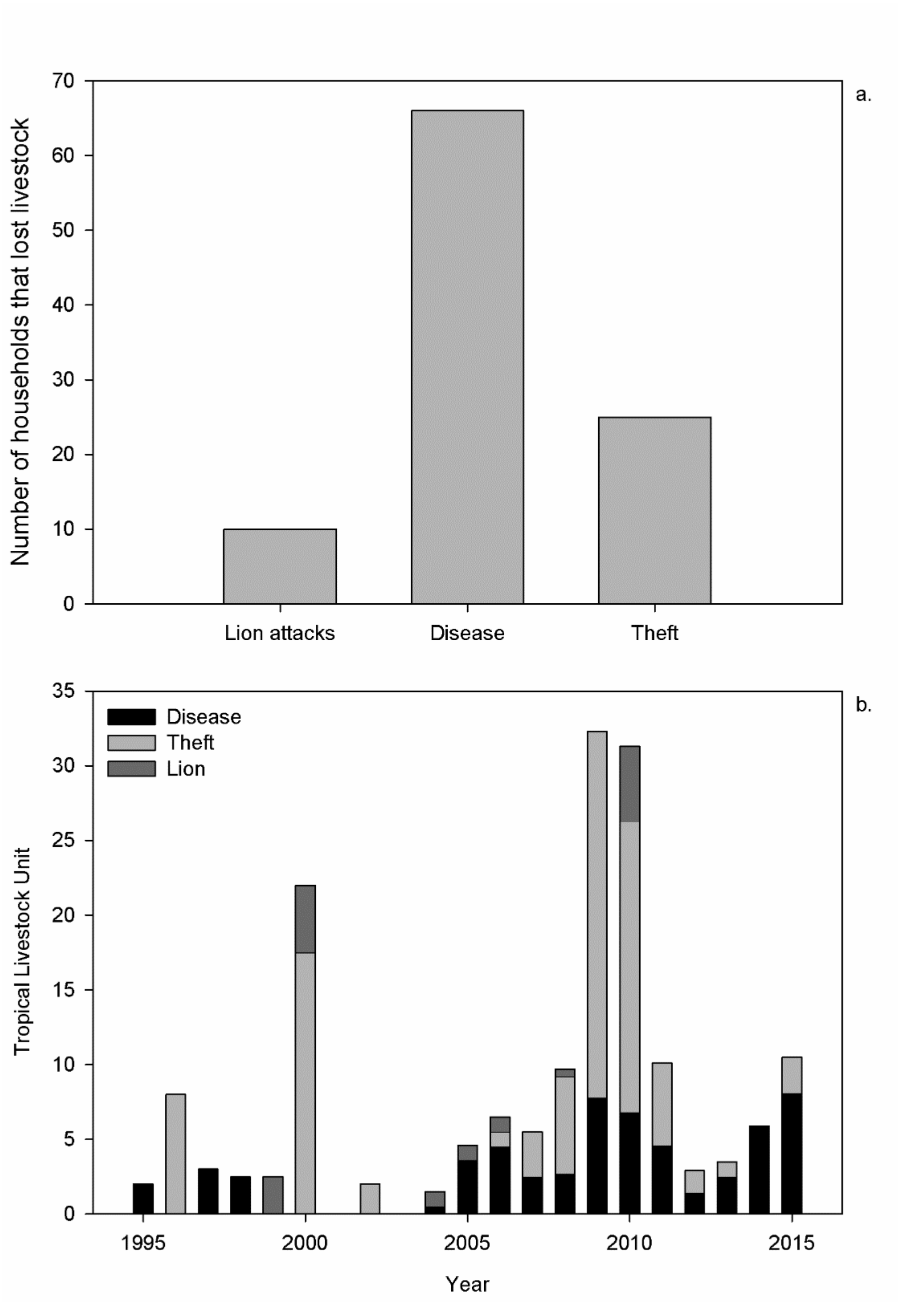

Fig. 2: Overview of livestock loss between 1995 and 2015 in Gambella region, Ethiopia. Three main factors linked to livestock loss in relation to number of individuals experiencing livestock loss (a) and magnitude of livestock loss, in Tropical Livestock Units, by each factor (b) (N=210).

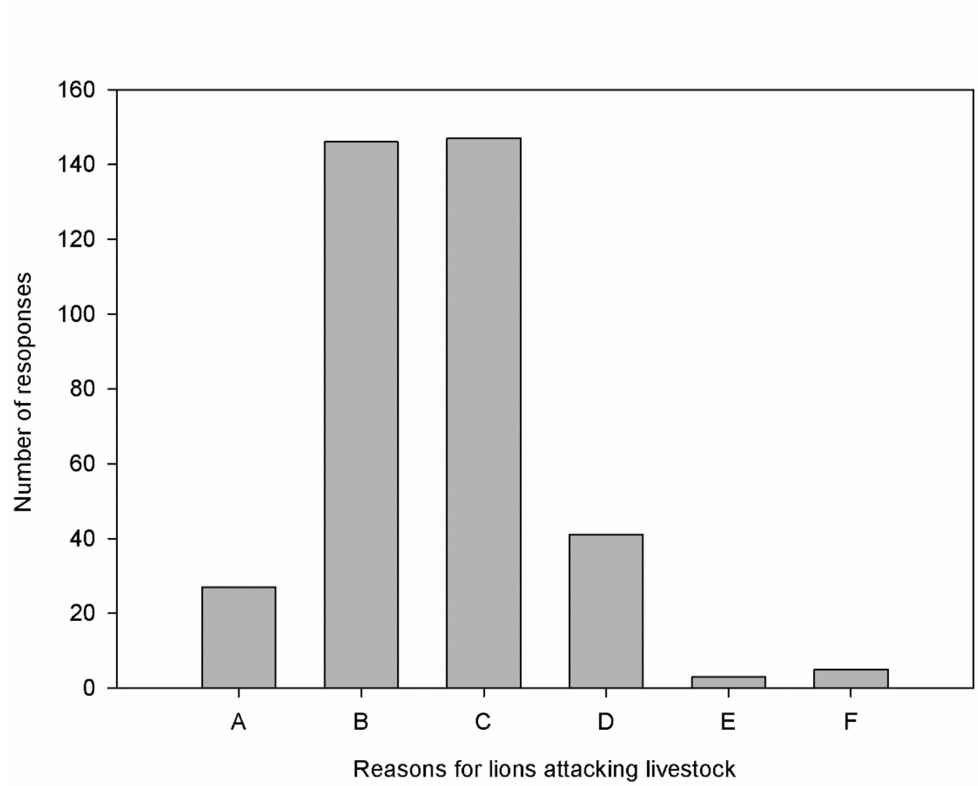

Fig. 3: Respondents' answers to the question 'why do lions attack livestock' in Gambella region, Ethiopia (A= lack of wild prey; B= because the livestock graze close to lions; C= because lions are violent in nature; D= because lions are habitual raiders; E= don't know; F= other reasons) (N=210)

All key-informant interviewees mentioned that hunting by the region's Special Police is a problem which has been reported by GNP officials to the regional government to no avail (*Special Police are police forces that receive para-military training and are armed to protect key regional facilities. They will intervene in situations that cannot be controlled by the conventional police, as a last resort for the regional government before it appeals for intervention by the federal government*). One key-informant stated: "the Special Police seem to have a wrong notion that the general rules do not apply to them so they kill wildlife as they please; and they carry the kills in the open too, unlike locals who try to hide when they see a GNP vehicle or staff". On the other hand, all key-informants (100%) stated that lion killing is a problem in Gambella region, but since it is an illegal act, locals do not report killing incidents, unless park scouts or other GNP personnel find the carcass in the field. During one of our data collection seasons, we found one lion carcass.

Key-informants mentioned that local people do not formally report depredation incidents as they happen, but raise the issue whenever they get the opportunity to meet with GNP staff formally or informally. As a result, the reports of depredation to GNP are intermittent (Table 1). Some of the key-informants reported that local people are starting to demand compensations from GNP for their claims of livestock loss. In 2015, local police officers killed a lion, claiming that it attacked their car.

Table 1: Livestock loss (expressed in Tropical Livestock Units) due to lion depredation reported to Gambella National Park, Ethiopia

Place	TLU	Year
Gambella town	4	2003
Metar	6	2004
Lare and Jikao	10	2010
Lare and Jikao	10.5	2016

Two of our six key-informants mentioned that some South Sudanese refugees are armed, further exacerbating the problem of poaching.

Attitudes towards lions

A little more than half of our respondents (53.8%) do not want lion numbers to increase in Gambella region. Among these respondents, more than half (62.83%) did not give a reason, the majority (19.47%) responded that it is because lions will kill people and livestock, 14.16% replied ‘it would just be bad’ if lion numbers increase, and 3.54% gave the reason that lions are useless.

According to most of our respondents (73%), lions do not have any cultural value in Gambella region. Additionally, the majority (57.6%) think that lions are not advantageous or benefit humans or the environment. The majority (67.62%) of our respondents answered that they like seeing lions in the wild, but when asked if lion killing should be allowed by law about half (52.4%) of our respondents answered yes. Only about 17.62% of our respondents want to see lions extirpated from Gambella, while 63.33% believe that it is important to conserve lions. Most of our respondents (83.33%) prefer the lions confined within a restricted area, like the national park.

Based on the index of internal reliability (Cronbach's $\alpha=0.678$), 67.8% of the variability in our attitude data is reliable. Spearman's correlation between livestock loss and desire to have lions extirpated from one's community showed a non-significant association ($\rho s=0.063$, $P=0.36$). The association between livestock wealth and extirpation of lions also appeared non-significant ($\rho s=0.029$, $P=0.67$). We found a significant association between education level and wanting lion numbers to increase in Gambella ($\rho s=0.426$, $P<0.01$). The association between where respondents live (the countryside or in town) and their view on the importance of conserving lions was borderline significant ($\rho s=-0.133$, $P=0.054$).

