



University of  
Massachusetts  
Amherst

## PRIDE IN OUR PRIDES: MITIGATING HUMAN-LION CONFLICT IN THE OKAVANGO DELTA, BOTSWANA

Item Type	Dissertation (Open Access)
Authors	LeFlore, Eric G
DOI	<a href="https://doi.org/10.7275/27245741">10.7275/27245741</a>
Rights	Attribution-NonCommercial-NoDerivatives 4.0 International
Download date	2026-06-09 14:48:01
Item License	<a href="http://creativecommons.org/licenses/by-nc-nd/4.0/">http://creativecommons.org/licenses/by-nc-nd/4.0/</a>
Link to Item	<a href="https://hdl.handle.net/20.500.14394/18770">https://hdl.handle.net/20.500.14394/18770</a>

**PRIDE IN OUR PRIDES: MITIGATING HUMAN-LION CONFLICT  
IN THE OKAVANGO DELTA, BOTSWANA**

A Dissertation Presented

by

ERIC G. LEFLORE

Submitted to the Graduate School of the  
University of Massachusetts Amherst in partial fulfillment of  
the requirements of the degree of

DOCTOR OF PHILOSOPHY

February 2022

Environmental Conservation

© Copyright by Eric G. LeFlore 2022  
All Rights Reserved

PRIDE IN OUR PRIDES: MITIGATING HUMAN-LION CONFLICT  
IN THE OKAVANGO DELTA, BOTSWANA

A Dissertation Presented

by

Eric G. LeFlore

Approved as to style and content by:

---

Todd K. Fuller, Co-Chair

---

Andrew B. Stein, Co-Chair

---

Peter W. Houlihan, Outside Member (Biology)

---

Paige S. Warren, Head  
Department of Environmental Conservation

---

Timothy O. Randhir, Graduate Program  
Director Environmental Conservation

## **DEDICATION**

For my family.

“Until the lions have their own historians,  
the history of the hunt will always glorify the hunter.”

-African proverb as recalled by Chinua Achebe

## ACKNOWLEDGMENTS

I would like to sincerely thank my committee members, Todd Fuller, Andrew Stein, and Peter Houlihan, for their guidance and support throughout this project. Todd, thank you for the countless meetings, new ideas, patience, reassuring presence, and, most importantly, for your mentorship and friendship. I have learned an incredible amount from you over our time together and owe much of my development as a conservation biologist and professor to you. Congratulations on your unbelievably productive and impressive career. It has truly been an honor working with you, and I cannot thank you enough for all you have done to help me along during my graduate and professional careers!

Andrew, thank you for starting this project with me. Embarking on this journey with you has been a dream come true. I thoroughly enjoyed our time in the field together and I hope we can continue working together more in the future. I'm thrilled to have been a part of CLAWS Conservancy and to have built Pride in Our Prides with you. It's been amazing to watch it continue to develop since I've left the field. You've done an amazing job shepherding this initiative along and it has already had a major impact on so many people and the conservation world. Thank you for including me in the program.

Peter, I sincerely appreciate you serving on my committee as an outside member. I've always appreciated your thoughtful questions throughout this process. Your expertise has made this project stronger, and I thank you for taking the time to be a part of my committee.

None of this work would have been possible without the translations, local knowledge, hard work, and positive attitude of Mathata "Pro" Tomeletso. Pro, my man, I

sincerely appreciate you, our friendship, and all you've done to help with this project. You were hired as a field assistant, but you quickly became a family member. The days we spent together in Botswana were truly some of the best days of my life. I will hold our time together fondly for the rest of my life, and I look forward to when we can spend more time together, laughing, and working to help your fellow community members while also protecting the biodiversity of the Delta. Thank you for sharing your culture with me and helping me learn so much about the region.

I sincerely thank the villagers, elders, and headmen from Beetsha, Eretsha, Gudigwa, Gunotsoga, and Seronga for not only welcoming me and accepting me into the community, but for being willing participants in this research with me. I appreciate you all sharing your culture and such a magical place with me. It was an honor working with you all and I look forward to new opportunities to do so again in the future. Christopher Dimbindo, thanks for sharing your tracking expertise with me and for all your hard work. Thanks to our great group of hard-working kraal builders: Raps, Kenneth, and Stallen.

I'd like to thank Greg and Sue Flaxman and staff members at Kadizora Camp, Jumbo Junction, Fallen Baobab, Kana Kara, and Mapula Lodge for logistical support. A big thank you to P. Sheller and Ngami Data Services for geographic information system data.

I would like to acknowledge the assistance from the Botswana Ministry of Environment, Wildlife, and Tourism and the Department of Wildlife and National Parks. In particular, I wish to thank Dr. Michael Flyman and Mavuna Mweze (in memoriam) for their support.

This project was funded through the generous support of National Geographic's Big Cats Initiative (grant numbers: B5-15 and B10-16), a J.W. Fulbright Research Scholarship, the University of Massachusetts, the Mellon Mays Graduate Initiative through the Social Science Research Council, and numerous private donations from tourists, wildlife enthusiasts, friends and family.

Crispin Sanderson, thank you for the Green Machine and for your perpetual mechanic advice. I learned so much in your shop, from actual auto mechanics to grit and perseverance. There's always a way to make a plan! Thanks for being the advisor to my alternate "PhD" in auto mechanics. A big thanks for all the help and laughs to the Fika Trading staff.

Thanks to Vince Shacks for sharing knowledge of this human-lion conflict with us, this project would not have gotten started without the tip.

Thank you, Robyn Currell and Steve Stockhall for being my home away from home, away from home. I cannot thank you enough for your generosity in opening up your home to me and providing me with researcher accommodations. Thanks for all the good food and great laughs.

To my Botswana researcher support network, thank you for the company, thoughtful wildlife research discussions, and the necessary conversations about anything but research. A special thanks go out to Rocío Pozo, Jeremy Cusack, Valli Fraser-Celin, Erin Must, Robynne Kotze, and Lindsey Rich. It was a blast spending time with you all. I look forward to the next time we run into each other at the Old Bridge.

John Finn and Kevin McGarigal, thank you both for teaching me how to code and analyze data in R. Jack, you are incredibly patient and knowledgeable. Kevin, your all

business approach to data analysis and your highly organized teaching style have given me an example to work towards in my scientific career. You both have shared valuable knowledge and given me the skills to overcome a plethora of analytical problems. I sincerely appreciate all the time you devoted to our meetings, courses, and my never-ending questions.

Members of the Fuller Lab Group throughout the years, thank you for being a part of my UMass journey. I appreciated your thoughtful suggestions and feedback when we would meet as a group. It was fantastic working with you all and I hope we have the opportunity to collaborate on projects in the future. Friends from the ECo Department, thanks for always cheering me on. Fletcher Clark, Jared Starr, Bridget MacDonald, Emily Hart, Kathy Zeller, and Melanie Klein, studying with you all certainly made all those problem sets more manageable!

A big thanks to my friends, who always show an interest in what I do. Brendan O'Hagan, thanks for all the support, friendship, and unbridled curiosity about all things wildlife related. Khary Polk, your undercover mentorship and unique interpretations of my research have been incredibly helpful throughout grad school.

An enormous thanks goes to my family for enjoying nature with me, whether on walks with dogs or hikes in national parks. Audrey MacLean, thank you for your unconditional support as I've navigated this challenging process. It's meant the world to me. A special thanks to my mother, Bonnie, to whom I owe every one of my successes. I would not have chased this career if it were not for your advice, love, and never-ending support. Thank you for all the laughter and for always being there for me.

## **ABSTRACT**

### **PRIDE IN OUR PRIDES: MITIGATING HUMAN-LION CONFLICT IN THE OKAVANGO DELTA, BOTSWANA**

**FEBRUARY 2022**

**ERIC G. LEFLORE, B.A., CONNECTICUT COLLEGE**

**M.S., UNIVERSITY OF MASSACHUSETTS AMHERST**

**Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST**

**Directed by: Dr. Todd K. Fuller & Dr. Andrew B. Stein**

Humans are having marked effects on the natural world, directly contributing to biodiversity declines around the globe. Large carnivores are disproportionately affected as they are wide-ranging, occur in low population densities, and are typically in conflict with humans. Large carnivores are now rare or absent from many ecosystems as their populations have plummeted and human-carnivore conflicts over livestock remain a main contributing factor. The situation is especially acute for the African lion (*Panthera leo*) as the species is in decline across Africa and has been extirpated from >80% of its historic range. Estimates show the population has decreased by ~90% in the last ~40 years and there are only ~20,000 lions left in the wild, most of which reside in protected reserves. Recently, the population stronghold in the Okavango Delta Region of northern Botswana was also shown to be in decline. This population is one of the largest in southern Africa and is one of only a handful of lion strongholds remaining on the continent.

Across five focal villages in the eastern panhandle of the Okavango Delta, I investigated human-lion conflict and established a community-based conflict mitigation program from October 2014 to December 2016. This multilevel study analyzed livestock

depredation events, tracked and monitored the local lion population, implemented and tested the efficacy of innovative conflict mitigation strategies, and examined the attitudes of local villagers towards predators and the established conflict mitigation program. Main conflict mitigation strategies included the establishment of an early-warning system linked to the movements of GPS satellite collared lions as well as a predator-proof livestock enclosure building program utilizing locally-sourced materials.

Through independent investigations, I found that lions were responsible for ~75% of livestock depredation events in the area and 116 livestock were killed in 102 confirmed wild carnivore attacks. Most (90%) attacks occurred while livestock were unattended and freely grazing in multi-use, communal areas. Valuation of verified losses totaled ~\$30,000 over the study period. Additionally, there were 50% more events reported to DWNP for compensation than were confirmed through independent investigations. Five lions (3 males & 2 females) were fitted with GPS satellite collars and home range size varied between the sexes but was not statistically different (males:  $\bar{x} = 584 \text{ km}^2$ ,  $n = 3$ ; females:  $\bar{x} = 319 \text{ km}^2$ ,  $n=2$ ). There was considerable spatial overlap in home ranges as neighboring collared individuals utilized high levels of shared space (female-female overlap:  $152 \text{ km}^2$ , representing 41-56% of respective home ranges; male-male overlap:  $125\text{-}434 \text{ km}^2$  shared space, representing 16-90% of respective home ranges). Lions varied space use temporally to avoid potentially costly interactions with neighboring individuals, and highest levels of overlap occurred during the wet and early dry seasons when flood waters minimized the amount of available land area.

In attempt to mitigate human-lion conflict and associated impacts, twelve predator-proof livestock enclosures (“kraals”) were constructed from locally-sourced

mophane (*Colophospermum mopane*) trees and villagers were shown how to construct the kraals for themselves. While they received strong reviews from villagers, only 66% of constructed kraals were regularly used to protect livestock overnight. Lion alert early-warning messages were dispersed throughout the villages when GPS satellite collared lions moved into areas of high livestock or human use. Collars were programmed with two “nested” electronic geofences denoting livestock grazing lands and village lands, enabling an email and text message notification to program staff who could then issue lion alert early warning to affected local stakeholders (within 5-8km of the breach location). Eighty-seven lion alerts (out of 101 geofence breaches) were dispersed to village headmen and elders and then passed throughout the community via a branching “phone tree”. The automated collar breach notification system was often delayed ( $\bar{x} = 8$  hours), inhibiting the distribution of lion alert messages. Villagers responded favorably to the lion alert program, though only 36% of surveyed farmers had actually received an alert by the end of 2016. In pre- (n = 201) and post- (n = 208) assessment interviews, 50% of farmers reported losing livestock to wild carnivores and respondents had strong negative attitudes towards lions and other carnivores in general. However, over the course of the study, villagers noted an increase in their tolerance of lions and an increase in the belief that coexistence with lions is possible. Respondents had negative attitudes towards the government-run compensation program, citing low and late payments, but were supportive of our mitigation strategies. Despite challenges encountered here, these efforts show targeted, intensive conflict management can positively impact stakeholder tolerance of carnivores, and with some updates and modifications this project can serve as a model for other systems where high levels of human-wildlife conflicts exist.

## TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS .....	vi
ABSTRACT.....	x
LIST OF TABLES .....	xvi
LIST OF FIGURES .....	xxi
CHAPTER	
1. INTRODUCTION .....	1
1.1. Introduction to Human-lion Conflict .....	1
1.2. Dissertation Format and Co-authorship.....	3
1.3. Permits, Approvals, and Funding .....	6
1.4. Literature Cited.....	7
2. LIVESTOCK DEPREDATION BY LARGE CARNIVORES IN NORTHERN BOTSWANA .....	10
2.1. Introduction.....	11
2.2. Study Area .....	15
2.3. Methods .....	16
2.4. Results.....	18
2.5. Discussion.....	21
2.6. Management Implications .....	25
2.7. Literature Cited.....	27
2.8. Tables & Figures.....	32
3. LION MOVEMENTS IN MULTI-USE AREA IN THE EASTERN PANHANDLE OF THE OKAVANGO DELTA, BOTSWANA.....	46
3.1. Introduction.....	47
3.2. Study Area .....	50
3.3. Methods .....	53
3.4. Results.....	56
3.4.1. Demographics & Monitoring.....	56
3.4.2. Home Range Size.....	56
3.4.3. Static Interactions.....	58
3.4.4. Dynamic Interactions .....	59
3.4.5. Proximity to Risk .....	62
3.5. Discussion.....	63
3.6. Literature Cited.....	66
3.7. Tables & Figures.....	72

4. LION ALERTS: STRATEGIES FOR MITIGATING HUMAN-LION CONFLICTS IN NORTHERN BOTSWANA .....	110
4.1. Introduction.....	112
4.2. Study Area .....	115
4.3. Methods .....	118
4.4. Results.....	121
4.5. Discussion.....	123
4.6. Literature Cited.....	128
4.7. Tables & Figures.....	132
5. HUMAN DIMENSIONS OF HUMAN-LION CONFLICT: A PRE- AND POST- ASSESSMENT OF A LION CONSERVATION PROGRAMME IN THE OKAVANGO DELTA, BOTSWANA.....	140
5.1. Introduction.....	141
5.2. Study Area .....	144
5.3. Methods .....	145
5.4. Results .....	147
5.4.1. Respondent Demographics .....	147
5.4.2. Perceptions of Wildlife, Conservation, and National Parks .....	148
5.4.3. Livestock Husbandry .....	150
5.4.4. Tolerance/Approval Scores.....	152
5.4.5. Perceptions of Conflict Mitigation Program.....	153
5.5. Discussion.....	154
5.5.1. Livestock Husbandry and Losses.....	154
5.5.2. Attitudes Towards Carnivores .....	156
5.5.3. Conflict Mitigation Program Efficacy .....	157
5.6. Conclusion .....	159
5.7. Literature Cited.....	160
5.8. Tables & Figures.....	166
6. CONCLUSION: THE FUTURE OF LION CONSERVATION IN AFRICA.....	171
6.1. Dissertation Summary .....	171
6.2. Future Directions .....	174
6.3. Literature Cited.....	178

## APPENDICES

A. CHAPTER 5 SUPPLEMENTAL MATERIALS .....	180
B. PRIDE IN OUR PRIDES INITIAL VILLAGER QUESTIONNAIRE .....	188
C. PRIDE IN OUR PRIDES FOLLOW-UP VILLAGER QUESTIONNAIRE.....	199
D. REVIEW OF LION EVOLUTION AND CONSERVATION GENETICS.....	206

BIBLIOGRAPHY.....231

## LIST OF TABLES

Table	Page
2.1. Percent (no. of events in parentheses) of Problem Animal Control (PAC) incidents by species reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana. ....	32
2.2. Percent (no. of events in parentheses) of Problem Animal Control (PAC) incidents by village reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana. ....	33
2.3. Percent of livestock lost (no. of livestock lost in parentheses) in all Problem Animal Control (PAC) incidents reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana (609 individual livestock were reported lost in 588 events). ....	34
2.4. Average livestock valuation from farmers (n=86) who lost livestock between October 2014 and December 2016 and the Botswanan government livestock compensation rates in U.S. dollars (USD) and Botswanan pula (BWP). ....	35
2.5. Government valuation (in USD) of livestock lost in all Problem Animal Control (PAC) incidents reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana. 609 individual livestock were reported lost in 588 events. ....	36
2.6. Percent (no. of incidents) of investigated depredation events that occurred at livestock kraals vs. in the veld attributed to each responsible carnivore species in the lion conflict study area in northern Botswana, October 2014-December 2016. ....	37
2.7. Confirmed total number (T) of individual livestock killed and injured (K/I) by predators from 102 investigated depredation events in the lion conflict study area in northern Botswana between October 2014 and December 2016. ....	38
2.8. Government valuation (in USD) of livestock killed by predators in 102 investigated depredation events in the lion conflict study area in northern Botswana during October 2014 to December 2016. ....	39
2.9. Investigated depredation events (n=102) from each village with associated attributes and management actions in the lion conflict study area in northern Botswana between October 2014 and December 2016. ....	40
3.1. Lion prides monitored in the northern Botswana study area from October-December 2014. ....	72

3.2. Lion prides monitored on the northern Botswana study area from January-December 2015. ....	73
3.3. Lion prides monitored in the northern Botswana study area from January-December 2016. ....	74
3.4. GPS satellite collar data for 5 collared lions in the northern Botswana study area between August 2015 and December 2016. ....	76
3.5. Seasonal 95% lion home range size estimates based on kernel density estimation ( <i>href</i> ) methods for 5 collared lions in the northern Botswana study area between August 2015 and December 2016. ....	77
3.6. Seasonal 50% lion home range size estimates based on kernel density estimation ( <i>href</i> ) methods for 5 collared lions in the northern Botswana study area between August 2015 and December 2016. ....	78
3.7. During the entire study period (Aug 2015-Dec 2016), 95% core home range estimates, and percent overlap (area of overlap), based on kernel density estimation ( <i>href</i> ) for simultaneously collared lions in the northern Botswana. Percent overlap with home range corresponds to the lions on top of contingency table. Lions that were not collared during the same timeframe and thus had no record of overlap are noted as “NR.” ....	79
3.8. During the entire study period (Aug 2015-Dec 2016), 50% core home range estimates, and percent overlap (area of overlap), based on kernel density estimation ( <i>href</i> ) for simultaneously collared lions in the northern Botswana. Percent overlap with home range corresponds to the lions on top of contingency table. Lions that were not collared during the same timeframe and thus had no record of overlap are noted as “NR.” ....	80
3.9. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation ( <i>href</i> ) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2015-Dec 2015. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table. ....	81
3.10. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation ( <i>href</i> ) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2015-Dec 2015. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table. ....	82
3.11. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation ( <i>href</i> ) for simultaneously collared lions in the northern Botswana study area during the wet season Jan 2016-Mar 2016. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table. ....	83

3.12. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the wet season Jan 2016-Mar 2016. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table. ....	84
3.13. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the early dry season Apr 2016-Jul 2016. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table.....	85
3.14. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the early dry season Apr 2016-Jul 2016. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table. ....	86
3.15. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2016-Dec 2016. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table.....	87
3.16. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2016-Dec 2016. Home ranges and overlap values presented in parentheses shown in km <sup>2</sup> , percent overlap with full home range extent corresponds to the lions on top of contingency table. ....	88
3.17. 95% contour Utilization Distribution Overlap Index (UDOI) for lion dyads having static interaction during the study. UDOI is a metric of static interaction that is a function of the product of the two individual's utilization distributions (UD). UDOI equals 0 when two home ranges do not overlap and 1 if two UD's are uniformly distributed with 100% overlap. Values >1 can occur if two UD's are nonuniformly distributed but have a high degree of overlap. Dyads without concurrent data noted as "NR.".....	89
3.18. 50% contour Utilization Distribution Overlap Index (UDOI) for lion dyads having static interaction over the course of the study. UDOI is a metric of static interaction that is a function of the product of the two individual's utilization distributions (UD). UDOI equals 0 when two home ranges do not overlap and 1 if two UD's are uniformly distributed with 100% overlap. Values >1 can occur if two UD's are nonuniformly distributed but have a high degree of overlap. Dyads without concurrent data noted as "NR." .....	91

- 3.19. Coefficients of association (Ca) for lion dyads having static interaction during the late dry season 2015 (top of contingency table) and wet season 2016 (bottom). Ca is a metric of dynamic interaction generated from the relationship between the number of relocations for both individuals within specified time/distance thresholds and the sum of n relocations for both individuals. Coefficients range from 0 to 1 with strong associations generally considered as >0.5 and weaker/no associations as <0.5. Individuals without relocations for the specified time period noted with “NR.” .....93
- 3.20. Coefficients of association (Ca) for lion dyads having static interaction during the early dry season 2016 (top of contingency table) and late dry season 2016 (bottom). Ca is a metric of dynamic interaction generated from the relationship between the number of relocations for both individuals within specified time/distance thresholds and the sum of n relocations for both individuals. Coefficients range from 0 to 1 with strong associations generally considered as >0.5 and weaker/no associations as <0.5. Individuals without relocations for the specified time period noted with “NR.” .....94
- 3.21. Lion proximity to human habitation across seasons (All = all relocations, LD15 = Late dry season 2015, W16 = Wet season 2016, ED16 = Early dry season 2016, LD16 = Late dry season 2016). Percentage (PCT) of individual lion’s relocations within 3 km of human habitation, median (Mdn) distance of all relocations to nearest point that is within 3 km of human habitation, and standard deviation (SD) of each lion’s distances to nearest point that is within 3 km of human habitation for the given season. ....95
- 3.22. Lion proximity to cattle grazing areas across seasons (Wet, Early Dry, and Late Dry). Percentage (PCT) of individual lion’s relocations within cattle grazing areas, median (Mdn) distance of all relocations to nearest cattle grazing area, and standard deviation (SD) of each lion’s distances to nearest cattle grazing area for the given season. ....96
- 4.1. Cattle posts listed for each village (with posts that received mophane kraals bolded) in the northern Botswana study area and lion alert messages sent to each village between August 2015 and December 2016. \*Matswii 2 received both a square and round kraal. ....132
- 4.2. GPS satellite collar data for 5 collared lions and associated number of independent geofence breaches and lion alerts sent in the northern Botswana study area between August 2015 and December 2016. The average duration (in hours) and standard deviation for each lion’s geofence breaches shown in parentheses ( $\bar{x}$ ,  $\sigma$ ). \*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition. ....133
- 5.1. Percent “yes” responses (no. of respondents in parentheses) to questions of conservation importance from initial surveys in 2014 (Village Center “VC” n=100, Cattle Post “CP” n=101, total n=201) and follow-up surveys in 2016 (VC n=111, CP n=97, total n=208) by location with associated  $\chi^2$  tests for homogeneity. Follow-up surveys also included questions regarding the established management interventions. Total percent “yes” responses (number of respondents in parentheses) and associated  $\chi^2$  goodness of fit tests also shown. Significant *p*-values denoted with an “\*.” .....166

- 5.2. Comparison by  $\chi^2$  tests for homogeneity for key questions involving wildlife, conservation, and livestock management from initial surveys in 2014 and follow-up surveys in 2016. Percent of respondents who answered “yes” shown (number of respondents in parentheses). All respondents answered questions about wildlife and conservation (2014 n=201, 2016 n=208) while only livestock owners answered questions about livestock management (2014 n=143, 2016 n=171). Significant *p*-values denoted with an “\*.” .....168
- 5.3. Mean tolerance/approval scores by location (village center “VC” and cattle post “CP”) for initial and follow-up surveys along with associated *t*-statistic. Further comparison by *t*-statistic of total mean tolerance scores between initial and follow-up surveys also shown. Significant *p*-values denoted with an “\*.” .....169

## LIST OF FIGURES

Figure	Page
2.1. Lion conflict study area in northern Botswana with locations of associated villages and connecting road, cattle posts, and lodges, and Wildlife Management Area boundaries. ....	41
2.2. Traditional kraal structures in northern Botswana. A: thorn branch style construction, B: thick wooden branch construction. Photos by E. LeFlore. ....	42
2.3. Number of problem animal control (PAC) reports filed with the Department of Wildlife and National Parks (DWNP) between 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana. * indicates an incomplete year of data. ....	43
2.4. Distribution of investigated depredation events documented in the lion conflict study area in northern Botswana during October 2014-December 2016. ....	44
2.5. Investigated depredation event hotspots in the lion conflict study area in northern Botswana during October 2014-December 2016 based on optimized hot spot analysis conducted in ArcGIS. ....	45
3.1. Map of the northern Botswana study area showing villages, cattle posts, safari lodges, government-defined management area (NG = Ngamiland) boundaries, and high risk areas for lions where they may encounter people or livestock. A: High human traffic areas (within 3 km of human habitation); B: Cattle grazing area during the wet season; C: Cattle grazing area during the early dry season; D: Cattle grazing area during the late dry season. Cattle grazing areas estimated based on field observations, expert elicitation, and data presented in Weise et al. (2019).....	97
3.2. All locations for collared lions in the northern Botswana study area between August 2015 and December 2016. A: Female 1 (Airstrip Pride); B: Female 2 (Cut-tail Pride); C: Male 1 (Xakampa Coalition); D: Male 2 (Airstrip Coalition); E: Male 3 (Xamaga Coalition). ....	98
3.3. All locations and 50% and 95% contours from kernel density estimation (href) for collared lions in the northern Botswana study area between August 2015 and December 2016. A: Female 1 (Airstrip Pride); B: Female 2 (Cut-tail Pride); C: Male 1 (Xakampa Coalition); D: Male 2 (Airstrip Coalition); E: Male 3 (Xamaga Coalition).....	99
3.4. 50% and 95% contours from kernel density estimation (href) for collared lions in the northern Botswana study area between August 2015 and December 2016. A: Female 1 (Airstrip Pride); B: Female 2 (Cut-tail Pride); C: Male 1 (Xakampa Coalition); D: Male 2 (Airstrip Coalition); E: Male 3 (Xamaga Coalition). ....	100

- 3.5. 50% and 95% contours from kernel density estimation (href) for collared female and male lions with unmarked individual sightings in the northern Botswana study area between August 2015 and December 2016. A: Females 50% (Female 1 - Airstrip Pride, Female 2 - Cut-tail Pride); B: Females 95% (Female 1 - Airstrip Pride, Female 2 - Cut-tail Pride); C: Males 50% (Male 1 - Xakampa Coalition, Male 2 - Airstrip Coalition, Male 3 - Xamaga Coalition). D: Males 95% (Male 1 - Xakampa Coalition, Male 2 - Airstrip Coalition, Male 3 - Xamaga Coalition). .....101
- 3.6. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2015. A: dyad 1 = Female 1(Airstrip Pride) : Male 1 (Xakampa Coalition); B: dyad 2 = F1(Airstrip Pride) : M2 (Airstrip Coalition); C: dyad 3 = F1 (Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : M1 (Xakampa Coalition); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : M1 (Xakampa Coalition). .....102
- 3.7. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2015. A: dyad 1 = Female 1(Airstrip Pride) : Male 1 (Xakampa Coalition); B: dyad 2 = F1(Airstrip Pride) : M2 (Airstrip Coalition); C: dyad 3 = F1 (Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : M1 (Xakampa Coalition); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : M1 (Xakampa Coalition). .....103
- 3.8. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the wet season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride). .....104
- 3.9. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the wet season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride). .....105
- 3.10. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the early dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride). .....106

3.11. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the early dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).....	107
3.12. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).....	108
3.13. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).....	109
4.1. Map of the lion conflict study area in northern Botswana as well as locations of PiOP sponsored predator-proof kraals (livestock enclosures) and lion alert electronic geofence boundaries in the lion conflict study area in northern Botswana. ....	134
4.2. Traditional kraal structures in northern Botswana. Top: thorn branch style construction, Bottom: thick wooden branch construction.....	135
4.3. Pride in Our Prides newly constructed predator-proof kraals in the lion conflict study area in northern Botswana. Top: Rectangular woven mophane branch kraal. Bottom: Portion of circular stacked mophane trunk kraal. ....	136
4.4. Male lion 95% kernel density estimation home ranges in the lion conflict study area in northern Botswana and lion alert electronic geofence boundaries in the lion conflict study area in northern Botswana. ....	137
4.5. Female lioness 95% kernel density estimation home ranges in the lion conflict study area in northern Botswana and lion alert electronic geofence boundaries in the lion conflict study area in northern Botswana. ....	138
4.6. Number of geofence breaches by month over the course of the human-lion conflict study in northern Botswana. ....	139
5.1. Study area map showing villages, cattle posts, safari lodges, and concession boundaries.....	170

# CHAPTER 1

## INTRODUCTION

### 1.1. Introduction to Human-lion Conflict

Wild carnivores and people have tenuously coexisted for millennia, but over recent decades these interactions have turned to consistent conflicts resulting in negative impacts on both people and carnivores (Woodroffe 2000, Ripple et al. 2014, van Eeden et al. 2018). Large carnivores are often no longer tolerated by humans as they frequently kill livestock and occasionally kill people (Woodroffe 2000, van Eeden et al. 2018). People often lethally remove livestock raiding carnivores in retaliatory and pre-emptive killings (Woodroffe and Frank 2005), and these killings are now the primary threat to large carnivores worldwide (Woodroffe 2001, Woodroffe et al. 2007, Ripple et al. 2014). Because of these killings, populations of large carnivores are declining, and their ranges are contracting (Dickman et al. 2011, Ripple et al. 2014).