Comparison with Kafa Biosphere Reserve

More economic loss is caused by lions in Kafa Biosphere Reserve (southwestern Ethiopia), than in and around GNP (Fig. 4) [10]. Between 1999 and 2013, communities around Kafa lost about 10 times more Tropical Livestock Units compared to communities in Gambella region.

The composite attitudinal index produced highest values for different measures of attitude in Kafa and Gambella. In Kafa, the highest value was for the importance of conserving lions, while in Gambella it was for depredation by lions being a concern. Results of the Mann Whitney U test show significant attitudinal differences between Kafa and Gambella, except for wanting lions to be extirpated from their respective regions (Table 2).

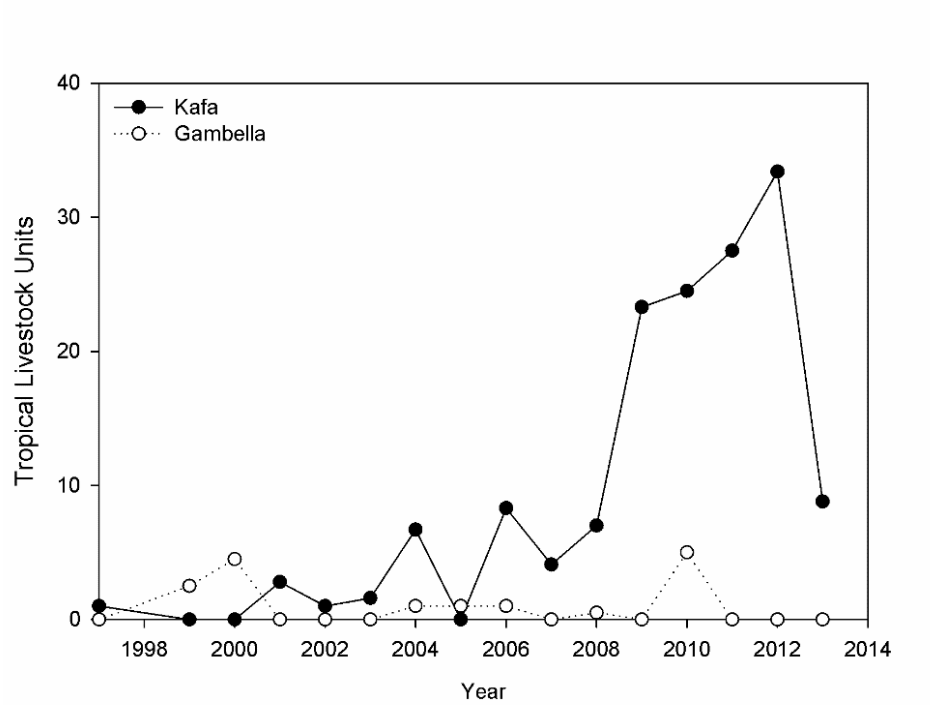

Fig. 4: Livestock loss comparison in Kafa and Gambella regions, Ethiopia

Table 2. Mean survey responses to statements that measured attitude in Kafa and Gambella regions in Ethiopia, and the p-value of Mann-Whitney U test for differences between the two areas

Statements	Gambella	Kafa	p-value
I like seeing lions in the wild	3.88	4.17	0.0004
It is important to conserve lions in Gambella/Kafa	3.78	4.54	<0.001
Presence of lions is a sign of a healthy environment	3.52	4.08	<0.001
I want lions extirpated from Gambella/Kafa	3.62	3.65	0.6774
Depredation by lions is a very concerning issue in Gambella/Kafa	4.16	3.88	0.01926

Discussion

We found that disease and theft are the leading causes of livestock loss in and around GNP, as previously reported in the literature [42, 43]. However, a mismatch was revealed between livestock depredation by lions and peoples' perception of risk that lions pose. Such a disparity has been reported in other studies. For example, local communities considered depredation the top livestock mortality factor in

Waza, Cameroon [44] and in Ruaha, Tanzania [43], although disease was more important in both cases. This subjective perception may be due to the resentment towards large and conflict-prone species [45]. Although most of our respondents stated they do not want lions to be extirpated from Gambella region, anecdotal evidence suggests that lion killing exists and lion population has declined. Despite the generally low overall impact of lions on local communities in GNP, there is a widely accepted notion that lions are dangerous animals with no cultural value.

Attitudes and behaviors could be shaped by actual attacks or by perceived risk [46]. The case in Gambella region is of the latter type, demonstrating that people's perception of risk often stems from rare and tragic events rather than many small ones that add up to a greater cumulative and/or historic effect [47]. Underlying factors, different from livestock depredation, are shaping local peoples' attitude towards lions in Gambella region. One factor can be the inherent, natural fear of lions [48] which is one of the key factors that shape attitude towards large carnivores [46]. We found education level to be another key factor in determining locals' attitude towards lions. Similar to the findings of Roskaft et al. [49], respondents with higher education level were more supportive of the idea of lion numbers increasing in GNP; this may be because higher education level has been linked to increased naturalistic scores (valuing outdoor recreational contact with wildlife) [50].

Conflicts foster negative attitudes, leading to unfavorable behaviors towards large carnivores. However, depending on the local culture, communities may be more tolerant, as in Kafa Biosphere Reserve, in southwestern Ethiopia. Although lion attacks are more common in Kafa, there are many cultural taboos and beliefs about lions that dissuade killing lions, thus creating the platform for coexistence [10]. In contrast, lions are reported to have practically no cultural value in Gambella region, indicating that local culture cannot be used to promote tolerance and coexistence as in Kafa. This demonstrates that issues of and potential solutions to human-lion conflicts should be understood and designed at a socially meaningful regional scale [29]. The opposite levels of intrinsic motivations in Kafa and Gambella towards tolerating lion attacks imply that approaches to these communities must be different when dealing with lion conservation [51]. Potential solutions for Gambella should also take into consideration the inter-ethnic conflicts [52].

Trophy hunting has a long history in Gambella, as it was one of the trade goods the region was known for [53]. Anecdotal evidence and informal communications with key-informants are filled with claims that lions are persecuted in Gambella. Additionally, Gambella's human population has increased due to relocation of Ethiopian highland settlers [32] and South Sudanese refugees, increasing the need for resources and likely leading to more poaching and land clearing. We propose that law enforcement be a priority to reduce poaching, as poaching can directly decrease lion population or indirectly by reducing prey availability. We strongly recommend working towards mitigating poaching by incorporating all stakeholders: local people, refugees, and the Special Police. Park rangers and other GNP staff might be intimidated when dealing with members of the Special Police, therefore EWCA needs to engage in discussions regarding this issue. Law enforcement, however weak, should be the same for locals and the Special Police.

The reward aspect of the carrot-and-stick approach in managing conflicts takes two forms: increasing tolerance of local people and reducing conflicts [54]. These could be achieved through activities like conservation education, economic incentives, and removing problem animals [55]. The conservation education should be composed of instrumental (predetermined guidelines) and emancipatory (after capacity building local people become part of the decision makers) perspectives [56]. In the case of GNP, communicating the major causes of livestock loss to the locals should reduce the misdirected resentment towards lions. This is particularly important since perceived damages by carnivores have been found to be more influential than actual attacks in guiding coexistence with carnivores [12]. Since depredation is claimed to increase in the wet season in Gambella, strict practices of mechanisms that limit livestock depredation [57] in the wet season could be part of the community conservation education. All of the above fall under the instrumental education aspect; the emancipatory approach could include locals taking part in discussions that guide conservation policies and managing conflicts. Interventions through education and outreach programs have been shown to have weak impacts on altering behavior [15, 58]. Hence, we suggest coupling the conservation education with “the stick”: strict law enforcement for bringing change in behavior [15, 59].

Bottom-up conservation in areas with power imbalance between participants, in places with little to no community-engagement in conservation, and where participants have no decision making power is challenging [60]. However, Moeliono [61] suggest that in places where conservation is the responsibility of governments, implementing local participation can be guided by steps in Arnstein’s ladder of participation [16]. The carrot-and-stick approach mentioned above encompasses the bottom five rungs of the ladder grouped into two levels; the non-participation (local people with no actual decision making power) and the degrees of tokenism (local people as part of the dialogue but not making decisions) [16]. After empowering local people with skills and capacities, communities can be guided up the participation ladder for true participation (i.e. the top three rungs; partnership, delegated power, and citizen control). The success of this true participation will depend on selecting the right participants, creating the right atmosphere, and making the process relevant to participants’ needs and priorities [60].

Allocating large tracts of land for commercial farming has intensified in Gambella region, with about 545,178 ha of land (16% of the region’s total area) leased between 2003 and 2014 [36]. Our data suggest no impact by these farms on the status of human-lion conflicts. However, the pressure for land can have a direct effect on the population of lions by causing prey depletion and habitat fragmentation. It may also bring lions into contact with people, often resulting in opportunities to prey upon livestock or attack people. It is important to note that there was a discrepancy in the extent of GNP between EWCA and the federal authority leasing land [62], hence the re-demarcation process of the park in 2011. Currently, agro-investment lands exist inside GNP, although some of the areas excised from the park are not converted to agricultural lands. GNP is not gazette, and with more land-leasing, another re-demarcation might occur. The impact of leasing “unused but protected” land [62] on lion populations (and other wildlife) needs to be studied.

It is likely that pro-carnivore attitude, mostly attributed to urbanites, might be considered as a way of dominance over rural residents [29]. Additionally, national parks created without taking locals' interests into consideration face challenges in serving the purpose for which they were established. This is because parks mostly overlook the political agency of local communities [63], considering locals only as resource users, and potentially leading to everyday forms of locals' resistance [64]. This compels us to question if lion killing in Gambella region is an enactment of a 'natural right' or if it is a way of resistance to a larger issue, an unfavorable protected area. Could changes on the lifestyles and livelihoods of local people be causing a resistance to conservation efforts [65]? Do local people resent the idea of conservation as it affects their lifestyle and livelihood and perceive killing wildlife as a way of pushing back [66, 67]? Gambella region is considered to support a viable lion population in Ethiopia [24]. However, without interventions to address the threats and a deeper understanding of causes of negative attitudes towards lions, the situation could change soon.

Acknowledgements

We thank all GNP staff, principally Galtuak Gatlok, Bemnet Regassa and Henok Tamiru for providing useful information and facilitating data collection. We are grateful to Haileyesus Matheos, Amare Mekonnen, Degu Tadie and Kassahun Abera for their advice about data collection. We thank all our data collectors for assisting with data collection and translation whenever local languages were used. Many thanks also to all our key-informants, survey participants and informal discussion participants for taking the time to answer our questions.

References

1. Bauer H, Packer C, Funston PF, Henschel P, Nowell K. *Panthera leo*: The IUCN Red List of Threatened Species; 2016 [cited 2017 August 14]. Available from: www.iucnredlist.org.
2. Patterson BD, Kasiki SM, Selempo E, Kays RW. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Park, Kenya. *Biological Conservation*. 2004;119(4):507–16. doi: https://doi.org/10.1016/j.biocon.2004.01.013.
3. Kissui BM. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation*. 2008;11(5):422–32. doi: 10.1111/j.1469-1795.2008.00199.x.
4. Woodroffe R. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*. 2000;3(2):165–73. doi: 10.1111/j.1469-1795.2000.tb00241.x.
5. Woodroffe R, Frank LG. Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation*. 2005;8:91–98.
6. Marchini S, Macdonald DW. Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. *Biological Conservation*. 2012;147(1):213–21. doi: http://dx.doi.org/10.1016/j.biocon.2012.01.002.
7. Treves A, Karanth KU. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*. 2003;17(6):1491–9. doi: 10.1111/j.1523-1739.2003.00059.x.

8. Dickman A, Marchini S, Manfredo M. The human dimension in addressing conflict with large carnivores. In: Macdonald DW, Willis KJ, editors. *Key topics in conservation biology*. 2. London: John Wiley & Sons, Ltd; 2013.
9. Lagendijk DDG, Gusset M. Human–carnivore coexistence on communal land bordering the Greater Kruger Area, South Africa. *Environmental Management*. 2008;42(6):971–6. doi: 10.1007/s00267-008-9204-5.
10. Gebresenbet F, Baraki B, Yirga G, Sillero-Zubiri C, Bauer H. A culture of tolerance: coexisting with large carnivores in the Kafa Highlands, Ethiopia. *Oryx*. 2017:1–10. Epub 03/20. doi: 10.1017/S0030605316001356.
11. Hazzah L, Borgerhoff Mulder M, Frank L. Lions and Warriors: social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biological Conservation*. 2009;142(11):2428–37. doi: https://doi.org/10.1016/j.biocon.2009.06.006.
12. Dorresteijn I, Milcu AI, Leventon J, Hanspach J, Fischer J. Social factors mediating human–carnivore coexistence: understanding thematic strands influencing coexistence in Central Romania. *Ambio*. 2016;45(4):490–500. doi: 10.1007/s13280-015-0760-7.
13. Waylen KA, Fischer A, McGowan PJK, Thirgood SJ, Milner-Gulland EJ. Effect of local cultural context on the success of community-based conservation interventions. *Conservation Biology*. 2010;24(4):1119–29. doi: 10.1111/j.1523-1739.2010.01446.x.
14. Twyman C. Participatory conservation? Community-based natural resource management in botswana. *Geographical Journal*. 2000;166(4):323–35. doi: 10.1111/j.1475-4959.2000.tb00034.x.

15. Baruch-Mordo S, Breck SW, Wilson KR, Broderick J. The Carrot or the stick? Evaluation of education and enforcement as management tools for human-wildlife conflicts. *PLOS ONE*. 2011;6(1):e15681. doi: 10.1371/journal.pone.0015681.

16. Arnstein SR. A ladder of citizen participation. *Journal of the American Institute of Planners*. 1969;35(4):216–24. doi: 10.1080/01944366908977225.

17. Henschel P, Bauer H, Sogbohoussou E, Nowell K. *Panthera leo* (West Africa subpopulation): The IUCN Red List of Threatened Species; 2015 [cited 2017 August 14]. Available from: http://www.iucnredlist.org/details/68933833/0.

18. Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, Dickman A, et al. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*. 2013;22(1):17–35. doi: 10.1007/s10531-012-0381-4.

19. Dolrenry S, Stenglein J, Hazzah L, Lutz RS, Frank L. A metapopulation approach to African lion (*Panthera leo*) conservation. *PLOS ONE*. 2014;9(2):e88081. doi: 10.1371/journal.pone.0088081.

20. White PA, Ikanda D, Ferrante L, Chardonnet P, Mesochina P, Cameriere R. Age estimation of African lions *Panthera leo* by ratio of tooth areas. *PLOS ONE*. 2016;11(4):e0153648. doi: 10.1371/journal.pone.0153648.

21. Curry CJ, White PA, Derr JN. Mitochondrial haplotype diversity in Zambian lions: bridging a gap in the biogeography of an iconic species. *PLOS ONE*. 2015;10(12):e0143827. doi: 10.1371/journal.pone.0143827.

22. Hayward MW, Hayward GJ, Tambling CJ, Kerley GIH. Do lions *Panthera leo* actively select prey or do prey preferences simply reflect chance responses via evolutionary

adaptations to optimal foraging? *PLOS ONE*. 2011;6(9):e23607. doi: 10.1371/journal.pone.0023607.

23. Sogbohossou EA, Bauer H, Loveridge A, Funston PJ, De Snoo GR, Sinsin B, De Iongh HH. Social structure of lions (*Panthera leo*) is affected by management in Pendjari Biosphere Reserve, Benin. *PLOS ONE*. 2014;9(1):e84674. doi: 10.1371/journal.pone.0084674.
24. Gebresenbet F, Bauer H, Hunter L, Gebretensae K, editors. Proceedings of the national lion conservation workshop 2009; Addis Ababa, Ethiopia.
25. IUCN. Conservation strategy for the lion in Eastern and Southern Africa. Pretoria: IUCN, 2006.
26. Ajzen I, Fishbein M. Attitude-behavior relations: A theoretical analysis and review of empirical research. *Psychological Bulletin*. 1977;84(5):888-918.
27. CSA. Census 2007 Report: Gambella Region. Addis Ababa, Ethiopia: Central Statistical Agency, 2007.
28. UNHCR. South Sudan Situation 2017 [cited 2017 August 22]. Available from: http://data.unhcr.org/SouthSudan/region.php?id=36.
29. Williams CK, Ericsson G, Heberlein TA. A quantitative summary of attitudes toward wolves and their reintroduction (1972-2000). *Wildlife Society Bulletin* (1973-2006). 2002;30(2):575-84.
30. Cascão AE. Resource-based conflict in South Sudan and Gambella (Ethiopia): when water, land and oil mix with politics. In: Dias AM, editor. *State and Societal Challenges in the Horn of Africa: Conflict and processes of state formation, reconfiguration and*

disintegration. Lisbon: Center of African Studies (CEA) ISCTE-IUL, University Institute of Lisbon 2013. p. 143–65.

31. Gebeyehu T. Ethnic conflict, interaction and cohabitation in Africa: The case of Nuer and Anuak. *Eastern Africa Social Science Research Review*. 2013;29(2):97–112.
32. Feyissa D. Land and the politics of identity. The case of Anywaa-Nuer relations in the Gambella region. In: Evers S, Spierenburg M, Wels H, editors. *Competing jurisdictions; Settling land claims in Ethiopia*. Afrika-Studiecentum Leiden, The Netherlands: Martinus Nijhoff publishers and VSP; 2005. p. 203–22.
33. Amare A. Wildlife resources of Ethiopia: Opportunities, challenges and future directions: From ecotourism perspective: A review paper. *Natural Resources*. 2015;6:405–22.
34. CMS. Inclusion of White-eared Kob (*Kobus kob leucotis*) on Appendix II Bonn, Germany: *Convention on Migratory Species*, 2014.
35. Duckworth F. *The wildlife situation in Gambela Awaraja, Southwest Ethiopia*. Addis Ababa, Ethiopia: report to Ethiopian Wildlife Conservation Organization (EWCO), 1973.
36. Gebresenbet F. Land Acquisitions, the politics of dispossession, and state-remaking in Gambella, western Ethiopia. *Afrika Spectrum*. 2016;51(1):5–28.
37. EWCA. Gambella National Park Undated [cited 2016 May 16,]. Available from: http://www.ewca.gov.et/en/gambella_national_park%20.
38. Schapira P, Monica M, Rolkier GG, Bauer H. Wildlife migration in Ethiopia and South Sudan longer than ‘the longest in Africa’: a response to Naidoo et al. *Oryx*. 2016;51(1):19. Epub 11/21. doi: 10.1017/S0030605316000363.

39. HoARECN. Launch of the biodiversity management programme 2013 [cited 2016 May 20,]. Available from: http://www.hoarec.org/index.php/en/2013-05-09-13-09-36/2013-05-09-13-09-57/centre-news/273-launch-of-the-the-biodiversitymanagement-programme.

40. Njuki J, Poole J, Johnson N, Baltenweck I, Pali P, Lokman Z, Mburu S. Gender, livestock and livelihood indicators. Nairobi, Kenya: International Livestock Research Institute, 2011.

41. McKnight PE, Najab J. Mann-Whitney U Test. The Corsini encyclopedia of psychology: John Wiley & Sons, Inc.; 2010.

42. Dar NI, Minhas RA, Zaman Q, Linkie M. Predicting the patterns, perceptions and causes of human–carnivore conflict in and around Machiara National Park, Pakistan. *Biological Conservation*. 2009;142(10):2076-82. doi: https://doi.org/10.1016/j.biocon.2009.04.003.

43. Dickman AJ, Hazzah L, Carbone C, Durant SM. Carnivores, culture and 'contagious conflict': Multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biological Conservation*. 2014;178:19-27. doi: http://dx.doi.org/10.1016/j.biocon.2014.07.011.

44. Tumenta PN, de Iongh HH, Funston PJ, Udo de Haes HA. Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx*. 2013;47(2):237–42. Epub 04/01. doi: 10.1017/S0030605311001621.