The African lion (*Panthera leo*) is a particularly acute example of this phenomenon as the species has been extirpated from approximately >80% of its historical range and is now found predominantly inside protected areas (Riggio et al. 2013). Lion populations continue to decline and only ~20,000 individuals remain on the continent, a drop of >90% based on estimates from the last ~50 years (Myers 1975, Nowell and Jackson 1996, Chardonnet 2002, Bauer and Van der Merwe 2004, Riggio et al. 2013, Bauer et al. 2015). Declines in lion populations are often directly related to conflicts over livestock (Loveridge et al. 2010). Therefore, addressing human-carnivore conflicts is critical for the successful conservation of the species.

While it is easy to focus on the declining lion population, the people living among lions are dealing with the costs and impacts associated with this conflict (Nyhus et al. 2005) and must not be overlooked. Human-lion conflicts are inherently complex (Dickman 2010) as people's attitudes and behaviors toward lions are based on a variety of factors (e.g., livestock losses, perceived threat of losses, community standing, emotional value of livestock, perceptions of wildlife conservation and ecotourism, etc.; Mishra 1997, Loveridge 2005, Naughton-Treves & Treves 2005, Mbaiwa et al. 2008, Dickman 2009). Local stakeholders, who bear the costs of living among lions, must be directly involved in the development and implementation of any conservation management plan.

Despite a plethora of research and applied conservation programs (Hazzah et al. 2014, Trinkel and Angelici 2016, van Eeden et al. 2018), widespread human-lion coexistence has yet to be realized (Bauer et al. 2015). The Okavango Delta of northern Botswana is home to one of the last remaining lion population strongholds and is an area of critical importance for lion conservation (Riggio et al. 2013, Funston 2014). The eastern panhandle of the Delta boasts some of the most sought-after wildlife game viewing in all of Africa and is also home to several agropastoralist communities (~5,000 people; Botswana Population and Housing Census 2011) and their livestock (~16,000 individuals; Weise et al. 2019). This sets the stage for potentially high levels of human-lion conflict. Following the high levels of conflict experienced in 2013, where numerous livestock were lost and ~30-50% of the local lion population were killed by villagers (Mweze 2014, pers. comm.), we initiated an assessment of human-lion conflict and established conflict mitigation strategies in the eastern panhandle of the Okavango Delta.

We developed a multilevel approach to address lion conservation and minimize human-lion conflicts designed specifically for rural Botswana that focused on the needs of the local people (i.e., to protect their livestock) as a way to protect biodiversity. If livestock are more protected and people become more tolerant of predators, the need to kill carnivores to protect their herds should be diminished (Ogada et al. 2003, Lichtenfeld et al. 2015). Through the establishment of a community-based conservation program (Pride in Our Prides), we investigated livestock losses to wild carnivores (Chapter 2, this document; LeFlore et al. 2019), monitored the local lion population (Chapter 3, this document), established conflict mitigation strategies including a locally sourced livestock enclosure building program and an early-warning system linked to lion GPS satellite collars to assist in fortifying livestock husbandry in the area (Chapter 4, this document; Weise et al. 2018, Weise et al. 2019), assessed local stakeholder's perceptions of lions and the associated conflict as well as their perceptions of the established conflict mitigation program (Chapter 5, this document; LeFlore et al. 2020),

## **1.2. Dissertation Format and Co-authorship**

The six chapters in this dissertation contain three body chapters (Ch. 2, 4, and 5) written in manuscript format for journal submission and one (Ch. 3) written in dissertation chapter format. These chapters are at various stages in the publication process in peer-reviewed journals, with chapters 2 and 5 already published, and chapter 3 and 4 to be submitted in the coming months after adapted and tailored to the appropriate journal. Although there are several co-authors for each of the four chapters, this dissertation represents my doctoral research. Below I list the contributions of all authors by chapter title.

## **Chapter 2**

LeFlore, E.G., T.K. Fuller, M. Tomeletso, and A.B Stein. 2019. Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation* 18:e00592. <https://doi.org/10.1016/j.gecco.2019.e00592>

I designed this study, conducted data collection, analysis, and manuscript preparation, and secured funding for the research. Fuller contributed to study design and conception, project oversight, and assisted with manuscript preparation. Tomeletso contributed to data collection. Stein contributed to study design and conception, secured funding for the research, provided oversight, and assisted with manuscript preparation.

## **Chapter 3**

Lion Movements in Multi-use Area in the Eastern Panhandle of the Okavango Delta, Botswana

Proposed authorship:

Eric G. LeFlore, Todd K. Fuller, Mathata Tomeletso, Frederick J. Verreynne, Peter W. Houlihan, Andrew B. Stein

I designed this study, conducted data collection, analysis, and manuscript preparation, and secured funding for the research. Fuller contributed to study design and conception, project oversight, and assisted with manuscript preparation. Tomeletso contributed to data collection. Verreynne assisted with data collection and study design. Houlihan contributed to study design and manuscript preparation. Stein contributed to study design

and conception, secured funding for the research, provided oversight, and assisted with manuscript preparation.

#### **Chapter 4**

Lion Alerts: Strategies for Mitigating Human-Lion Conflicts in Northern Botswana

Proposed authorship:

Eric G. LeFlore, Todd K. Fuller, Mathata Tomeletso, Andrew B. Stein

I designed this study, conducted data collection, analysis, and manuscript preparation, and secured funding for the research. Fuller contributed to study design and conception, project oversight, and assisted with manuscript preparation. Tomeletso contributed to data collection. Stein contributed to study design and conception, secured funding for the research, provided oversight, and assisted with manuscript preparation.

#### **Chapter 5**

LeFlore E.G., T.K. Fuller, M. Tomeletso, T.C. Dimbindo, and A.B Stein. 2020. Human dimensions of human–lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana. *Environmental Conservation* 47:182-189. <https://doi.org/10.1017/S0376892920000120>

I designed this study, conducted data collection, analysis, and manuscript preparation, and secured funding for the research. Fuller contributed to study design and conception, project oversight, and assisted with manuscript preparation. Tomeletso and Dimbindo contributed to data collection. Stein contributed to study design and conception, secured funding for the research, provided oversight, and assisted with manuscript preparation.

### **1.3.Permits, Approvals, and Funding**

This research was conducted with the approval of the Botswana Ministry of Environment, Wildlife, and Tourism (MEWT) and the Department of Wildlife and National Parks (DWNP) under research permit number: EWT 8/36/4 XXVII (61). Lion radio collars were deployed with government approval under supplemental darting permit numbers WP/RES 15/2/2 XXVII (22) & WP/RES 15/2/2 XXVII (141). Vertebrate field research was approved through University of Massachusetts (UMass) Amherst Institutional Animal Care and Use Committee (Protocol #2014-0083) and human subject questionnaire surveys were approved through UMass Amherst Institutional Review Board (Protocol ID: 2019-5619).

This research was funded by National Geographic's Big Cats Initiative (grant numbers: B5-15 and B10-16), a J.W. Fulbright Research Scholarship, a UMass Amherst Northeast Alliance for Graduate Education and the Professoriate Fellowship, a UMass Amherst Graduate School Dissertation Research Grant, and the Mellon Mays Graduate Initiative through the Social Science Research Council.

#### 1.4. Literature Cited

- Bauer, H. and S. Van der Merwe. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38:26–31.
- Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. Hunter, D. 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.
- Botswana Population and Housing Census. 2011. URL [www.catalog.ihnsn.org/index.php/catalog/4243/download/55990](http://www.catalog.ihnsn.org/index.php/catalog/4243/download/55990). Accessed on October 15, 2015.
- Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA, Paris, France.
- Dickman, A.J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict: *Animal Conservation* 13: 458–466.
- Dickman, A.J. 2009. Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania. Ph.D. Thesis, University College London, London, United Kingdom.
- Funston, P. 2014. The Kavango-Zambezi Transfrontier Conservation Area – critical for African lions. *Cat News* 60: 4-7.
- Hazzah, L., S. Dolrenry, L. Naughton, C.T.T. Edwards, O. Mwebi, F. Kearney, and L. Frank. 2014. Efficacy of Two Lion Conservation Programs in Maasailand, Kenya. *Conservation Biology* 28: 851-860.
- LeFlore E.G., T.K. Fuller, M. Tomeletso, T.C. Dimbindo, and A.B Stein. 2020. Human dimensions of human–lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana. *Environmental Conservation* 47:182-189.
- LeFlore, E.G., T.K. Fuller, M. Tomeletso, and A.B. Stein. 2019. Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation* 18: e00592.
- Lichtenfeld, L.L., C. Trout, and E.L. Kisimir. 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodivers Conserv* 24: 483-491.
- Loveridge, A.J. 2005. Conflict synthesis. In *Lion Conservation Research: From Conflict to Socioecology*. Workshop 3 & 4, eds A.J. Loveridge, T. Lynam, and D.W. Macdonald, Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.

- Loveridge, A.J., Hemson, G., Davidson, Z. & Macdonald, D.W. (2010) African lions on the edge: reserve boundaries as ‘attractive sinks’. *In* *Biology and Conservation of Wild Felids*, pp. 283–304. eds D.W. Macdonald and A.J. Loveridge. Oxford University Press, Oxford, United Kingdom.
- Mbaiwa, J.E., B.N. Ngwenya, and D.L. Kgathi. 2008. Contending with unequal and privileged access to natural resources and land in the Okavango Delta, Botswana. *Singapore Journal of Tropical Geography* 29: 155-172.
- Mishra, C. 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24: 338-343.
- Mweze, M. 2014. Botswana Department of Wildlife and National Parks. Personal Communication. October 2014, Seronga, Ngamiland, Botswana.
- Myers, N. 1975. The silent savannahs. *International Wildlife* 5: 5–10.
- Naughton-Treves, L. and A. Treves. 2005. Socio-ecological factors shaping local support for wildlife: crop raiding by elephants and other wildlife in Africa. *In* *People and Wildlife: Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 252-277. Cambridge, UK: Cambridge University Press.
- Nowell, K. and P. Jackson. 1996. *Wild Cats: Status Survey and Conservation Action Plan*. World Conservation Union, Gland, Switzerland 5577.
- Nyhus, P.J., S.A. Osofsky, P. Ferraro, F. Madden, and H. Fischer. 2005. Bearing the cost of human-wildlife conflict: the challenges of compensation schemes In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 107–121. Cambridge University Press, Cambridge, UK.
- Ogada, M.O., R. Woodroffe, N.O. Oguge, and L.G. Frank. 2003. Limiting Depredation by African Carnivores: the Role of Livestock Husbandry. *Conservation Biology* 17: 1-10.
- Riggio, J., A. Jacobson, L. Dollar, H. Bauer, A. Dickman, P. Funston, P. Henschel, H. de Iongh, L. Lichtenfeld, C. Packer, and S. Pimm. 2013. The size of savannah Africa: a lion’s view. *Biodiversity and Conservation* 22:17–35.
- Trinkel, M., and F.M. Angelici. 2016. The decline in the lion population in africa and possible mitigation measures. *In* *Problematic Wildlife*, pp. 45–68. ed F. M. Angelici. Springer International Publishing, Switzerland.
- van Eeden, L. M., A. Eklund, J.R.B. Miller, J.V. López-Bao, G. Chapron, M.R. Cejtin, et al. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16: e2005577.

- van Eeden, L.M., A. Eklund, J.R.B. Miller, J.V. López, G. Chapron, M.R. Cejtin, M.S. Crowther, C.R. Dickman, J. Frank, M. Kropfel, D.W. Macdonald, J. McManus, T.K. Meyer, A.D. Middleton, T.M. Newsome, W.J. Ripple, E.G. Ritchie, O.J. Schmitz, K.J. Stoner, M. Tourani, and A. Treves. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16(9): e2005577.
- Weise, F. J., M.W. Hayward, R. Casillas Aguirre, M. Tomeletso, P Gadimang, M.J. Somers, et al. 2018. Size, shape and maintenance matter: a critical appraisal of a global carnivore conflict mitigation strategy – livestock protection kraals in northern Botswana. *Biological Conservation* 225: 88–97.
- Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. Lions at the Gates: Transdisciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution* 6: 242.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165–173.
- Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. *In Carnivore Conservation*. pp. 61–92. eds J.L. Gittleman, S. Funk, D.W. Macdonald, and R.K. Wayne. Cambridge University Press, Cambridge, United Kingdom.
- Woodroffe, R. and L.G. Frank. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* 8: 91-98.
- Woodroffe, R., L.G. Frank, P.A. Lindsey, S.M.K ole Ranah, S. Romañach. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity Conservation* 16:1245–1260.

**CHAPTER 2**

**LIVESTOCK DEPREDATION BY LARGE CARNIVORES IN NORTHERN  
BOTSWANA**

**Abstract.** Human-carnivore conflict is a leading cause of large carnivore declines and minimizing these conflicts is vital to maintaining viable carnivore populations. Often, however, conservation agencies and governments do not have a proper understanding of conflicts prior to establishing mitigation programs or are unable to collect the appropriate data to verify claims of livestock loss. We investigated livestock depredation events in the Eastern Panhandle of the Okavango Delta, Botswana between October 2014 and December 2016 and compared these investigations with concurrent Problem Animal Control (PAC) information from the Botswana Department of Wildlife and National Parks (DWNP) compensation program. Only animals killed in livestock enclosures or while being herded qualify for reimbursement through the compensation program, but DWNP is typically unable to verify claims. We identified wildlife sign at the depredation event location and collected information from the livestock owner to determine the species responsible for the attack, time of the attack, the livestock lost, and the husbandry methods employed. In total, 116 livestock were killed and 13 more injured in 102 confirmed wild carnivore attacks. Most (90%) attacks occurred while livestock were unattended and freely grazing in multi-use, communal areas. Cows, oxen (castrated male cows) and calves (*Bos taurus* and *B. t. indicus*) were killed most often and African lions (*Panthera leo*) were responsible for 74% of investigated attacks, while African wild dogs (*Lycaon pictus*) accounted for 13%, leopard (*Panthera pardus*) 8%, and spotted hyena

(*Crocuta crocuta*) 5%. Valuation of verified losses totaled ~\$30,000 over the study period. There were 50% more events reported to DWNP for compensation than we confirmed through independent investigations. In its current form, the compensation program does not seem sustainable, nor does it enable the verification of claims. While such programs should not be abandoned, compensation programs designed to provide monetary resources for losses caused by predators should require timely reporting and in-depth investigation of depredation events. Additional conflict mitigation strategies should target increasing livestock husbandry methods in the area, with a specific focus on herding.

## **2.1. Introduction**

People and predators have tenuously coexisted for millennia, but over recent decades the level of conflict has increased due to rising human populations and changes in human activities (Woodroffe 2000, Conover 2002, Graham et al. 2005, Madden and McQuinn 2014). Large carnivores are typically no longer tolerated by humans as they frequently kill livestock and occasionally kill people (Woodroffe 2000, van Eeden et al. 2018). Predators are often killed in retaliation, and these killings are the primary threat to large carnivores worldwide (Woodroffe 2001, Woodroffe et al. 2007). Because of this, populations of these species are declining and their ranges are contracting (Dickman et al. 2011). The removal of large carnivores can have major cascading impacts on ecological communities, destabilizing ecosystems and their food webs (Ripple et al. 2014, Newsome et al. 2017). In addition to their ecological importance, large carnivores are extremely valuable as a source of monetary income from ecotourism, however local communities bear the considerable costs of living with these predators (Macdonald et al. 2010). The

impact of livestock depredation where carnivore distributions overlap with farming practices can have a negative effect on local farmers, causing loss of income and food while also adversely impacting rural development (Treves and Karanth 2003, Graham et al. 2005, Woodroffe et al. 2007, Thorn et al. 2013). Given that retaliatory killings are a major threat to large carnivores, mitigating human-carnivore conflict (HCC) is vital to achieving successful carnivore conservation; however, this requires site-specific management based on both biological and social data (Treves and Karanth 2003, Inskip and Zimmerman 2009).

HCC has increasingly been studied around the globe in an attempt to better understand the drivers of conflict and enable coexistence with large carnivores (e.g., Palmeira et al. 2008, Aryal et al. 2014, Ohrens et al. 2015, Singh et al. 2015). In a literature review focused on the conservation of African carnivores, Winterbach et al. (2013) identified a number of ecological (e.g., livestock predation), socioeconomic (e.g., people's attitudes towards carnivores), and political (e.g., conservation policy development and implementation) factors as key drivers of large carnivore conservation. Researchers, governments, and conservation agencies have made a concerted effort to study and establish conflict mitigation strategies that target these drivers, which include but are not limited to evaluations of livestock predation (e.g., Lichtenfeld et al. 2015, Weise et al. 2018), people's attitudes towards carnivores (e.g., Hemson et al. 2009, Thorn et al. 2012), and conservation policy development and implementation (e.g., Dickman et al. 2011, Mossaz et al. 2015, Ravenelle and Nyhus 2017). Despite these and numerous other studies, there is no consensus as to the most effective conflict mitigation

interventions (Eklund et al. 2017). Therefore, site-specific factors should direct mitigation strategies (Treves and Karanth 2003, Inskip and Zimmerman 2009).

Governments try to reduce conflicts and alleviate the financial burden for farmers who lose livestock to predators through compensation programs, but often factors impacting those losses are not well understood (Mabille et al. 2015). In an attempt to facilitate human-carnivore coexistence, the Botswanan government established a compensation program under the purview of the Department of Wildlife and National Parks (DWNP; DWNP 1998). The program was overhauled in 2013, increasing reimbursement levels to 100% of averaged market value for losses to African lions (*Panthera leo*) and 35% for losses to other species of conservation concern, i.e., African wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*), and leopards (*Panthera pardus*; DWNP 2013). While the program is only supposed to reimburse losses for animals killed in livestock enclosures or while being herded, DWNP officials are typically not able to verify claims of livestock depredation due to limited resources, which results in false claims being paid out. Implementing conflict mitigation strategies without proper understanding of the system and levels of conflict can result in wasted resources and can even have negative overall effects on wildlife conservation and attitudes towards wildlife (Graham et al. 2005, Nyhus et al. 2005).

Here we assess the level of HCC in the eastern Panhandle of the Okavango Delta, Botswana to help inform conflict mitigation strategies. According to DWNP, 30-50% of the local lion population was removed by villagers as a result of targeted killings and indiscriminate poisoning events in response to high numbers of livestock losses in 2013 (Mweze 2014, pers. comm.). The lion is often responsible for livestock losses and, as a

result, killed in retaliation (Ikanda and Packer 2008, Hazzah et al. 2009, Hemson et al. 2009). HCC is the leading cause of lion population declines across the continent (Woodroffe 2001) and lions have been extirpated from over 80% of their historic range (Riggio et al. 2013). Lion populations throughout Africa are vanishing quickly with current estimates hovering around 20,000 individuals (Chardonnet 2002, Bauer and Van der Merwe 2004, Riggio et al. 2013, Bauer et al. 2015, Bauer et al. 2016). Human-lion conflict mitigation is a high priority for the species' long-term persistence (Woodroffe 2001), and more secure livestock husbandry practices, e.g., predator-proof livestock enclosures and sound herding practices (Ogada et al. 2003, Lichtenfeld et al. 2015), have proven effective at decreasing conflicts with lions and other predators (Breitenmoser et al. 2005, Woodroffe et al. 2007).

Following the high levels of conflict experienced in 2013, we initiated an assessment of HCC and established conflict mitigation strategies in the eastern Panhandle. Our aim was to independently assess the levels of livestock depredation and compare those records to DWNP Problem Animal Control (PAC) data. The PAC data are the basis for the national compensation program that aims to minimize conflicts by reimbursing villagers for losses incurred from predators. We hypothesized that there would be more depredation (PAC) events reported to DWNP than we identified through independent investigations as our program was new to the community and DWNP runs the compensation program. Additionally, we predicted that lions and spotted hyenas would be responsible for the highest percentage of livestock loss in the area (Ogada et al. 2003, Kolowski and Holekamp 2006, Mponzi et al. 2014). We predicted that villagers filed false depredation reports blaming lions when spotted hyenas (*Crocuta crocuta*) were

responsible for losses to receive compensation. As such, lions would be named in a larger percentage of the PAC reports to DWNP compared to our independent investigations. For our independent depredation investigations, we hypothesized that most depredation events would happen in the veld as opposed to the village due to a very limited herding culture in the area.

## **2.2. Study Area**

This study was conducted in the eastern panhandle of the Okavango Delta of northern Botswana (between  $-18.986419^{\circ}$ ,  $22.449220^{\circ}$  and  $-18.563485^{\circ}$ ,  $22.936769^{\circ}$ ; Fig. 2.1) and lies within a portion of the Kavango-Zambezi Transfrontier Conservation Area (KAZA) which has been identified as an area of critical importance for lion conservation (Funston 2014). The Okavango Delta is within the northern portion of the Kalahari Desert and is a freshwater alluvial system that supports one of southern Africa's most sought-after wildlife tourism regions. Large carnivores found in the area include the African lion, leopard, cheetah, spotted hyaena, and African wild dog.

Our research efforts encompassed portions of government defined wildlife management areas (WMAs) NG 11, NG 12, NG 22, NG 23, and NG 23A (Ngamiland) which are gazetted as multiuse areas, including human habitation, conservation, and photographic tourism areas (Fig. 2.1). NGs 11 and 12 are multiuse WMAs where people live, farm and utilize natural resources. NG 22 is designated as a community-run wildlife conservation area, while NGs 23 and 23A are leased to ecotourism companies for photographic tourism. In NGs 11 and 12 east of Seronga, people are concentrated in four villages (Beetsha, Eretsha, Gudigwa, and Gunotsoga) and in smaller familial settlements called cattle posts. Village populations, including the people living at associated cattle

posts, range from approximately 700-1600 people (Botswana Population and Housing Census 2011). The local villagers are subsistence farmers who keep livestock (cattle, *Bos taurus/indicus*; goat, *Capra hircus*; horse, *Equus caballus*; and donkey *Equus asinus*) and grow crops. Average herd size in the area is approximately 12 individuals per farmer (LeFlore, unpublished data). Livestock are typically protected overnight in thorn branch enclosures or thick, wooden branch enclosures, referred to locally as “kraals” (Fig. 2.2). Historically, there was a strong herding culture, but, as herd boys are now going to school and moving to more developed areas, these herding practices have been largely abandoned.

In conjunction with our conflict investigations described in this manuscript, we established a range of conflict mitigation strategies. We developed an early warning system linked to lion GPS satellite collars and issued “lion alerts” to villagers via a “telephone tree” when collared individuals moved into areas where livestock typically graze and within ~5-8km of villages (see Weise et al. 2019). Additionally, we built 12 predator-proof kraals at cattle posts with historically high levels of conflict (see Weise et al. 2018, Chapter 4 this document). We employed five local villagers to help with these efforts and worked closely with community members and leadership. We also regularly led educational sessions in the villages and at local schools to share project updates and information about local lion prides.

### **2.3. Methods**

Problem Animal Control (PAC) data were collected from the Department of Wildlife and National Parks’ (DWNP) Seronga office between October 2014 and December 2016; years of inquiry were 2009-2016. These data were extracted from

DWNP documents where villagers reported their livestock losses to DWNP, the police, and/or wildlife volunteers. The reports contained information such as: date of incident, village, cattle post (when applicable), species responsible, and number and species of livestock lost. These reports were compiled from the area villages by DWNP to enable compensation payments for livestock losses. We organized these reports into a spreadsheet and calculated descriptive statistics and Chi-square goodness of fit tests using R Statistical software (R version 2.15.1). Chi-square tests were based on the best available estimates of large carnivore relative abundance from density estimates in published literature (lion = 5.8/100km<sup>2</sup>, Cozzi et al. 2013; spotted hyena = 14.4, Cozzi et al. 2013; African wild dog = 3.5, Creel et al. 2004; leopard = 1.5, Winterbach 2008).

When a depredation event occurred, farmers were encouraged to work with our conflict research and mitigation program by village chiefs and elders as the information they provided assisted with the implementation of future conflict mitigation. When livestock farmers reported losses to us, we would accompany them to the kill site. We documented the GPS location, probable time of the incident and habitat. We looked for tracks and sign of carnivore species to determine the species responsible for the incident, i.e. killing bites, claw marks, feeding style, predator spoor, among others. Since villagers were self-reporting incidents, we only investigated the depredation events that were brought to our attention. Descriptive statistics and Chi-squared goodness of fit tests were calculated using R Statistical software and based on published species population densities as above. We used a Pearson's product moment correlation test to compare the number of depredation events per village to village specific attributes (estimated values for human population, livestock population, number of livestock per person, and number

of cattle posts) and village specific management actions (number of employees from our research program, number of predator-proof kraals built, number of lion alerts issued and an estimate of our overall effort/time spent in each village). The estimates of livestock per village were obtained from Botswanan Department of Veterinary Services records and our effort/time spent per village was estimated post hoc.

An Optimized Hot Spot Analysis (Arc GIS Version 10.5.1; based on the Getis-Ord  $G_i^*$  statistic) was conducted to see if investigated depredation event locations were significantly clustered together (optimal fixed distance band based on peak clustering at 6.5 km with resulting heat map grid cell size of 4.7 km<sup>2</sup>). PAC data did not have an associated point location and could not be included in this analysis. The hot spot analysis relies on z-scores for all investigated depredation event locations in the dataset, with significantly positive scores indicating significant clustering of high predation locations (hot spots) and significantly negative scores indicating significant clustering of low predation locations (cold spots). A heat map depicting warm/hot spots (areas with a higher chance of depredation event occurring, e.g., positive z-scores) and cool/cold spots (areas with lower chance of a depredation event occurring, e.g., negative z-scores) was created based on these results.

## **2.4. Results**

For the focal villages (Beetsha, Eretsha, Gudigwa, and Gunotsoga), governmental PAC records showed that five carnivore species were reported to kill livestock from 2009 through 2016, totaling 588 individual reports (Table 2.1). Of all PAC reported incidents, lions were reported to be responsible for significantly more events (81%, n=477) than expected when accounting for species estimated relative abundance of large carnivores as

described above ( $\chi^2 = 1195.73$ ,  $df = 4$ ,  $p < 0.001$ ). African wild dogs were responsible for 13% ( $n=79$ ) of reported events, leopards for 4% ( $n=22$ ), spotted hyenas 1% ( $n=7$ ), and caracal (*Caracal caracal*) depredations represent less than 1% of all reports ( $n = 1$ ; not included in Chi-squared test). The number of reports spiked in 2012 and 2013, totaling 113 and 159 reports, respectively, and totaling 46% of all reported events during the eight-year span (Fig. 2.3 & Table 2.1). The most (38%,  $n = 225$ ) PAC reports came from the village of Gudigwa (Table 2.2), followed by Gunotsoga (22%,  $n = 132$ ), Eretsha (22%,  $n = 128$ ), and Beetsha (18%,  $n = 103$ ). There was a significant difference in the number of reports received from each village ( $\chi^2 = 9.44$ ,  $df = 3$ ,  $p = 0.024$ ). In the 588 PAC events, four species totaling 609 individual livestock were claimed to have been lost, with bovids (cattle and goats) making up 94% (Table 2.3). During every year between 2009 and 2016, bovids made up at least 91% of the animals reported killed by predators. Over the same time frame, the Botswanan government valued the livestock lost to predators at \$185,590 USD for focal villages (Tables 2.4 and 2.5). Excluding 2009, a year of incomplete records, farmers in the four focal villages claimed livestock losses valued at an average of US\$25,576 per year between 2010 and 2016.