45. Dickman AJ. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation*. 2010;13(5):458–66. doi: 10.1111/j.1469-1795.2010.00368.x.

46. Dickman AJ, Hazzah L. Money, myths and man-eaters: complexities of human–wildlife conflict. In: Angelici FM, editor. *Problematic wildlife A cross-disciplinary approach*. Switzerland: Springer International Publishing; 2016. p. 339–56.

47. Naughton-Treves L, Treves A. Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In: Woodroffe R, Thirgood S, Rabinowitz A, editors. *People and wildlife: conflict or coexistence*? Cambridge: Cambridge University Press.; 2005. p. 252–77.

48. Kruuk H. Hunter and hunted: Relationships between carnivores and people. Cambridge, UK: Cambridge University Place; 2002.

49. Roskaft E, Handel B, Bjerke T, Kaltenborn BP. Human attitudes towards large carnivores in Norway. *Wildlife Biology*. 2007;13(2):172–85.

50. Bjerke T, Reitan O, Kellert SR. Attitudes toward wolves in southeastern Norway. *Society & Natural Resources*. 1998;11(2):169–78. doi: 10.1080/08941929809381070.

51. Rode J, Gómez-Baggethun E, Krause T. Motivation crowding by economic incentives in conservation policy: A review of the empirical evidence. *Ecological Economics*. 2015;117:270–82. doi: https://doi.org/10.1016/j.ecolecon.2014.11.019.

52. Feyissa D. The cultural construction of state borders: the view from Gambella. *Journal of Eastern African Studies*. 2010;4(2):314–30. doi: 10.1080/17531055.2010.487341.

53. Zewde B. An overview and assessment of Gambella trade (1904-1935). *The International Journal of African Historical Studies*. 1987;20(1):75–94. doi: 10.2307/219279.

54. Sillero-Zubiri C, Laurenson MK. Interactions between carnivores and local communities: conflict or co-existence? In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK,

editors. *Carnivore Conservation*. Cambridge, UK: Cambridge University Press; 2001. p. 282–312.

55. Sillero-Zubiri C, Sukumar R, Treves A. Living with wildlife: the roots of conflict and the solutions. In: Macdonald DW, editor. *Key topics in conservation biology*: Blackwell Publishing; 2006. p. 255–72.
56. Wals AEJ. Learning our way out of unsustainability: The role of environmental education In: Nathan PE, editor. *The Oxford handbook of environmental and conservation philosophy*. New York: Oxford University Press; 2012. p. 628–44.
57. Ogada MO, Woodroffe R, Oguge NO, Frank LG. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology*. 2003;17(6):1521–30. doi: 10.1111/j.1523-1739.2003.00061.x.
58. Gore ML, Knuth BA, Scherer CW, Curtis PD. Evaluating a conservation investment designed to reduce human–wildlife conflict. *Conservation Letters*. 2008;1(3):136–45. doi: 10.1111/j.1755-263X.2008.00017.x.
59. Keane A, Jones JPG, Edwards-Jones G, Milner-Gulland EJ. The sleeping policeman: understanding issues of enforcement and compliance in conservation. *Animal Conservation*. 2008;11(2):75–82. doi: 10.1111/j.1469-1795.2008.00170.x.
60. Reed MS, Ceno JSD. Mediation and conservation conflicts: from top-down to bottom-up. In: Young JC, Wood KA, Gutiérrez RJ, Redpath SM, editors. *Conflicts in Conservation: Navigating Towards Solutions. Ecological* Reviews. Cambridge: Cambridge University Press; 2015. p. 226–239.
61. Moeliono M. Hands off, hands on: communities and the management of national parks in Indonesia. In: Sodhi NS, Acciaioli G, Erb M, Tan AK-J, editors. *Biodiversity and human*

livelihoods in protected areas: case studies from the Malay Archipelago. Cambridge, UK: Cambridge University Place; 2007. P. 165–186.

62. Nalepa RA, Short Gianotti AG, Bauer DM. Marginal land and the global land rush: a spatial exploration of contested lands and state-directed development in contemporary Ethiopia. *Geoforum*. 2017;82:237–51. doi: http://dx.doi.org/10.1016/j.geoforum.2016.10.008.
63. Schwartzman S, Moreira A, Nepstad D. Rethinking tropical forest conservation: perils in parks. *Conservation Biology*. 2000;14(5):1351–7. doi: 10.1046/j.1523-1739.2000.99329.x.
64. Scott JC. Everyday forms of resistance. *The Copenhagen journal of Asian studies*. 1989;4(1):33–62.
65. Holmes G. Protection, politics and protest: understanding resistance to conservation. *Conservation and Society*. 2007;5(2):184–201.
66. Goldman MJ, de Pinho JR, Perry J. Beyond ritual and economics: Maasai lion hunting and conservation politics. *Oryx*. 2013;47(4):490–500. Epub 05/14. doi: 10.1017/S0030605312000907.
67. Benjaminsen TA, Svarstad H. The death of an elephant: conservation discourses versus practices in Africa. *Forum for Development Studies*. 2010;37(3):385–408. doi: 10.1080/08039410.2010.516406.

CHAPTER V

LIMITATIONS AND FUTURE DIRECTIONS

Inherent limitations are common when using modelling approaches, and there could be potential errors too (Segurado and Araujo 2004, Marmion et al. 2009, Sequeira et al. 2018). Having different resolutions of input layers forced me to keep analyses to the smallest resolution. Approximations that are involved with different products (for example: land cover from European Space Agency (ESA), human population density from Food and Agriculture Organization of the United Nations (FAO), and prey species richness from IUCN) might also reduce the accuracy of the models. Classifications used for different stages of my analyses (for example: suitability classifications of land cover and human population density layers for refining ecological niche models, and creating the resistance surfaces by using suitability classifications of human population density, land cover, and prey species richness) could also have introduced some bias, while maintaining simplicity of the outputs. Despite the limitations, identifying potential suitable distributions via ecological niche modeling and further filtering the distributions using important factors is a cost-effective and reliable technique that can provide much-needed information to assist the management and conservation of sub-Saharan large carnivores.

The potential distribution maps produced in my second chapter can be validated by being used for surveys. The least-cost optimal pathways can also be used to establish functional corridors that connect large carnivore populations. Future studies should include fine scale studies of intraguild interactions, large carnivore dispersals, transboundary connectivity, and conserving free ranging large carnivore populations.

Limitations of the human-carnivore conflict chapters (third and fourth chapters) include gaps created due to the personalistic nature of ethnographic data collection (for example: failure to ask questions in the same exact wording, recording everything respondents say, etc), which vary from one data collector to the other. Another potential limitation could be the cultural differences between locals and the researcher, and not having enough time to assimilate into the local culture to learn/understand cultural contexts. For example, in Kafa locals mostly address lions by including a respectful prefix before the noun 'lion', which is not common in most parts of Ethiopia. Communication gaps, perhaps caused by mis-translation, might also have introduced some bias into the results of the surveys and the focus group discussions. Household surveys were prepared in English and then translated to Amharic (the federal working language), a second language to the majority of local people (including most of the data collectors). On the fly translation of answers to survey questions from local languages to Amharic was common in both study sites. This also might have introduced some bias.

Despite the limitations, the results from these chapters could be used to manage lion populations in Gambella National Park and lion and leopard populations in Kafa Biosphere Reserve. Although majority of existing literature focuses on cost and benefit issues as determinants of conflict outcomes (Dickman et al. 2011, Marchini and Macdonald 2012), my study demonstrated the importance of culture of tolerance in managing human-carnivore conflicts. However, relying on the culture of tolerance is not sufficient as urbanization and globalization could easily erode these cultural beliefs. Other ways of encouraging tolerance must be designed. These could start by providing environmental/conservation education, then grow to participatory approaches that engage locals from planning to decision-making and implementation stages. Increasing carnivore-related benefits might also be useful in fostering tolerance.

In Gambella, a well-planned and executed conservation education can help to shift the public attention from the prejudicially accused lions to theft and livestock disease. This, however, might call for an interdisciplinary approach because carnivore ecologists alone will not be able to deal with the human-human or human-livestock conflicts.

Human-carnivore conflicts are complex and hence multi-disciplinary, multi-scale analyses are necessary to understand the entire context. For example, Ericsson and Heberlein (2003) showed that negative attitudes for wolves are common among urban dwellers with little contact with the countryside or the wolves, while Williams et al. (2002) showed that positive attitudes towards wolves are common among people with little experience with the wolves. This illustrates that the notion 'lions are tolerated in Kafa because they are rare' does not hold water, and that region-specific, small-scale studies are important to draw conclusions. Additionally, environmental value orientation (how people evaluate the environment based on their emotional and cognitive principles), which affects attitude towards carnivores, might be affected by how locals perceive central governments (Gangaas et al. 2015). As a result, region specific political ecology studies are needed to understand how locals in Kafa and Gambella perceive central governments and/or conservation regulations/policies, and how land use patterns relate to existing social, economic, and political conditions to facilitate large carnivore conservation in these areas.

In conclusion, large carnivores in sub-Saharan Africa are declining rapidly because of the exponentially growing human population, which leads to habitat encroachment and fragmentation. Focusing on the conservation of large carnivore populations within Protected Areas is not a sound plan as most Protected Areas are small in size, aggravating edge effects and potential extinctions (Woodroffe and Ginsberg 1998). Therefore, conservationists must identify free ranging large carnivore populations by surveying as much suitable areas as possible to include the free ranging populations in management plans. Levels of human-carnivore conflicts and tolerance should also be identified to encourage existing balances of co-existence or to mitigate conflicts and develop cultures of tolerance.

References

Dickman, A. J., E. A. Macdonald, and D. W. Macdonald. 2011. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences* **108**:13937–13944.

Ericsson, G., and T. A. Heberlein. 2003. Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. *Biological Conservation* **111**:149–159.

Gangaas, K. E., B. P. Kaltenborn, and H. P. Andreassen. 2015. Environmental attitudes associated with large-scale cultural differences, not local environmental conflicts. *Environmental Conservation* **42**:41–50.