Between October 2014 and December 2016, we investigated 102 livestock depredation events, of which lions were responsible for 75 (74%; Table 2.6), significantly more events than expected when accounting for species estimated relative abundance ( $\chi^2 = 156.75$ ,  $df = 4$ ,  $p < 0.001$ ). During these 102 investigated depredation events a total of 129 individual livestock (cattle, goat, horse, donkey) were attacked, 116 individuals killed with another 13 injured (Table 2.7). Bovid were taken most often, comprising 97% of all livestock killed. During the study, the value of killed livestock totaled \$29,925

USD (Table 2.8). Focusing on complete data years of 2015 and 2016, the average yearly loss to predators in the study area was \$14,188 USD. Of the 102 events, 79% (n = 80) were filed with DWNP for reimbursement through the governmental compensation program. Significantly more depredation events (90%, n = 92; Table 2.6) happened in the veld while livestock are grazing and unattended, as opposed to at the kraal (10%, n = 10;  $\chi^2 = 65.922$ , df = 1,  $p < 0.001$ ). On only six occasions were there people with the herd that was attacked. Most attacks occurred in NG 12 (vs. NG 11) where livestock are typically grazing due to water and food availability and where more predators are believed to be (Fig. 2.4).

In our investigations, the most depredation events occurred in Beetsha (39%, n = 40; Table 9), followed by Eretsha (28%, n = 29), Gunotsoga (19%, n = 19), Gudigwa (8%, n = 8), and Seronga (5%, n = 5). There was a significant difference in the number of events per village ( $\chi^2 = 68.118$ , df = 5,  $p < 0.001$ ). When standardized by the estimated number of livestock and separately by the estimated number of livestock per person, there was still a significant difference between the number of depredation events per village ( $\chi^2 = 22.975$ , df = 4,  $p < 0.001$ ;  $\chi^2 = 14.915$ , df = 4,  $p = 0.005$ ). Our conservation efforts and management activities centered on where there were the most depredation events (Table 2.9). The number of livestock depredation events per village was positively correlated, but not significantly, with estimated livestock population ( $r = 0.76$ ,  $p = 0.21$ ), estimated number of livestock per person ( $r = 0.74$ ,  $p = 0.15$ ), the number of our employees ( $r = 0.75$ ,  $p = 0.15$ ), the number of predator-proof kraals built by our program ( $r = 0.79$ ,  $p = 0.11$ ), and the number of lion alerts ( $r = 0.87$ ,  $p = 0.06$ ; Table 9). There was a significant positive correlation between the number of reported depredation events per village and

the estimated amount of effort and time spent in the corresponding village ( $r = 0.93$ ,  $p = 0.02$ ). The number of depredation events per village was not correlated with the human population ( $r = -0.37$ ,  $p = 0.53$ ) or the number of cattle posts ( $r = -0.05$ ,  $p = 0.94$ ) in the respective village.

On average, investigated depredation events took place 6.1 km from the nearest village center (standard deviation “ $\sigma$ ” = 2.7 km) and 2.7 km from the nearest cattle post ( $\sigma = 2.2$  km). A spatial assessment (optimized hotspot analysis) of investigated depredation events yielded two major depredation hotspots, southeast of Eretsha and east of Beetsha where depredation events were significantly clustered (Fig. 2.5). Warm and hot spots had positive z-score values while cool and cold spots had negative z-score values; all red-hot spots incorporated areas where depredation events were significantly clustered with  $p$ -values  $< 0.01$  (Fig. 2.5).

## **2.5. Discussion**

While we confirmed lions were responsible for about 75% of losses, local farmers reported to the government that lions were responsible for over 80% of depredation events. A direct comparison between individual PAC reports and our investigated events was not possible due to a lack of fine grain information in PAC reports. As independent investigators, villagers may have been unaware of our research program, and we recognize this as a potential bias in our data. Villagers were not compensated for losses to spotted hyenas but did receive compensation for livestock lost to lions. Further, villagers recognize the limited resources available to DWNP and report losses suffered to spotted hyenas as losses to lions. We recorded a 7% increase for reported losses to spotted hyenas, with a corresponding decrease in lion records compared to the DWNP PAC data.

African wild dog and leopard records were similar between the two analyses, so the discrepancy in lion-hyena reporting is likely due to false claims to DWNP for compensation. The lack of compensation for losses to spotted hyena does not give local farmers any incentive to accurately report depredation events when they happen, especially if there is no government investigation of depredation events. Additionally, 21% of our investigated depredation events were not reported to DWNP for compensation, some because they were not eligible for reimbursement (i.e. losses to spotted hyena) or would yield below market value for the lost stock (i.e. losses to leopard and wild dog) and others (i.e. losses to lion) because farmers were frustrated with the compensation program.

Lions were the major culprits in all reported livestock depredation events, affirming local opinions about which predators were most harmful to rural farmer's livelihoods. Lions are known to cause the most damage in some circumstances (e.g., Laikipia District, Kenya, Ogada et al. 2003) but spotted hyenas have been shown to cause the most damage in others (e.g., outside Massai Mara National Reserve, Kenya, Kolowski and Holekamp 2006; Massai Steppe, Tanzania, Mponzi et al. 2014). Cattle were the most common domestic prey choice (implicated in 96% of investigated livestock attacks and 92% of PAC data livestock lost) as lions predominantly prey on large ungulates (Hayward and Kerley 2005) and cattle are the most prevalent domestic animal in the area. Where lions take the most livestock, larger livestock (cattle) are taken most frequently (Ogada et al. 2003), and where spotted hyenas are the worst offenders, smaller stock (sheep and goats) are lost most frequently (Kolowski and Holekamp 2006, Mponzi et al. 2014). While there were correlations between the number of depredation

events per village and both the estimated numbers of cattle and estimated number of cattle per person, none were statistically significant. As the number of livestock increases the chance of depredation also increases. Similarly, there was a non-significant, positive correlation between the number of depredation events and the number of project employees, the number of predator-proof kraals built, and the number of lion alerts sent per village. Mitigation efforts were more intensive in areas with higher rates of conflict and there was a significant correlation between the number of depredation events and an estimate of our efforts/time spent in each village. We investigated conflicts when they occurred and thus spent more time in villages with higher levels of conflict. We recognize that our simultaneous involvement in conflict mitigation could have biased the number of reports we received from villagers. Though we established the same mitigation practices in all focal villages, the intensity of these mitigation efforts differed as a result of conflict intensity. Furthermore, community members from the village of Gudigwa were more apprehensive about our program likely leading to a reporting bias in our independent investigations compared to DWNP PAC data. However, the level of this bias is not directly quantifiable, and we present our results with this caveat.

The total value of livestock we confirmed were lost to predators was ~US\$30,000 in just over two years, with average yearly losses totaling ~US\$14,000. Based on the estimated local population (Botswana Population and Housing Census 2011) and average household sizes in the area (LeFlore, unpublished data), that level of loss equates to about US\$25 per household per year. Between 2009 and 2016, the value of all livestock losses reported to the government was ~US\$185,600, an average of US\$25,575 per year across four villages and US\$45 per household. There was a drop in reported livestock losses in

2014 which was likely due to villagers killing 30-50% of lion population in 2013 following high levels of conflict. Additionally, elevated levels of reported conflicts in 2012 and 2013 could actually be representative of losses, but could also have been artificially inflated in connection to the compensation program revision in 2013. Typically, all farmers do not experience losses at similar levels; losses are disproportionately distributed amongst farmers, affecting a minority of individuals (Thirgood et al. 2005, Dickman et al. 2011). Suffering the loss of even one individual to a depredation event could lead to a hefty economic toll for a farmer: as much as twenty times the average per household yearly rate of loss (e.g., average market value of a bull = US\$565). Given average herd sizes in the study area, suffering even one event could be extremely detrimental to local farmers and more than one in a year could be catastrophic (Thirgood et al. 2005).

Most depredation events occurred while livestock were either grazing unguarded or left unattended in the veld overnight. Livestock husbandry is quite limited in the region (Hemson et al. 2009, Weise et al. 2018), and there is no longer a strong herding culture. As children and teenagers are now going to school there are fewer young men to take responsibility for herding the livestock. Traditional livestock herding and husbandry efforts have largely been abandoned in western Europe, North and South America, and portions of Africa (Breitenmoser et al. 2005). In East Africa a strong herding culture persists, primarily due to continued risk of livestock theft (Frank 1998, Ogada et al. 2003, Frank et al. 2005, Woodroffe et al. 2007), and most of the livestock losses occur at and around the “boma” (kraal/livestock enclosure; Ogada et al. 2003, Frank et al. 2006). In our area, livestock are most at risk away from cattle posts and villages in conflict hotspots

southeast of Eretsha and east of Beetsha where depredation events were significantly clustered. Sound livestock husbandry and herding practices are vital to minimize conflict with predators (Ogada et al. 2003, Breitenmoser et al. 2005 Woodroffe et al. 2007).

Overall, there were 50% more depredation events reported to DWNP than were reported to and investigated by us between 2015 and 2016, years of complete data (Tables 2.1 & 2.8). While we were likely unable to investigate every depredation event that actually occurred, given our extensive efforts to establish and maintain positive relationships with community members and continued presence in the area, it seems unlikely that an additional 50% of depredation events occurred and were not reported to us. Instead, we postulate this discrepancy is a result of the factors described above, and villagers are likely falsely reporting losses, purposefully or not, to receive compensation from the government by reporting animals lost to drought, starvation, or disease as animals lost to predators. On at least 5 occasions we were called to investigate a dead animal with no signs of predator attack. Without adequate resources to investigate claims of livestock loss, DWNP has limited ability to determine which claims are accurate and which are attempts to take advantage of the compensation system.

## **2.6. Management Implications**

It is beneficial for villagers to receive compensation for losses and alleviate the economic burden of predator conflict (Naughton-Treves et al. 2003, Nyhus et al. 2005), however the government-run compensation program is unable to sustainably reimburse claims in its current form. To ensure that the program is not being exploited, rigorous and prompt investigation of claims should be established. Ineffective compensation programs may actually increase retaliatory killings (Nyhus et al. 2005). While the program has

shortcomings, it should not be abandoned altogether because, similar to other regions, villagers support and expect reimbursement so ceasing payments can cause increased retaliation and hostility (Bangs et al. 1998, Naughton-Treves et al. 2003, Treves et al. 2009). Furthermore, compensation programs lacking adequate incentives for farmers to properly care for livestock can lead to poor livestock husbandry and disregard for preventative measures (Dyar and Wagner 2003, Swenson and Andren 2005).

Compensation schemes in Botswana and around the globe must include a variety of factors to be effective (see Nyhus et al. 2005). The most critical factors include: correct and speedy confirmation of losses; timely and fair payments; clear protocols, rules and guidelines that connect payment and appropriate conservation management practices; and an understanding of the cultural and socio-economic systems. Our work underscores the importance of investigating depredation events as a part of compensation programs.

Finally, our results show that most losses occur in the veld and while livestock are unguarded. Therefore, we suggest conflict mitigation efforts focus on increasing herding and livestock husbandry practices in the region. In many cases, conflict mitigation programs focus on securing the livestock enclosure (e.g., our efforts, Lichtenfeld et al. 2015). However, this may not be the most effective strategy in Botswana (Weise et al. 2018). Governments and conservation organizations would be wise to assess damages prior to establishing mitigation strategies.

## 2.7. Literature Cited

- Aryal, A., D. Brunton, W. Ji, R.K. Barraclough, and D. Raubenheimer. 2014. Human–carnivore conflict: Ecological and economical sustainability of predation on livestock by snow leopard and other carnivores in the Himalaya. *Sustainability Science* 9:321–329.
- Bangs, E.E., S.H. Fritts, J.A. Fontaine, D.W. Smith, K.M. Murphy, C.M. Mack, and C.C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho and Wyoming. *Wildlife Society Bulletin* 26:785–793.
- Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. Hunter, D. 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. doi: 10.1073/pnas.1500664112.
- Bauer, H., C. Packer, P.F. Funston, P. Henschel, and K. Nowell. 2016. *Panthera leo*. The IUCN Red List of Threatened Species 2016: e.T15951A115130419. <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en>
- Bauer, H. and S. Van der Merwe. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38:26–31.
- Botswana Population and Housing Census. 2011. Available at [www.catalog.ihnsn.org/index.php/catalog/4243/download/55990](http://www.catalog.ihnsn.org/index.php/catalog/4243/download/55990). Accessed on October 15, 2015.
- Breitenmoser U., C. Angst, J-M. Landry, C. Breitenmoser-Würsten, J.D.C. Linnell, and J-M. Weber. 2005. Non-lethal techniques for reducing depredation. In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 49–71. Cambridge University Press, Cambridge, UK.
- Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA, Paris, France.
- Conover, M. 2002. *Resolving Human–Wildlife Conflicts: The Science of Wildlife Damage Management*. Lewis, Florida.
- Cozzi, G., F. Broekhuis, J.W. McNutt and B. Schmid. 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation*. DOI: 10.1007/s10531-013-0564-7.
- Creel, S., M.G.L. Mills, and J.W. McNutt. 2004. Demography and Population Dynamics of African Wild Dogs in Three Critical Ecosystems. In: D.W. Macdonald & C. Sillero-Zubiri (eds) *The Biology & Conservation of Wild Canids*. pp. 337–350. Oxford University Press.

- Dickman A.J., E.E. Macdonald, 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.
- Department of Wildlife and National Parks, 1998. *Guidelines for Compensation*. Department of Wildlife and National Parks, Gaborone.
- Department of Wildlife and National Parks, 2013. *Compensation Guidelines for Damages Caused by Elephants and Lion*. Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism. Government of Botswana, Gaborone, Botswana.
- Dyar, J.A. and J. Wagner. 2003. Uncertainty and species recovery program design. *Journal of Environmental Economics and Management* 45:505–522.
- Eklund, A., J.V. López-Bao, M. Tourani, G. Chapron, and J. Frank. 2017. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific Reports* 7:2097. DOI:10.1038/s41598-017-02323-w
- Frank, L.G. 1998. *Living with lions: carnivore conservation and livestock in Laikipia District, Kenya*. Development Alternatives, Bethesda, Maryland.
- Frank, L., G. Hemson, H. Kushnir, and C. Packer. 2006. *Lions, conflict and conservation*. Background paper for the east and southern African lion conservation workshop Johannesburg, South Africa, 8-13 January 2006.
- Frank, L.G., R. Woodroffe, M.O. Ogada. 2005. People and predators in Laikipia District, Kenya. *In*: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 286–304. Cambridge University Press, Cambridge, UK.
- Funston, P. 2014. The Kavango-Zambezi Transfrontier Conservation Area – critical for African lions. *Cat News* 60:4–7.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122:159–171.
- Hayward, M.W. and G.I.H. Kerley. 2005. Prey preferences of the lion (*Panthera leo*). *The Journal of Zoology* 267:309–322.
- Hazzah, L., M. Borgehoff Mulder, and L. Frank. 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.
- Hemson, G., S. Maclennan, G. Mills, P. Johnson, D. Macdonald. 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.

- Ikanda, D., C. Packer. 2008. Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania. *Endangered Species Research* 6:67–74.
- Inskip, C. and A. Zimmermann. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43:18–34.
- Kolowski, J.M. and K.E. Holekamp. 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* 128:529–541.
- Lichtenfeld, L.L., C. Trout, and E.L. Kisimir. 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodiversity Conservation* 24:483–491.
- Mabille, G., A. Stein, T. Tveraa, A. Myrseth, H. Brøseth, and J. D. C. Linnell. 2015. Sheep farming and large carnivores: What are the factors influencing claimed losses? *Ecosphere* 6:82.
- Macdonald, D.W., A.J. Loveridge, and A. Rabinowitz. 2010. Felid futures: crossing disciplines, borders and generations. In: D.W. Macdonald, A.J. Loveridge (eds) *Biology and Conservation of Wild Felids*. Oxford University Press, Oxford. pp. 599–649.
- Madden, F. and B. McQuinn. 2014. Conservation's blind spot: the case for conflict transformation in wildlife conservation. *Biological Conservation* 178: 97–106. <https://doi.org/10.1016/j.biocon.2014.07.015>
- Mossaz, A., R.C. Buckley, and J.G. Castley. 2015. Ecotourism contributions to conservation of African big cats. *Journal for Nature Conservation* 28:112–118. <http://dx.doi.org/10.1016/j.jnc.2015.09.009>
- Mponzi, B.P., C.A. Lepczyk, and B.M. Kissui. 2014. Characteristics and distribution of livestock losses caused by wild carnivores in Maasai Steppe of northern Tanzania. *Human-Wildlife Interactions* 8:218–227.
- Mweze, M. 2014. Botswana Department of Wildlife and National Parks. Personal Communication. October 2014, Seronga, Ngamiland, Botswana.
- Naughton-Treves, L., R. Grossberg, and A. Treves 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology* 17:1500–1511.
- Newsome, T.M., A.C. Greenville, D. Čirović, C.R. Dickman, C.N. Johnson, M. Krofel, M. Letnic, W.J. Ripple, E.G. Ritchie, S. Stoyanov, and A.J. Wirsing. 2017. Top predators constrain mesopredator distributions. *Nature Communications* 8:15469. DOI: 10.1038/ncomms15469

- Nyhus, P.J., S.A. Osofsky, P. Ferraro, F. Madden, and H. Fischer. 2005. Bearing the cost of human-wildlife conflict: the challenges of compensation schemes In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 107–121. Cambridge University Press, Cambridge, UK.
- Ogada, M.O., R. Woodroffe, N.O. Oguge, and L.G. Frank. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* 17:1–10.
- Ohrens, O., A. Treves, and C. Bonacic. 2015. Relationship between rural depopulation and puma-human conflict in the high Andes of Chile. *Environmental Conservation* doi:10.1017/S0376892915000259.
- Palmeira, F.B.L., P.G. Crawshaw Jr., C.M. Haddad, K.M.P.M.B. Ferraz and L. M. Verdade. 2008. Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biological Conservation* 141:118–125.
- R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <<http://www.r-project.org>>.
- Ravenelle, J., Nyhus, P.J., 2017. Global patterns and trends in human-wildlife conflict compensation. *Conservation Biology* 31: 1247–1256. <https://doi.org/10.1111/cobi.12948>
- Riggio, J., A. Jacobson, L. Dollar, H. Bauer, A. Dickman, P. Funston, P. Henschel, H. de Iongh, L. Lichtenfeld, C. Packer, and S. Pimm. 2013. The size of savannah Africa: a lion's 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. DOI: 10.1126/science.1241484
- Singh, R., P. Nigam, Q. Qureshi, K. Sankar, P.R. Krausman, S. P. Goyal, and K.L. Nicholason. 2015. Characterizing human-tiger conflict in and around Ranthambhore Tiger Reserve, western India. *European Journal of Wildlife Research* 61:255–261.
- Swenson, J.E. and H. Andren. 2005. A tale of two countries: large carnivore depredations and compensation schemes in Sweden and Norway. In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 323–339. Cambridge University Press, Cambridge, UK.
- Thirgood, S., R. Woodroffe, and A. Rabinowitz. 2005. The impact of human-wildlife conflict on human lives and livelihoods. In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 13–26. Cambridge University Press, Cambridge, UK.

- Thorn, M., M. Green, F. Dalerum, P.W. Bateman, and D.M. Scott. 2012. What drives human-carnivore conflict in the North West Province of South Africa? *Biological Conservation* 150:23–32.
- Thorn, M., M. Green, D. Scott, K. Marnewick. 2013. Characteristics and determinants of human-carnivore conflict in South African farmland. *Biodiversity Conservation* 22:1715–1730.
- Treves, A., R.L. Jurewicz, L. Naughton-Treves, and D.S. Wilcove. 2009. The price of tolerance: wolf damage payments after recovery. *Biodiversity and Conservation* 18:4003–4021.
- Treves, A. and K.U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491–1499.
- van Eeden, L.M., A. Eklund, J.R.B. Miller, J.V. López, G. Chapron, M.R. Cejtin, M.S. Crowther, C.R. Dickman, J. Frank, M. Krofel, D.W. Macdonald, J. McManus, T.K. Meyer, A.D. Middleton, T.M. Newsome, W.J. Ripple, E.G. Ritchie, O.J. Schmitz, K.J. Stoner, M. Tourani, and A. Treves. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16(9): e2005577. <https://doi.org/10.1371/journal.pbio.2005577>
- Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. 2019. Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution*. 6:242. doi: 10.3389/fevo.2018.00242
- Weise, F.J., M.W. Hayward, R. Casillas Aguirre, M. Tomeletso, P. Gadimang, M.J. Somers, and A.B. Stein. 2018. Size, shape, and maintenance matter: a critical appraisal of a global carnivore mitigation strategy – Livestock protection kraals in northern Botswana. *Biological Conservation* 225:88–97.
- Winterbach, C. 2008. Draft national predator strategy, Botswana. Department of Wildlife and National Parks, Gaborone.
- Winterbach, H.E.K., C.W. Winterbach, M.J. Somers, and M.W. Hayward. 2013. Key factors and related principles in the conservation of large African carnivores. *Mammal Review* 43:89–110.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165–173.
- Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. In: Gittleman, J. L., Funk, S., Macdonald, D. W. & Wayne, R. K. (eds) *Carnivore Conservation*. pp. 61–92. Cambridge: Cambridge University Press.
- Woodroffe, R., L.G. Frank, P.A. Lindsey, S.M.K. ole Ranah, S. Romañach. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity Conservation* 16:1245–1260.

## 2.8. Tables and Figures

Table 2.1. Percent (no. of events in parentheses) of Problem Animal Control (PAC) incidents by species reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana.

	2009 <sup>a</sup>	2010	2011	2012	2013	2014	2015	2016	Total
Predator	(24)	(53)	(46)	(113)	(159)	(47)	(80)	(66)	(588)
Lion	71	25	72	80	93	89	89	95	81
Wild dog	8	64	26	16	4	2	6	2	13
Leopard	21	9	0	4	1	6	3	2	4
Spotted hyena	0	2	2	1	1	2	0	2	1
Caracal	0	0	0	0	1	0	0	0	0
Unknown	0	0	0	0	0	0	3	0	0
Percent	4	9	8	19	27	8	14	11	

<sup>a</sup> indicates an incomplete year of data.

Table 2.2. Percent (no. of events in parentheses) of Problem Animal Control (PAC) incidents by village reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana.

Village	2009 <sup>a</sup> (24)	2010 (53)	2011 (46)	2012 (113)	2013 (159)	2014 (47)	2015 (80)	2016 (66)	Total (588)
Beetsha	8	6	13	26	12	28	25	17	18
Eretsha	33	9	11	19	11	36	40	33	22
Gudigwa	46	72	76	48	30	19	16	26	38
Gunotsoga	13	13	0	7	47	17	19	24	22
Percent	4	9	8	19	27	8	14	11	

<sup>a</sup> indicates an incomplete year of data.

Table 2.3. Percent of livestock lost (no. of livestock lost in parentheses) in all Problem Animal Control (PAC) incidents reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana (609 individual livestock were reported lost in 588 events).

	2009 <sup>a</sup>	2010	2011	2012	2013	2014	2015	2016	Total
Livestock	(24)	(53)	(46)	(113)	(159)	(47)	(89)	(76)	(609)
<b>Bovids</b>									
Cow	42	53	59	60	60	45	46	46	54
Calf	27	13	9	8	9	15	10	22	12
Bull	12	13	15	15	10	13	24	9	14
Ox	8	13	15	6	11	21	15	14	12
Goat	12	2	0	4	1	0	0	3	2
Subtotal	100	94	98	93	91	94	94	95	94
<b>Equids</b>									
Horse	0	0	0	5	6	4	2	3	4
Donkey	0	4	0	1	3	2	3	3	2
Subtotal	0	4	0	6	8	6	6	6	6
Unknown	0	2	2	1	1	0	0	0	1
Percent	4	9	8	19	26	8	15	12	

<sup>a</sup> indicates an incomplete year of data.

Table 2.4. Average livestock valuation from farmers (n=86) who lost livestock between October 2014 and December 2016 and the Botswanan government livestock compensation rates in U.S. dollars (USD) and Botswanan pula (BWP).

Livestock	Farmer value USD (BWP)	Government value USD (BWP)
Bull	425 (4,130)	565 (5,500)
Ox	320 (3,100)	310 (3,000)
Cow	295 (2,860)	310 (3,000)
Calf	220 (2,150)	100 (1,000)
Horse	310 (3,000)	255 (2,500)
Goat	100 (1,000)	45 (450)
Donkey	50 (500)	20 (200)

Table 2.5. Government valuation (in USD) of livestock lost in all Problem Animal Control (PAC) incidents reported to the Department of Wildlife and National Parks (DWNP) during 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana. 609 individual livestock were reported lost in 588 events.

	2009 <sup>a</sup>	2010	2011	2012	2013	2014	2015	2016	Total
Livestock Lost	(26)	(53)	(46)	(113)	(159)	(47)	(89)	(76)	(609)
<b>Bovids</b>									
Cow	3,410	8,680	8,370	21,080	29,760	6,510	12,710	10,850	101,370
Calf	700	700	400	900	1,400	700	900	1,700	7,400
Bull	1,695	3,955	3,955	9,605	9,040	3,390	11,865	3,955	47,460
Ox	630	2,170	2,170	2,170	5,580	3,100	4,030	3,410	23,250
Goat	135	45	0	180	45	0	0	90	495
Subtotal	6,560	15,550	14,895	33,935	45,825	13,700	29,505	20,005	179,975
<b>Equids</b>									
Horse	0	0	0	1,530	2,295	510	510	510	5,355
Donkey	0	40	0	20	80	20	60	40	260
Subtotal	0	40	0	1,550	2,375	530	570	550	5,615
<b>Total</b>	<b>6,560</b>	<b>15,590</b>	<b>14,895</b>	<b>35,485</b>	<b>48,200</b>	<b>14,230</b>	<b>30,075</b>	<b>20,555</b>	<b>185,590</b>

<sup>a</sup> indicates an incomplete year of data.

Table 2.6. Percent (no. of incidents) of investigated depredation events that occurred at livestock kraals vs. in the veld attributed to each responsible carnivore species in the lion conflict study area in northern Botswana, October 2014-December 2016.

Species	Veld (92)	Kraal (10)	Total (102)
Lion	67	8	74
Wild dog	13	0	13
Spotted hyena	7	1	8
Leopard	4	1	5
Unknown	1	0	1
Percent	90	10	

Table 2.7. Confirmed total number (T) of individual livestock killed and injured (K/I) by predators from 102 investigated depredation events in the lion conflict study area in northern Botswana between October 2014 and December 2016.