Marchini, S., and D. W. Macdonald. 2012. Predicting ranchers' intention to kill jaguars: Case studies in Amazonia and Pantanal. *Biological Conservation* **147**:213–221.

Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. Evaluation of consensus methods in predictive species distribution modelling. *Diversity and distributions* **15**:59–69.

Segurado, P., and M. B. Araujo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* **31**:1555–1568.

Sequeira, A. M. M., P. J. Bouchet, K. L. Yates, M. Kerrie, and M. J. Caley. 2018. Transferring biodiversity models for conservation: Opportunities and challenges. *Methods in Ecology and Evolution* **9**:1250–1264.

Williams, C. K., G. Ericsson, and T. A. Heberlein. 2002. A quantitative summary of attitudes toward wolves and their reintroduction (1972-2000). *Wildlife Society Bulletin* (1973-2006) **30**:575–584.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside Protected Areas. *Science* **280**:2126–2128.

APPENDICES

Appendix 1

Supplementary Material I: Number and source of occurrence points

Species	GBIF	Vertnet	Inaturalist	Yalden	Self and colleagues' fieldwork	OSU Vertebrate Museum collections
Cheetah	95	9	47	45	11	4
AWD	46	18	30	8	52	0
Lion	204	104	0	65	49	2
Leopard	254	95	0	28	7	2

Appendix 2

Supplementary Material II: Habitat suitability per large carnivore

Agriculture	Forest	Grassland	Wetland	Shrubland	Sparse vegetation	Others

ID	Class	AWD	Cheetah	Lion	Leopard
10	Rainfed crops	NO	NO	NO	LOW
11	Herbaceous cover	LOW	LOW	LOW	MEDIUM
12	Tree or shrub cover	YES	MEDIUM	YES	YES
20	Irrigated or post-flooding cropland	NO	NO	LOW	LOW
30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	NO	LOW	LOW	YES
40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	LOW	LOW	MEDIUM	YES
50	Tree cover, broadleaved, evergreen, closed to open (>15%)	YES	LOW	YES	YES
60	Tree cover, broadleaved, deciduous, closed to open (>15%)	YES	LOW	YES	YES
61	Tree cover, broadleaved, deciduous, closed (>40%)	YES	LOW	YES	YES
62	Tree cover, broadleaved, deciduous, open (15-40%)	YES	LOW	YES	YES
70	Tree cover, needleleaved, evergreen, closed to open (>15%)	YES	LOW	YES	YES
80	Tree cover, needleleaved, deciduous, closed to open (>15%)	YES	LOW	YES	YES
90	Tree cover, mixed leaf type (broadleaved and needleleaved)	YES	LOW	YES	YES
100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	YES	LOW	YES	YES
110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	YES	MEDIUM	YES	YES
120	Shrubland	YES	YES	YES	YES
122	Deciduous shrubland	YES	YES	YES	YES
130	Grassland	YES	YES	YES	YES
150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	YES	YES	YES	YES
151	Sparse tree (<15%)	YES	YES	YES	YES
152	Sparse shrub (<15%)	YES	YES	YES	YES
153	Sparse herbaceous cover (<15%)	YES	YES	YES	YES
160	Tree cover, flooded, fresh or brakish water	LOW	LOW	MEDIUM	MEDIUM
170	Tree cover, flooded, saline water	LOW	LOW	MEDIUM	MEDIUM
180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	NO	NO	YES	YES
190	Urban areas	NO	NO	NO	NO
200	Bare areas	LOW	LOW	LOW	YES
201	Consolidated bare areas	LOW	LOW	LOW	MEDIUM
202	Unconsolidated bare areas	LOW	LOW	YES	YES
210	Water bodies	NO	NO	NO	NO

Appendix 3

Supplementary Material III: Home range sizes of large carnivores and sources

Key: Lion | African wild dog | Cheetah | Leopard

Homerange (sq km)	Reference
26 to 220, in some cases it may exceed 2000	Stuart C&Stuart T (2008)
65 (woodland) to 184 (grassland) in Serengeti	Hunter (2011)
500 (in Serengeti)	Hunter (2011)
2800 (Kalhari)	Hunter (2011)
2721 to 6542 (Kunene, NW Namibia)	Hunter (2011)
20 to 500	Orsdol etal (1985)
25 to 51 (Nairobi Park)	Schaller (1972)
6 to 10 times (25 to 51) (in Kalhari)	Schaller (1972)
263 (Ethosha NP)	Stander (1991)
150 (Ethosha NP)	Stander (1991)
325 (Ethosha NP)	Stander (1991)
550 (Ethosha NP)	Stander (1991)
2075 (Ethosha NP)	Stander (1991)
550 (Ethosha NP)	Stander (1991)
590 (Ethosha NP)	Stander (1991)
250 (Ethosha NP)	Stander (1991)
650 (Ethosha NP)	Stander (1991)
630 (in Waza)	Bauer and Iongh (2005)
1015 (Waza, using 100% minimun convex polygon)	Tumenta_etal_2013
641 (waza, 95% kernel-density estimation)	Tumenta_etal_2013
195 (Benoue NP)	Schoe, 2007
200 ± 141 (Pendjari BR, with 95% MCP)	Eto_thesis
256 ± 154 (Pendjari BR, with 100% MCP)	Eto_thesis
388 (Females, in Hwange)	Loveridge etal_2009
478 (Males in Hwange)	Loveridge etal_2009

Homerange (sq km)	Reference
400 to 1500	Stuart C&Stuart T (2008)
150 to 2460	Hunter (2011)
423 to 1318	Hunter (2011)
50 to 260	Hunter (2011)
1000	Frame, Malcolm, Frame, and van Lawick, 1979
500	Creel&acdonald, 1999
1500-2000	(Frame et al 1979)
500	Gorman_ etal (1998)
650	
250	Fuller &Kat (1990)
1110	Reiche, 1981
357 to 930	Mills&Gorman (1997)
50-200	Fuller, Kat, et al 1992
3900	Van Lawick and Van Lawik-Goodal (1971)
160	Schaller (1972)
800 to 1500	Stuart C&Stuart T (2008)
40 - males in serengeti	Stuart C&Stuart T (2008)
175 - in Kruger	Stuart C&Stuart T (2008)
37 in Serengeti	Hunter (2011)
126 to 195 (Kruger)	Hunter (2011)
777 (Serengeti)	Hunter (2011)
1829 (Namibia)	Hunter (2011)
1608.4 (Namibia)	
1642 (Namibian)	Marker 2002 (IUCN)
50 to 130	In Walker's carnivores of the World
700 to 1500	In Walker's carnivores of the World
126	Broomhall_etal_2003
195	Broomhall_etal_2004
150	Broomhall_etal_2005
171	Broomhall_etal_2006
833	Caro, 1994
777	Caro, 1994
1651	Marker et al (2007)
10 to several hundred sq kms	Stuart C&Stuart T (2008)
188.4 to 451.2 - in northern Namibia	Hunter (2011)
488.7 to 2321.5 - in Kalhari	Hunter (2011)
42 (male) and 65 (female)	Odden etal (2014)
37.13 (adult males)	Mizutani & Jewell (1998)
2182 (Central Kalhari)	Bothma et al 1997

Homerange (sq km)	Reference
8 to 63	Walker's carnivores of the World
5.6 to 29.9	Bailey (1993)
16.5 to 96.1	Bailey (1993)

Appendix 4

Supplementary Material IV: List of prey species used for creating the friction layer

No.	List of prey species
1	*Aepyceros melampus* (Impala)
2	*Allenopithecus nigroviridis* (Allen's Swamp Monkey)
3	*Allochrocebus lhoesti* (L'Hoest's Monkey)
4	*Allochrocebus preussi* (Preuss's Monkey)
5	*Allochrocebus solatus* (Sun-tailed Monkey)
6	*Ammodorcas clarkei* (Dibatag)
7	*Cephalophus adersi* (Aders' Duiker)
8	*Cephalophus callipygus* (Peters' Duiker)
9	*Cephalophus dorsalis* (Bay Duiker)
10	*Cephalophus harveyi* (East African Red Duiker, Harvey's Duiker, Harvey's Red Duiker)
11	*Cephalophus jentinki* (Jentink's Duiker)
12	*Cephalophus leucogaster* (White-bellied Duiker)
13	*Cephalophus natalensis* (Natal Duiker, Natal Red Duiker, Red Forest Duiker)
14	*Cephalophus niger* (Black Duiker)
15	*Cephalophus nigrifrons* (Black-fronted Duiker)
16	*Cephalophus ogilbyi* (Ogilby's Duiker)
17	*Cephalophus rufilatus* (Red-flanked Duiker)
18	*Cephalophus silvicultor* (Yellow-backed Duiker)
19	*Cephalophus spadix* (Abbott's Duiker, Minde)
20	*Cephalophus weynsi* (Weyns's Duiker)
21	*Cephalophus zebra* (Banded Duiker, Zebra Antelope, Zebra Duiker)
22	*Ceratotherium simum* (White Rhinoceros)
23	*Cercopithecus ascanius* (Red-tailed Monkey)
24	*Cercopithecus campbelli* (Campbell's Monkey)
25	*Cercopithecus cephus* (Moustached Monkey)
26	*Cercopithecus denti* (Dent's Monkey)
27	*Cercopithecus diana* (Diana Monkey)
28	*Cercopithecus dryas* (Dryas Monkey)
29	*Cercopithecus erythrogaster* (Red-bellied Monkey)
30	*Cercopithecus erythrotis* (Red-eared Monkey)
31	*Cercopithecus hamlyni* (Owl-faced Monkey)
32	*Cercopithecus lowei* (Lowe's Monkey)
33	*Cercopithecus mitis* (Blue Monkey)
34	*Cercopithecus mona* (Mona Monkey)
35	*Cercopithecus neglectus* (De Brazza's Monkey)
36	*Cercopithecus nictitans* (Putty-nosed Monkey)

No.	List of prey species
37	*Cercopithecus petaurista* (Spot-nosed Monkey)
38	*Cercopithecus roloway* (Roloway Monkey)
39	*Cercopithecus sclateri* (Sclater's Monkey)
40	*Chlorocebus aethiops* (Grivet Monkey)
41	*Chlorocebus cynosuros* (Malbrouck Monkey)
42	*Chlorocebus djamdjamensis* (Bale Monkey)
43	*Chlorocebus pygerythrus* (Vervet Monkey)
44	*Chlorocebus sabaeus* (Green Monkey)
45	*Chlorocebus tantalus* (Tantalus Monkey)
46	*Connochaetes gnou* (Black Wildebeest)
47	*Connochaetes taurinus* (Common Wildebeest)
48	*Equus quagga* (Plains zebra)
49	*Erythrocebus patas* (Patas Monkey)
50	*Eudorcas albonotata* (Mongalla Gazelle)
51	*Eudorcas rufifrons* (Red-fronted Gazelle)
52	*Eudorcas thomsonii* (Thomson's gazelle)
53	*Eudorcas tilonura* (Eritrean Gazelle, Heuglin's Gazelle)
54	*Gazella cuvieri* (Cuvier's Gazelle, Edmi)
55	*Gazella dorcas* (Dorcas Gazelle)
56	*Gazella leptoceros* (Slender-horned Gazelle)
57	*Gazella spekei* (Speke's Gazelle)
58	*Giraffa camelopardalis* (Giraffe)
59	*Kobus ellipsiprymnus* (Waterbuck)
60	*Kobus kob* (kob)
61	*Kobus leche* (Southern Lechwe)
62	*Kobus megaceros* (Nile Lechwe)
63	*Kobus vardonii* (Puku)
64	*Litocranius walleri* (Gerenuk)
65	*Madoqua guentheri* (Guenther's Dik-dik)
66	*Madoqua kirkii* (Kirk's Dik-dik)
67	*Madoqua piacentinii* (Silver Dik-dik)
68	*Madoqua saltiana* (Salt's Dik-dik)
69	*Miopithecus ogouensis* (Northern Talapoin Monkey)
70	*Miopithecus talapoin* (Southern Talapoin Monkey)
71	*Nanger dama* (Addra Gazelle, Dama Gazelle, Mhorr Gazelle)
72	*Nanger granti* (Grant's Gazelle)
73	*Nanger soemmerringii* (Gazelle de Soemmerring, Soemmerring's Gazelle)
74	*Oryx gazella* (Gemsbok)
75	*Phacochoerus aethiopicus* (Desert warthog)

No.	List of prey species
76	*Phacochoerus africanus* (Common warthog)
77	*Philantomba maxwellii* (Maxwell's Duiker)
78	*Philantomba monticola* (Blue Duiker)
79	*Potamochoerus larvatus* (Bushpig)
80	*Raphicerus campestris* (Steenbok)
81	*Raphicerus melanotis* (Cape Grysbok)
82	*Raphicerus sharpei* (Sharpe's Grysbok)
83	*Redunca arundinum* (Southern Reedbuck)
84	*Redunca fulvorufula* (Mountain Reedbuck)
85	*Redunca redunca* (Bohor Reedbuck, Common Reedbuck)
86	*Sus scrofa* (Wild boar) (youngs)
87	*Sylvicapra grimmia* (Common Duiker)
88	*Syncerus caffer* (African Buffalo)
89	*Tragelaphus angasii* (Nyala)
90	*Tragelaphus buxtoni* (Mountain Nyala)
91	*Tragelaphus derbianus* (Derby's Eland, Giant Eland, Lord Derby's Eland)
92	*Tragelaphus oryx* (Common Eland)
93	*Tragelaphus scriptus* (Bushbuck)
94	*Tragelaphus strepsiceros* (Greater Kudu)

Appendix 5

Supplementary Material V: The top 25% least-cost corridors

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
AWD-13	37768472	31.59	No	Tanzania		No	650	650	1300	0	NA
AWD-8	23678282	27.50	No	Kenya		No	41600	35750	77350	5850	13.22
AWD-11	28984052	137.87	No	Tanzania		No	3900	4550	8450	650	13.00
AWD-7	19615732	76.36	No	Tanzania		No	3250	3900	7150	650	11.00
AWD-3	12809262	25.62	No	Zambia		YES	14950	19500	34450	4550	7.57
AWD-17	43551492	25.62	No	Mali		No	2600	1950	4550	650	7.00
AWD-19	47996288	103.25	No	Mozambique		YES	8450	5200	13650	3250	4.20
AWD-27	61848588	25.80	No	South Africa		No	650	1300	1950	650	3.00
AWD-23	50979568	93.99	No	Mozambique		No	15600	6500	22100	9100	2.43
AWD-2	12369718	40.13	No	Tanzania		No	1300	3250	4550	1950	2.33
AWD-16	41831020	61.66	No	Kenya		No	5200	1950	7150	3250	2.20
AWD-15	40989640	25.62	No	Congo		No	10400	30550	40950	20150	2.03
AWD-24	53798900	128.09	Yes	Tanzania	Mozambiq ue	Yes	5850	18850	24700	13000	1.90
AWD-6	18133148	36.23	No	Mozambique		Yes	650	5200	5850	4550	1.29
AWD-5	17493424	57.21	No	Zambia		Yes	3900	36400	40300	32500	1.24
AWD-18	43551492	102.47	No	Zambia		Yes	22100	1300	23400	20800	1.13
AWD-1	10887134	65.41	No	Kenya		YES	1950	35750	37700	33800	1.12
AWD-20	48599780	208.65	Yes	Chad	C. African Republic	Yes	57850	2600	60450	55250	1.09
AWD-25	57968104	65.41	Yes	South Sudan	Ethiopia	Yes	1300	34450	35750	33150	1.08
AWD-14	37768472	40.13	No	Kenya		YES	41600	1300	42900	40300	1.06

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
AWD-12	30742232	76.86	No	Zambia		YES	36400	1899950	1936350	1863550	1.04
AWD-9	23758246	159.93	Yes	Kenya	Tanzania	Yes	35750	650	36400	35100	1.04
AWD-21	49478872	27.50	No	South Africa		No	1899950	19500	1919450	1880450	1.02
AWD-10	28801988	61.66	No	Tanzania		No	650	65000	65650	64350	1.02
AWD-4	14931570	34.35	No	Kenya		No	68900	650	69550	68250	1.02
AWD-26	59779608	65.41	No	Angola		No	1899950	6500	1906450	1893450	1.01
AWD-22	49478872	27.50	No	South Africa		No	1899950	1950	1901900	1898000	1.00
CHE-18	39073272	81.27346	No	Tanzania		No	103500	131500	235000	28000	8.39
CHE-15	28221096	155.7271	No	Tanzania		No	9000	20000	29000	11000	2.64
CHE-9	24150844	80.23812	No	South Africa		No	2500	1000	3500	1500	2.33
CHE-11	25886420	91.17065	Yes	DR Congo	Sudan	Yes	12500	4500	17000	8000	2.13
CHE-21	44606376	22.30319	No	Mozambique		Yes	13000	4500	17500	8500	2.06
CHE-24	45464548	27.6018	No	Kenya		No	624500	212000	836500	412500	2.03
CHE-27	51297332	44.60637	No	Kenya		No	1500	500	2000	1000	2.00
CHE-1	85386.13	57.78433	Yes	Kenya	Tanzania	Yes	37000	9000	46000	28000	1.64
CHE-5	17842550	22.30319	No	DR Congo		Yes	3000	500	3500	2500	1.40
CHE-34	57988288	22.30319	No	Central African Republic		No	13000	1500	14500	11500	1.26
CHE-22	44606376	22.30319	No	Cote D'Ivoire		Yes	9000	1000	10000	8000	1.25
CHE-28	52267584	36.66709	No	Mozambique		Yes	4500	500	5000	4000	1.25
CHE-35	58351720	37.32599	No	Sudan		No	121000	9500	130500	111500	1.17
CHE-26	46454032	116.9052	No	Zimbabwe		Yes	500	8000	8500	7500	1.13
CHE-14	27687652	57.69366	No	Kenya		No	37000	630500	667500	593500	1.12
CHE-7	21253024	57.93493	No	Tanzania		No	9000	500	9500	8500	1.12
CHE-6	18505660	59.62918	No	Tanzania		No	20000	1000	21000	19000	1.11
CHE-8	21253024	53.84466	No	Tanzania		No	20000	1000	21000	19000	1.11

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
CHE-32	55500980	90.68473	No	Zambia		No	3092000	116000	3208000	2976000	1.08
CHE-20	41260896	22.30319	No	Mozambique		No	116000	4000	120000	112000	1.07
CHE-17	34569940	22.30319	No	Tanzania		No	133000	2500	135500	130500	1.04
CHE-19	39650996	27.6018	No	Tanzania		No	133000	2500	135500	130500	1.04
CHE-29	53032908	49.75438	No	Zambia		Yes	116500	1500	118000	115000	1.03
CHE-16	30011710	37.32599	No	Kenya		Yes	212000	2000	214000	210000	1.02
CHE-25	45721532	22.30319	No	Angola		No	29000	3092000	3121000	3063000	1.02
CHE-30	53686152	105.4439	No	Mozambique		Yes	128000	1000	129000	127000	1.02
CHE-36	58351720	41.9657	No	Kenya		No	1500	212500	214000	211000	1.01
CHE-12	26763824	22.30319	No	Tanzania		No	500	106000	106500	105500	1.01
CHE-3	14497072	22.30319	No	Tanzania		No	128000	500	128500	127500	1.01
CHE-31	53844656	30.33314	No	Central African Republic		No	169500	500	170000	169000	1.01
CHE-4	15420900	26.24286	No	Zimbabwe		No	3092000	8000	3100000	3084000	1.01
CHE-13	26763824	44.60637	No	Kenya		No	212000	500	212500	211500	1.00
CHE-23	44606376	22.30319	No	Ethiopia		Yes	500	213500	214000	213000	1.00
CHE-2	5384466	36.66709	No	South Africa		No	3092000	1500	3093500	3090500	1.00
CHE-10	24309346	27.6018	No	South Africa		No	3092000	500	3092500	3091500	1.00
CHE-33	56873124	22.30319	No	South Africa		No	3104000	500	3104500	3103500	1.00
LEOP-37	8032161	24.43023	No	Kenya		Yes	150	150	300	0	NA
LEOP-39	9161870	77.4496	No	DR Congo		Yes	300	300	600	0	NA
LEOP-52	19223246	15.75038	No	Uganda		Yes	150	150	300	0	NA
LEOP-14	3495136	23.2602	No	Tanzania		No	4866300	4260450	9126750	605850	15.06
LEOP-28	5242704	34.95136	No	Tanzania		No	4260300	4870500	9130800	610200	14.96
LEOP-32	6478421	41.42178	No	Ghana		No	228300	194100	422400	34200	12.35
LEOP-18	4219002	17.46795	No	Kenya		Yes	150	300	450	150	3.00
LEOP-33	6690436	30.61655	No	DR Congo		Yes	150	300	450	150	3.00
LEOP-2	1765044	17.47568	No	Tanzania		No	1800	4050	5850	2250	2.60