Livestock	Lion	Wild dog	Spotted hyena	Leopard	Unknown	All Species		Percent
	T (K/I)	T (K/I)	T (K/I)	T (K/I)	T (K/I)	T	(K/I)	
<b>Bovids</b>								
Cow	47 (42/5)	8 (6/2)	5 (5/0)	1 (1/0)	1 (1/0)	62	(55/7)	48
Calf	21 (19/2)	2 (2/0)	4 (4/0)	5 (4/1)	0 (0/0)	32	(29/3)	25
Ox	21 (18/3)	3 (3/0)	0 (0/0)	0 (0/0)	0 (0/0)	24	(21/3)	19
Bull	4 (4/0)	1 (1/0)	0 (0/0)	0 (0/0)	0 (0/0)	5	(5/0)	4
Goat	1 (1/0)	1 (1/0)	0 (0/0)	0 (0/0)	0 (0/0)	2	(2/0)	1
Subtotal	94 (84/10)	15 (13/2)	9 (9/0)	6 (5/1)	1 (1/0)	125	(112/13)	97
<b>Equids</b>								
Horse	2 (2/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	2	(2/0)	1
Donkey	2 (2/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	2	(2/0)	1
Subtotal	4 (4/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	4	(4/0)	3
<b>Total</b>	<b>98 (88/10)</b>	<b>15 (13/2)</b>	<b>9 (9/0)</b>	<b>6 (5/1)</b>	<b>1 (1/0)</b>	<b>129 (116/13)</b>		
<b>Percent</b>	<b>76</b>	<b>12</b>	<b>7</b>	<b>5</b>	<b>1</b>			

Table 2.8. Government valuation (in USD) of livestock killed by predators in 102 investigated depredation events in the lion conflict study area in northern Botswana during October 2014 to December 2016.

	2014 <sup>a</sup>	2015	2016	Total
Livestock Lost	5	50	61	116
Depredation Events	5	44	53	102
<hr/>				
Livestock Valuation (In USD)				
Bovids				
Cow	1,240	7,440	8,370	17,050
Calf	0	1,400	1,500	2,900
Bull	0	0	2,825	2,825
Ox	310	2,480	3,720	6,510
Goat	0	45	45	90
Subtotal	1,550	11,365	16,460	29,375
Equids				
Horse	0	255	255	510
Donkey	0	40	0	40
Subtotal	0	295	255	550
<hr/>				
Total	1,550	11,660	16,715	29,925
<hr/>				

<sup>a</sup> indicates an incomplete year of data.

Table 2.9. Investigated depredation events (n=102) from each village with associated attributes and management actions in the lion conflict study area in northern Botswana between October 2014 and December 2016

Village	Village <u>Attributes</u>					<u>Management Actions</u>			
	No. events	Est. human population	Est. livestock population	Est. no. livestock/person	No. cattle posts	No. employees	Pct. effort/time	No. kraals	No. alerts
Beetsha	40	1,585	4,122	3	8	3	30	3	26
Eretsha	29	912	1,678	2	4	2	30	4	19
Gudigwa	8	725	1,176	2	11	1	15	2	9
Gunotsoga	19	953	824	1	6	0	20	2	23
Seronga	5	3,716	2,002	1	4	1	5	1	0
Unknown	1	-	-	-	-	-	-	-	-
Total	102	7,891	9,802	1	33	7	100	12	77
Correlation to no. events (r)		-0.37	0.67	0.74	-0.05	0.75	0.93	0.79	0.87
<i>p</i> -value		0.53	0.21	0.15	0.94	0.15	0.02	0.11	0.06

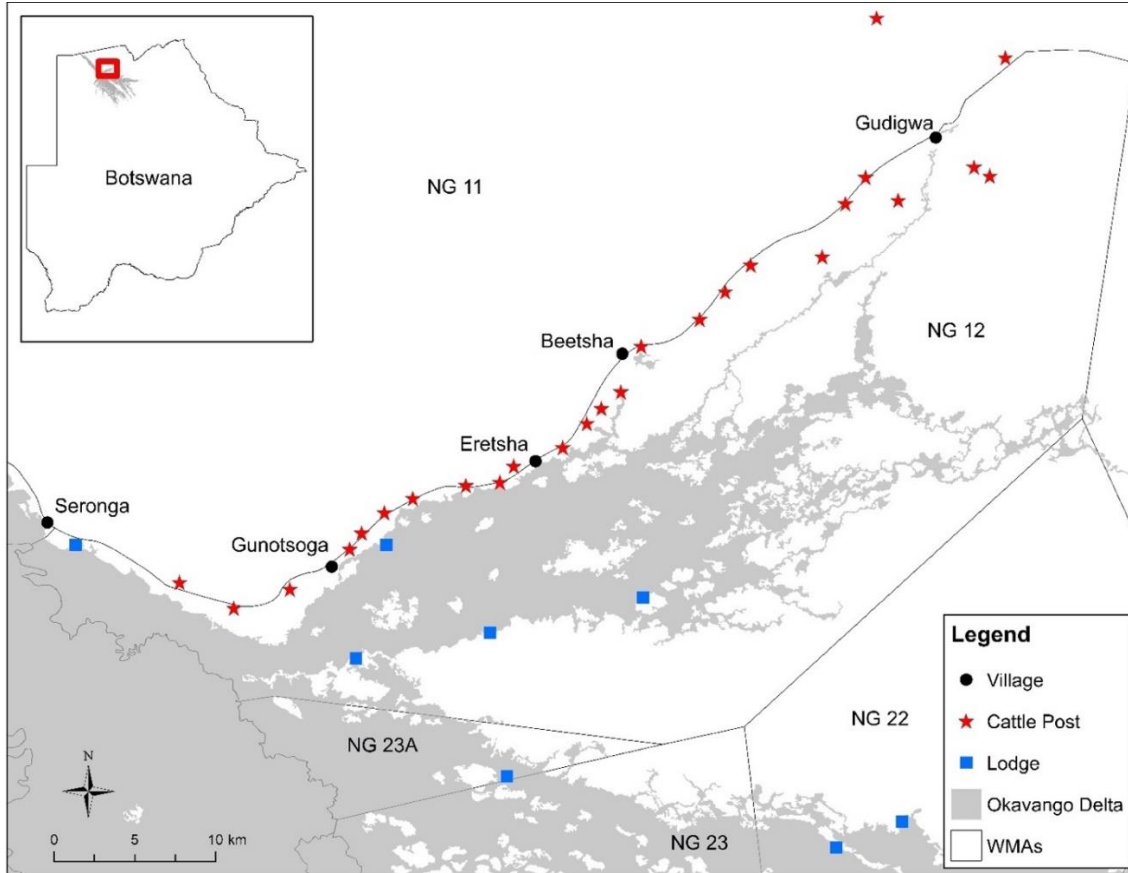


Figure 2.1. Lion conflict study area in northern Botswana with locations of associated villages and connecting road, cattle posts, and lodges, and Wildlife Management Area boundaries.



A:



B:

Figure 2.2. Traditional kraal structures in northern Botswana. A: thorn branch style construction, B: thick wooden branch construction. Photos by E. LeFlore.

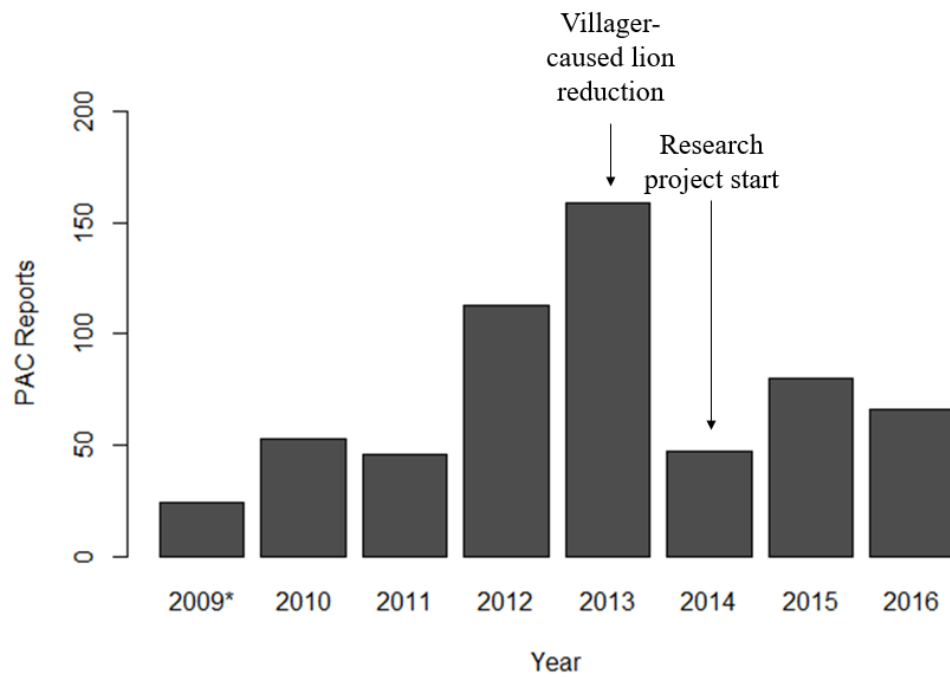


Figure 2.3. Number of problem animal control (PAC) reports filed with the Department of Wildlife and National Parks (DWNP) between 2009-2016 for focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the lion conflict study area in northern Botswana.

\* indicates an incomplete year of data.

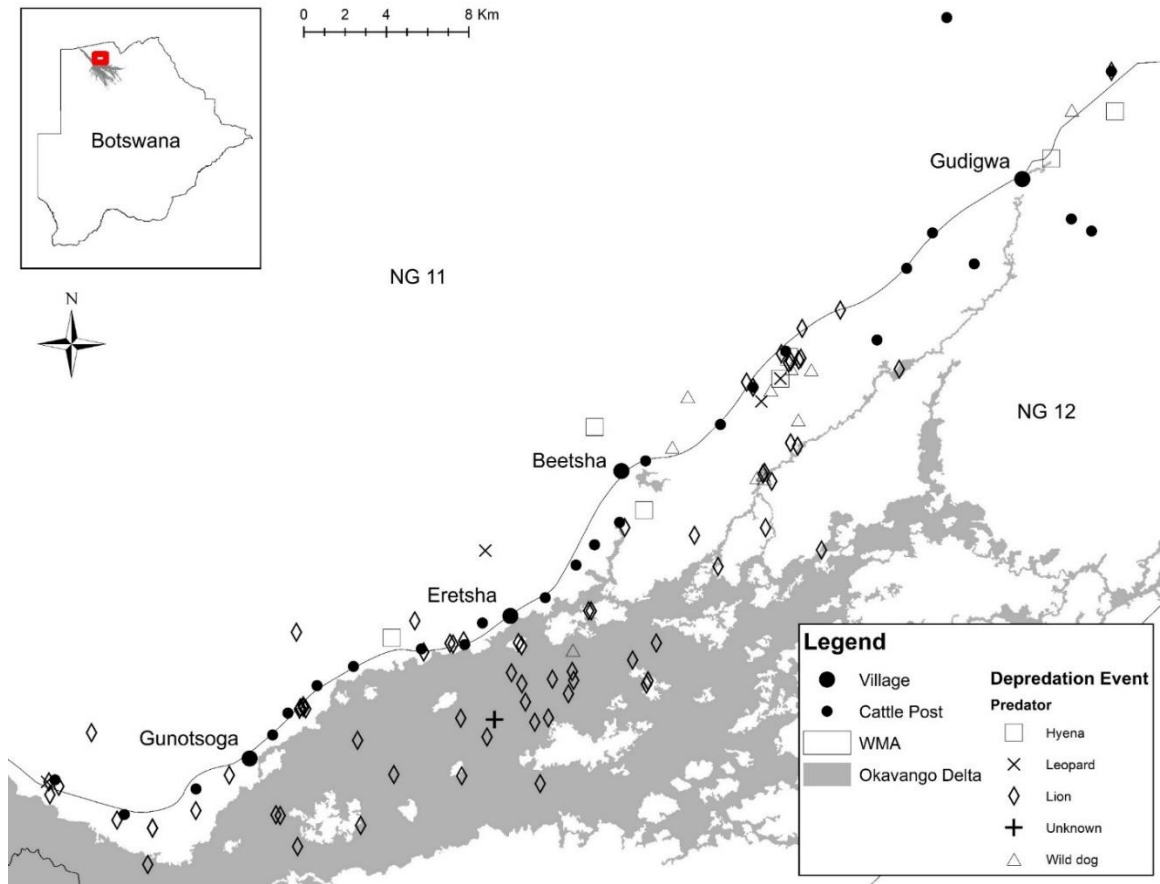


Figure 2.4. Distribution of investigated depredation events documented in the lion conflict study area in northern Botswana during October 2014-December 2016.

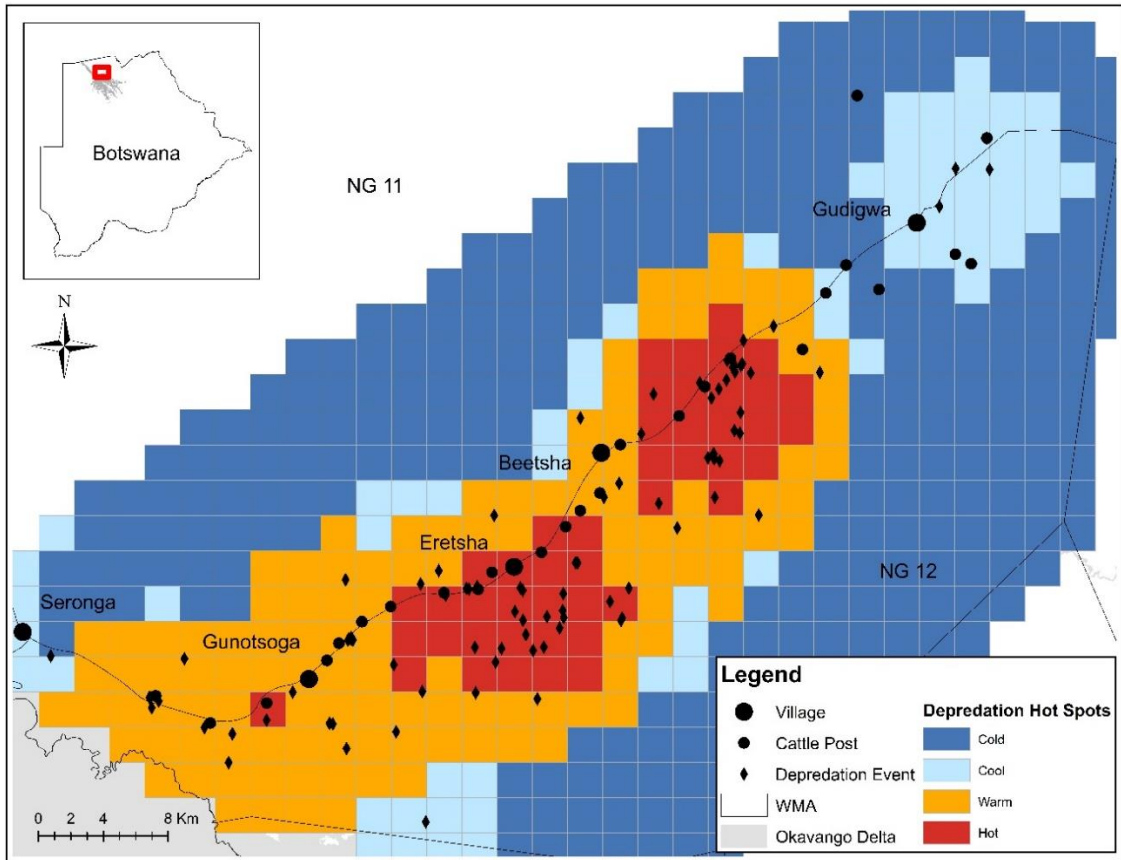


Figure 2.5. Investigated depredation event hotspots in the lion conflict study area in northern Botswana during October 2014-December 2016 based on optimized hot spot analysis conducted in ArcGIS.