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
LEOP-19	4219002	29.43106	No	DR Congo		No	1650	300	1950	1350	1.44
LEOP-20	4219002	17.358	No	DR Congo		Yes	1650	300	1950	1350	1.44
LEOP-35	7714138	29.43106	No	Tanzania		No	150	1050	1200	900	1.33
LEOP-21	4219002	34.20723	No	Togo		No	1350	150	1500	1200	1.25
LEOP-54	20389332	24.71434	No	DR Congo		No	1650	150	1800	1500	1.20
LEOP-3	2471434	12.35717	No	Tanzania		No	1800	150	1950	1650	1.18
LEOP-55	22242908	52.10241	No	Ethiopia		No	150	2250	2400	2100	1.14
LEOP-27	4942869	37.07151	No	Ghana		Yes	194250	5550	199800	188700	1.06
LEOP-45	12657006	120.0996	No	Central African Republic		No	4260300	71850	4332150	4188450	1.03
LEOP-49	16451978	140.4714	No	Central African Republic		No	50250	4260300	4310550	4210050	1.02
LEOP-4	2471434	41.23079	No	Mozambique		No	4866300	11400	4877700	4854900	1.00
LEOP-11	2983285	17.358	No	Uganda		Yes	4260300	7350	4267650	4252950	1.00
LEOP-5	2471434	132.7948	No	DR Congo		No	87150	150	87300	87000	1.00
LEOP-6	2471434	63.64141	No	Uganda		No	4260300	4800	4265100	4255500	1.00
LEOP-15	3495136	33.37605	No	Uganda		No	4866300	4800	4871100	4861500	1.00
LEOP-7	2471434	470.8228	Yes	Uganda	Tanzania	No	4260300	4200	4264500	4256100	1.00
LEOP-56	22242908	364.7169	Yes	Sudan	Ethiopia	Yes	4260300	2250	4262550	4258050	1.00
LEOP-16	3707152	24.71434	No	Tanzania		No	4260300	1800	4262100	4258500	1.00
LEOP-30	5966570	29.83285	No	DR Congo		No	4260300	1650	4261950	4258650	1.00
LEOP-8	2471434	127.2828	Yes	DR Congo	Uganda	No	4260300	1500	4261800	4258800	1.00
LEOP-44	11121454	37.07151	No	Zimbabwe		No	4866300	900	4867200	4865400	1.00
LEOP-9	2471434	12.35717	No	Tanzania		No	4260600	750	4261350	4259850	1.00
LEOP-50	17300040	24.83202	No	Mozambique		No	4866300	750	4867050	4865550	1.00
LEOP-31	5966570	42.19002	No	Zimbabwe		No	4866300	600	4866900	4865700	1.00
LEOP-29	5454719	47.69452	No	Kenya		No	4260300	450	4260750	4259850	1.00
LEOP-24	4730853	41.12221	Yes	Uganda	DR Congo	No	4260600	450	4261050	4260150	1.00
LEOP-38	8225989	39.72753	No	Kenya		No	450	4261500	4261950	4261050	1.00

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
LEOP-25	4730853	17.70917	No	Tanzania		No	4866300	450	4866750	4865850	1.00
LEOP-42	10909438	41.78823	No	Tanzania		No	4866300	450	4866750	4865850	1.00
LEOP-17	3707152	43.54114	No	DR Congo		No	4260300	300	4260600	4260000	1.00
LEOP-10	2471434	12.35717	No	Central African Republic		No	4260450	300	4260750	4260150	1.00
LEOP-12	2983285	21.44827	No	Uganda		Yes	4262250	300	4262550	4261950	1.00
LEOP-23	4219002	28.02092	Yes	DR Congo	Uganda	Yes	4263150	300	4263450	4262850	1.00
LEOP-1	24714.34	12.35717	No	Tanzania		No	4260300	150	4260450	4260150	1.00
LEOP-13	2983285	21.44827	No	Uganda		Yes	4260300	150	4260450	4260150	1.00
LEOP-26	4730853	40.88744	No	Tanzania		No	4260300	150	4260450	4260150	1.00
LEOP-34	6690436	33.80544	No	DR Congo		No	4260300	150	4260450	4260150	1.00
LEOP-43	11015446	50.17281	Yes	Kenya	Tanzania	Yes	4260300	150	4260450	4260150	1.00
LEOP-46	14210746	12.35717	No	DR Congo		No	4260300	150	4260450	4260150	1.00
LEOP-36	7714138	23.2602	No	Tanzania		No	4866300	150	4866450	4866150	1.00
LEOP-40	9885737	12.35717	No	Zimbabwe		No	4866300	150	4866450	4866150	1.00
LEOP-47	15446464	29.44104	No	DR Congo		Yes	4866300	150	4866450	4866150	1.00
LEOP-51	17899708	35.73506	No	Mozambique		Yes	4866300	150	4866450	4866150	1.00
LEOP-53	20097030	22.76818	No	Zimbabwe		No	4866900	150	4867050	4866750	1.00
LEOP-41	9885737	12.35717	No	Zimbabwe		No	4867800	150	4867950	4867650	1.00
LION-4	5384466	30.33314	No	DR Congo		No	500	500	1000	0	NA
LION-24	21920524	107.6893	No	DR Congo		No	3000	2500	5500	500	11.00
LION-14	13923078	57.78433	No	Tanzania		No	1500	2000	3500	500	7.00
LION-15	13923078	57.78433	No	Tanzania		No	1000	1500	2500	500	5.00
LION-29	33454780	22.30319	No	Zimbabwe		No	1000	500	1500	500	3.00
LION-37	41260896	22.30319	No	Kenya		No	1500	3000	4500	1500	3.00
LION-16	13923078	99.75003	No	Zambia		No	9500	4500	14000	5000	2.80
LION-33	40145736	22.30319	No	Eritrea		No	2000	5500	7500	3500	2.14
LION-38	41260896	22.30319	No	Eritrea		No	5500	2000	7500	3500	2.14

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
LION-19	16190281	147.1477	Yes	South Africa	Mozambique	Yes	5000	1500	6500	3500	1.86
LION-27	26922328	250.3515	No	DR Congo		Yes	3000	17000	20000	14000	1.43
LION-32	37691260	34.97284	Yes	Zambia	Zimbabwe	Yes	1500	9500	11000	8000	1.38
LION-34	40145736	22.30319	No	Ethiopia		No	1000	7000	8000	6000	1.33
LION-25	23768180	220.5042	No	Central African Republic		No	35000	4000	39000	31000	1.26
LION-35	40145736	22.30319	No	Central African Republic		No	35000	3500	38500	31500	1.22
LION-1	44606.38	22.30319	No	Tanzania		No	29000	2500	31500	26500	1.19
LION-30	34378604	319.2375	Yes	Central African Republic	DR Congo	Yes	1000	14000	15000	13000	1.15
LION-21	19690206	178.6891	No	Zambia		Yes	9500	500	10000	9000	1.11
LION-31	36384768	326.6124	No	Zambia		Yes	9500	500	10000	9000	1.11
LION-26	25659816	44.60637	No	Tanzania		No	177000	5000	182000	172000	1.06
LION-5	6690956	22.30319	No	Mozambique		No	161000	3000	164000	158000	1.04
LION-12	12999250	76.80675	No	Tanzania		No	2000	161000	163000	159000	1.03
LION-20	17459888	80.08751	No	Mozambique		Yes	1733500	7000	1740500	1726500	1.01
LION-22	19690206	53.84466	Yes	Uganda	Kenya	Yes	1733500	5500	1739000	1728000	1.01
LION-10	11692760	72.29883	No	Mozambique		No	161000	500	161500	160500	1.01
LION-9	11099892	78.39327	No	Mozambique		No	1733500	5000	1738500	1728500	1.01
LION-28	30024146	124.6939	No	Zambia		Yes	1733500	1500	1735000	1732000	1.00
LION-7	7614785	52.63632	Yes	DR Congs	Sudan	Yes	1733500	1000	1734500	1732500	1.00
LION-8	8921275	66.90956	No	Central African Republic		No	1733500	1000	1734500	1732500	1.00
LION-23	21253024	53.84466	No	Kenya		No	1733500	1000	1734500	1732500	1.00
LION-17	13923078	57.78433	Yes	Zambia	Zimbabwe	Yes	2823000	1000	2824000	2822000	1.00
LION-2	2297229	66.90956	No	Tanzania		No	1733500	500	1734000	1733000	1.00
LION-11	11692760	98.05578	No	South Africa		No	1733500	500	1734000	1733000	1.00
LION-13	12999250	94.60202	Yes	Uganda	Kenya	Yes	1733500	500	1734000	1733000	1.00

ID	Path cost	Length (Km)	Trans boun dary	Country 1	Country 2	Passes throug h a NP	Area of Patch 1 (Sq. Km)	Area of Patch 2 (Sq. Km)	Sum of areas	Absolute difference	(Sum of areas)/ (Absolute difference)
LION-36	40145736	22.30319	No	Kenya		No	1733500	500	1734000	1733000	1.00
LION-3	4460638	22.30319	No	Zambia		No	2823000	500	2823500	2822500	1.00

Appendix 6: Questionnaire used for data collection in chapter IV

S1 Questionnaire

Date: _______________ Coordinates of the house/location: _________________________

I. Socio-economic characteristics of the respondent

1. District: _________________________
2. Sex: ____________
3. Date of birth: _________________________
4. Place of birth: _________________________
5. How long have you lived in Gambella? _________________________
6. Education level: A. Illiterate B. Read and write C. Primary/middle school D. High school E. Diploma and above
7. What is the family composition of your household?
   Spouse ________ Children ____ (M) _____ (F) Relatives______ Others_________
8. Occupation

II. Economic level of the household

9. Average land holding in hectares?
   a. <0.25 b. 0.26-0.5 c. 0.51-0.75 d. 0.76-1 e. >1 f. I don't have a land
   (If you said you do not have land, please pass to question 13)
10. Do you produce crops? a. Yes b. No
11. If yes, is your harvest usually enough to feed your family? a. Yes b. No
12. How long do you generally consume your harvest before you start buying food?
13. What is the estimated average annual total household annual income in ETB?
    a. ≤500 b. 501-1000 c. 1001-2000 d. 2001-3000 d. >3000

III. Lion management, knowledge and perception

14. Pleas tick the alternative that the best describes your opinion
    (Key: 1-Strongly disagree, 2-Disagree, 3- Neutral, 4- Agree and 5- Strongly agree)

No.	**Questions**	**1**	**2**	**3**	**4**	**5**
1	Lion is bad animal					
2	The presence of lions is a sign of a healthy environment					
3	Depredation by lions is a very concerning issue in Gambella					
4	Lions are known for attacking and injuring people					
5	I would be afraid to go into the forest/filed if there are lions					

6	Lion is dangerous to humans					
7	It is important to conserve lions in Gambella					
8	I like seeing lions in the wild					
9	I want lions extirpated from Gambella					
10	Lions should only live in restricted places in Gambella					
11	Killing of lions should be strictly regulated by law					
12	Killing of lions should be allowed by law					
13	Lions have ample prey in the wild					
14	The number of lions in Gambella has notably increased in the past ten years					
15	Lions habitat destruction is a problem in Gambella					

IV. Carnivore knowledge

15. Which carnivore species do you recognize from the pictures?
1. ________ 2. ________ 3. ________ 4. ________ 5. ________ 6. ________

16. Which species (from the pictures in Qn #15) have you ever seen?
1. ________ 2. ________ 3. ________ 4. ________ 5. ________ 6. ________

17. Which of the tracks can you identify (from the provided picture of tracks)?
1. ________ 2. ________ 3. ________ 4. ________ 5. ________ 6. ________

18. According to you, among the above given carnivores (in Qn #15) which are the most dangerous?
(Give a score: 1: extremely dangerous, 2: very dangerous and 3: dangerous)
1. __________________ 2. _________________ 3. ____________________

Why do you think these carnivores are dangerous?
____

19. Do you want lion numbers to increase in Gambella? a. Yes b. No
Why? ____

20. Do you think lions have any advantages? a. Yes b. No
If yes, please mention some of their benefits?
____

21. Do lions have a special meaning/importance in your culture? a. Yes b. No

If yes, please explain in detail:

____

22. Do you know any carnivore body parts that are used for preparing traditional medicines?
a. Yes b. No; If yes, please explain in detail:
Which animal? _________________
Which part of its body? _____________________________
For which disease? ____
23. What are the common prey types for lions in Gambella?

____

24. Do people kill lions in Gambella? a. Yes b. No
If yes, please explain why

____

V. Livestock depredation

25. Do you have livestock? a. Yes b. No
If yes, please fill the table below. If No, please move to question 33.

Livestock species	Sex		Age level		
	Male	Female	Young	Adult	Old
Cow					
Donkey					
Sheep					
Goat					
Ox					
Others					

26. Did you lose livestock as a result of lion depredation? If yes, please fill the table below.

Species	Sex	Age	Number	Depredation place	Year
Cattle					
Donkey					
Sheep					
Goat					
Others					

27. Do you think you can avoid depredation? a. Yes b. No

28. What method you use to limit/avoid livestock depredation?

a. Dog c. Guard/Shepherd

b. Enclosures/Fences d. Fire

a. Others; please specify: ____

29. According to you, among the above given depredation mitigation options, which are effective? Give a score of 1 to 3: from the most effective to effective)

1. 2. 3.

30. How far away is your livestock grazing area from your house?

Dry season ______________________ Wet season ______________________

31. Have you ever lost livestock due to disease? a. Yes b. No

If yes, please give details:

a. Which animals did you lose? How many? _____________ ____________
b. Which disease? _____________________________________
c. When? Month ___________________ Year ___________________

32. Have you ever lost livestock due to theft? a. Yes b. No

If yes, please give details:

a. Which animals did you lose? How many? _______________ ______________
b. Where were they stolen from and how? ________________________________
c. When were they stolen? Month _______________ Year _________________

33. What can be a suitable remedial measure to reduce depredation by lions?

a. Killing all lions
b. Killing the problem causing individual lions
c. Relocating all the lions
d. Keeping livestock in a strongly fenced area
e. Better protection of livestock
f. Others; please explain ____

34. In your opinion; what is the trend of livestock attacks by lions these last five years?

a. It has increased
b. It has decreased
c. It has not changed
d. I do not know

35. Do you think people who lost livestock to lion attacks should be compensated? a. Yes
    b. No
    Why? ____

36. When do you think the livestock predation by lions takes place?
    a. Mornings (6:00-12:00)
    b. Afternoons (12:00-18:00)
    c. Nights (18:00-23:00)
    d. Around and past midnight to Dawn (23:00-6:00)
    e. I do not know

37. In your opinion, why do lions attack livestock?
    a. Lack of wild prey
    b. Because livestock graze close to (and inside) lion habitats
    c. Because they are violent in nature
    d. Because they are habitual raiders
    e. I do not know
    f. Other reasons; please explain: ____________________________________

38. Do lions attack people? a. Yes b. No

39. If yes, what preventive techniques do you use to avoid being attacked by a lion?
    ____
    ____

40. Has anyone from your immediate family been attacked by a lion?
    a. Yes b. No
    If yes:
    a. What type of attack was it? ____
    b. Where did it happen? ____
    c. How did it happen? ____
    d. When did it happen? Month _____________ Year ________________

41. Do you have any comments, observations or recommendations about livestock production, lion conservation, and the problem of depredation?
    ____
    ____
    ____
    ____
    ____

Appendix 7: Internal Review Board

Oklahoma State University Institutional Review Board

Date:	Wednesday, April 09, 2014
IRB Application No	AS1434
Proposal Title:	Carnivore Conservation in Ethiopia with a Focus on Kafa Biosphere Reserve, Southwestern Ethiopia
Reviewed and Processed as:	Expedited

Status Recommended by Reviewer(s): Approved Protocol Expires: 4/8/2015

Principal Investigator(s):

Fikirte Gebresenbet Erda	Jacqueline Vadjunec
21 N Univ Pl Apt 10	337 Murray Hall
Stillwater, OK 74078	Stillwater, OK 74078

The IRB application referenced above has been approved. It is the judgment of the reviewers that the rights and welfare of individuals who may be asked to participate in this study will be respected, and that the research will be conducted in a manner consistent with the IRB requirements as outlined in section 45 CFR 46.

☒ The final versions of any printed recruitment, consent and assent documents bearing the IRB approval stamp are attached to this letter. These are the versions that must be used during the study.

As Principal Investigator, it is your responsibility to do the following:

1.Conduct this study exactly as it has been approved. Any modifications to the research protocol must be submitted with the appropriate signatures for IRB approval. Protocol modifications requiring approval may include changes to the title, PI advisor, funding status or sponsor, subject population composition or size, recruitment, inclusion/exclusion criteria, research site, research procedures and consent/assent process or forms
2.Submit a request for continuation if the study extends beyond the approval period. This continuation must receive IRB review and approval before the research can continue.
3.Report any adverse events to the IRB Chair promptly. Adverse events are those which are unanticipated and impact the subjects during the course of the research; and
4.Notify the IRB office in writing when your research project is complete.

Please note that approved protocols are subject to monitoring by the IRB and that the IRB office has the authority to inspect research records associated with this protocol at any time. If you have questions about the IRB procedures or need any assistance from the Board, please contact Dawnett Watkins 219 Cordell North (phone: 405-744-5700, dawnett.watkins@okstate.edu).

Sincerely,

Shelia M. Kennison

Shelia Kennison, Chair
Institutional Review Board

VITA

Fikirte Gebresenbet Erda

Candidate for the Degree of

Doctor of Philosophy

Dissertation: DISTRIBUTION AND HABITAT CONNECTIVITY OF LARGE CARNIVORES IN SUB-SAHARAN AFRICA AND HUMAN-CARNIVORE CONFLICTS IN WESTERN ETHIOPIA

Major Field: Integrative Biology

Biographical:

Education:

Completed the requirements for the Doctor of Philosophy in Integrative Biology major at Oklahoma State University, Stillwater, Oklahoma in July, 2018.

Completed the requirements for the Master of Science in Dryland Biodiversity at Addis Ababa University, Addis Ababa, Ethiopia in 2008.

Completed the requirements for the Bachelor of Education in Biology at Jimma University, Jimma, Ethiopia in 2005.

Experience:

Graduate Research/Teaching Associate, Department of Integrative Biology, Oklahoma State University, Stillwater, OK. 2012-Present.
Lecturer, Department of Wildlife and Ecotourism Management, Mekelle University, Mekelle, Ethiopia. 2008-2010.

Professional Memberships:

Society for Conservation Biology
Biological Society of Ethiopia
Ethiopian Wildlife and Natural History Society (EWNHS)
Large carnivore working group of Ethiopia