## CHAPTER 3

### LION MOVEMENTS IN MULTI-USE AREA IN THE EASTERN PANHANDLE OF THE OKAVANGO DELTA, BOTSWANA

**Abstract** - As global large carnivore populations continue to decline due to human actions, maintaining viable populations beyond protected area borders is critical. African lions (*Panthera leo*) ranging beyond protected area borders regularly prey on domestic livestock causing humans to retaliate or even preemptively kill lions to minimize impacts of lost livestock. To understand how lions navigate high conflict areas in human-dominated landscapes, lions were observed and monitored in the eastern Panhandle of the Okavango Delta between October 2014 and December 2016, and five lions were fitted with GPS satellite collars from August 2015 to December 2016. Lion prides and coalitions were small, with all prides having four or fewer females and all coalitions having two or fewer males. Home range size varied between the sexes but was not statistically different (males:  $\bar{x} = 584 \text{ km}^2$ ,  $n = 3$ ; females:  $\bar{x} = 319 \text{ km}^2$ ,  $n=2$ ). There was considerable spatial overlap in home ranges as neighboring collared individuals utilized high levels of shared space (female-female overlap:  $152 \text{ km}^2$ , representing 41-56% of respective home ranges; male-male overlap:  $125\text{-}434 \text{ km}^2$  shared space, representing 16-90% of respective home ranges). However, lions varied their space use temporally to avoid potentially costly interactions with neighboring individuals, as evidenced by low coefficients of association ( $<0.08$ ). Highest levels of overlap occurred during the wet and early dry seasons when flood waters minimized the amount of available land area. All collared individuals minimized time in close proximity ( $<3 \text{ km}$ ) to human habitation, but

some individuals were able to rely heavily on areas where unmonitored livestock grazed. While most lions exist within protected areas, anthropogenic impacts beyond protected area boundaries can impact critical populations within protected areas. Studying systems beyond park boundaries with high levels of human-lion conflict while also establishing conservation programs which account for both ecological and sociocultural dimensions will better aid lion conservation efforts moving forward.

### **3.1. Introduction**

Large carnivore populations and geographic ranges are declining around the globe as species in the order Carnivora face pressures like habitat loss and conflicts with humans (Ripple et al. 2014). Few protected areas are large enough to provide ample space for wide-ranging large carnivores (Winterbach et al. 2014), and many species range beyond protected area (PA) boundaries where they interact with a growing human population (Woodroffe and Ginsberg 1998, Wittemeyer et al. 2008). Human-dominated landscapes outside PAs pose many threats to large carnivores (e.g., legal [Packer et al. 2011] and illegal hunting [Liberg et al. 2012], and human-wildlife conflicts [Treves and Karanth 2003]) and contribute to population declines both inside and outside reserves (Woodroffe and Ginsberg 1998).

The African lion (*Panthera leo*) is representative of the challenges facing large carnivores living outside reserve boundaries as the species has been extirpated from approximately 87% of its historical range and is now found predominantly inside PAs (Riggio et al. 2013). Lion populations continue to decline and only ~20,000 individuals remain on the continent (Chardonnet 2002, Bauer and Van der Merwe 2004, Riggio et al. 2013, Bauer et al. 2015, Bauer et al. 2016). Anthropogenic impacts at reserve boundaries

and beyond have contributed to these declines, impacting lion population density, population structure, and increasing mortality in juveniles, dispersing subadults, and adults (Loveridge et al. 2010, Elliot et al. 2014). Declines in lion populations are often directly related to conflicts over livestock (Loveridge et al. 2010). Understanding the movements of large carnivores in human-dominated landscapes beyond reserve boundaries is critical in order to minimize conflicts with humans and maintain healthy populations.

Lions are social felids and the largest of the African carnivores (Estes 1991). They feed on a variety of prey with large ungulates being most common (Hayward and Kerley 2005). Lions have a complex social system and are found in prides and male coalitions. Prides consist of several related adult females and their dependent young (Stander 1992). Females will cooperate to hunt (Stander 1992), rear young (Bertram 1975), and defend both the territory and young (Packer et al. 1990). Females usually remain resident in their natal pride while males are expelled when they reach sexual maturity (Van Orsdol et al. 1985). Males form coalitions which typically consist of related males (Bertram 1976) that dispersed from their natal pride at the same time, but coalitions can also consist of unrelated males (Packer and Pusey 1982). These coalitions are nomadic before they take over a pride of females by challenging and ousting resident male coalitions (Bygott et al. 1979, Van Orsdol et al. 1985). The length of a coalition's tenure can be linked to its size (Van Orsdol et al. 1985), though on average for coalitions of two males, lengths have ranged from 18 months in Serengeti (Bygott et al. 1979) to 90 months in Queen Elizabeth National Park (Van Orsdol 1981).

Males predominantly hold the responsibility of defending home ranges, but females will also defend against intruding conspecifics (Van Orsdol et al. 1985). Lions will defend their territories through roaring, scent marking, patrolling, and via direct aggressive conflicts with intruders (Schaller 1972, Van Orsdol et al. 1985). Home ranges can vary in size from 20 km<sup>2</sup> to 500 km<sup>2</sup> (Van Orsdol et al. 1985, Tuqa et al. 2014, Valeix et al. 2012), and even larger home ranges have been noted in arid areas (>2700 km<sup>2</sup>; Funston 2001). There can be considerable overlap when large home ranges exist but there is typically little overlap with smaller home ranges (Schaller 1972, Van Orsdol 1981, Van Orsdol et al. 1985). Home ranges of resident males and females are not always the same size as a single coalition of males can control an area that incorporates the home ranges of multiple female prides (Van Orsdol et al. 1985).

Radio telemetry and GPS satellite tracking collars have been extensively used to study lion ecology and are well-documented – Scheel and Packer (1991) investigated hunting behavior, Tambling et al. (2010) used GPS collars to locate feeding sites, Valeix et al. (2011) focused on movements through patch networks, among many others. Our study focused on the lion population of the eastern Panhandle of the Okavango Delta in a human-dominated landscape where villagers reported high levels of livestock losses to lions and other wild carnivores (LeFlore et al. 2019). We monitored the local lion population and investigated their movements within the highly dynamic Delta ecosystem to understand how lions navigate a high conflict zone outside the borders of PAs. We estimated home range size, space use and overlap, and proximity to areas of risk (human habitation and livestock grazing areas) for collared individuals. We hypothesized that home ranges would be smaller than average home ranges seen in other areas because of

high levels of food availability (both wild and domestic; Fynn et al. 2015) present in the area (e.g., Van Orsdol et al. 1985). Furthermore, we anticipated high levels of overlap and space sharing between neighboring prides and coalitions because of the dynamic nature and seasonality of the Delta system and conflict area (Kotze et al. 2018, Hemson 2003).

### **3.2. Study Area**

The eastern panhandle of the Okavango Delta of northern Botswana lies within the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA), an area of critical importance for lion conservation (Funston 2014). The KAZA TFCA is c. 440,000 km<sup>2</sup>, spans five countries, includes 36 protected areas, and is home to one of the largest lion populations in Africa (c. 3,500 lions; Funston 2014), classifying it as a lion stronghold (Riggio et al. 2013). The eastern panhandle connects the Delta to the rest of the KAZA TFCA and supports people, their livestock, and plentiful wildlife (Ramberg et al. 2006, Fynn et al. 2015). Our research encompassed government-defined management areas slated for uses ranging from human habitation and natural resource consumption (Ngamilands [NGs] 11 and 12) to wildlife management and community/internationally run ecotourism (NGs 22, 23 and 23A) (Figure 3.1). The area lies north of Moremi Game Reserve and west of Chobe National Park, the southern extremes of the KAZA TFCA in Botswana and critical lion habitat (Riggio et al. 2013, Funston 2014). A national hunting ban in Botswana outlawed both safari and subsistence hunting in 2014 (Mbaiwa 2018), though retaliatory lion killings still occur in the study area (Mweze 2014, pers. comm.). The area contains a wide assemblage of wild herbivores (Fynn et al. 2015) and is one of the most sought-after wildlife viewing areas in Africa.

While the Okavango Delta is not a true delta, it is a large inland alluvial fan of the Okavango River and is one of the largest inland “deltas” in the world (McCarthy et al. 2003). The Okavango River is one of southern Africa’s largest rivers and discharges about 10 km<sup>3</sup> of water into the Delta each year (McCarthy et al. 2000, Kgathi et al. 2006). The Delta is composed of a shifting matrix of river channels, swamps and islands (McCarthy et al. 2003). The system is fed by seasonal rains that fall in the Okavango River catchment area in Angola and flow into the Okavango River and, to a lesser degree, local rainfall (Wolski and Savenije 2006). The annual flooding of the Delta is also seasonal, and there is a lag between Angolan rains and peak flooding in the Okavango Delta. The Delta is typically at its lowest across the entire Delta in February and March, when 2,500-4,000 km<sup>2</sup> remain flooded, and at its highest during August, when 6,000-12,000 km<sup>2</sup> are inundated, opposite of the local rainy season (McCarthy et al. 2003). The eastern Panhandle study area is inundated by the early waves of flooding, when waters reach the panhandle starting in February (McCarthy et al. 2003). Waters remain high into July when they begin slowly receding from our study area and push further southeast to the rest of the Delta. The yearly cycling of the floods is not congruent with the rainy season, which runs from November to March (Wolski and Savenije 2006), so the Delta becomes an important water source in the dry Kalahari environment (McCarthy et al. 2003). Based on temperature, surface water levels, and annual precipitation in 2016, we defined three seasons. The wet season ran from January to March and was characterized by warm days, heavy rainfall, and rising flood waters in the Delta. The early dry season spanned April to July when the flood waters reached their peak and began receding, little to no rain, and cool winter temperatures. The late dry season spanned August to

December and was characterized by the drying of the Delta to its lowest levels where water only remained in permanent channels and hot summer days with temperatures regularly  $>30^{\circ}$  C.

With the cyclical nature of the floods, there are three major hydro-ecological zones in the region: permanent swamp, regularly flooded seasonal floodplains, and occasionally flooded floodplains (Wolski and Savenije 2006). The floodplains of the Delta are predominantly sandy and the soils accumulate little organic matter. Areas of the Delta with perennial water, permanent swamps, sustain obligate aquatic plant species like papyrus (*Cyperus papyrus*) and reed beds of *Phragmites australis* and *Typha bulrushes* (Kgathi et al. 2006, Wolski and Savenije 2006). Emergent sedges dominate areas that seasonally flood, and drier, occasionally flooded areas support various species of grasses (Wolski and Savenije 2006). Islands support riparian forests of semi-deciduous species comprised of phreatophytic species and salinity resistant grasses (Wolski and Savenije 2006). Dryland forests which do not flood are fed by rains (Wolski and Savenije 2006) and, in our study area, are composed of Mopane (*Colophospermum mopane*) woodlands (Kgathi et al. 2006).

Local villagers (population c. 5,000; Botswana Population and Housing Census 2011) are agropastoralists, keeping livestock (cattle, *Bos taurus/Bos indicus*; goat, *Capra hircus*; horse, *Equus caballus*; and donkey, *Equus asinus*) and tending crops (e.g., sorghum [*Sorghum sp.*], millet [*Pennisetum sp.*], and watermelon [*Citrullus lanatus*]) during the growing season (typically December–April). Livestock populations have risen dramatically in the area. Official cattle counts show the population almost doubling over the previous decade (from c. 6,000 in 2006 to c. 11,000 in 2017; Department of

Veterinary Services, Seronga office), though actual numbers are likely higher as the Dept. of Veterinary Services is not always able to survey all herds due to logistical constraints. Livestock are occasionally protected overnight (~60% of farmers reported protecting livestock every night in enclosures) in traditional thorn branch or wooden post enclosures, referred to locally as ‘kraals,’ but roam freely during the day (LeFlore et al. 2019, 2020). People live in villages and cattle posts (smaller familial settlements). With extensive human and livestock activity in the area (Fig 3.1), the area poses a risk to free-ranging lions. While unguarded livestock represent an easy prey option for lions, people kill lions in response to lost livestock or even the perceived threat of losing livestock (LeFlore et al. 2019, 2020). This landscape of risk exists within a critical area for lion conservation and may inhibit lion movements around the southern portion of the KAZA TFCA or even the dispersal of lions throughout the region.

### **3.3. Methods**

We began tracking lion activity in NG’s 11, 12, 22, 23, and 23A in October 2014. We used spoor tracking and received tips from local safari guides to locate and identify the various prides and coalitions in the area. Lions were photographed to identify individuals based on their unique whisker spot pattern and identifying marks (e.g., scars, ear notches, etc.; Schaller 1972). Data on demographics, location, pride composition, behavior, and prey species were recorded when lions were observed. Pride composition and demographic information enabled the selective deployment of GPS satellite collars between August 2015 and February 2016 under authority of the Botswanan Department of Wildlife and National Parks (research permit number: EWT 8/36/4 XXVII (61), darting permit numbers WP/RES 15/2/2 XXVII (22) & WP/RES 15/2/2 XXVII (141)).

Five lions were fitted with Telonics Iridium TGW-4570-3 units (Telonics Inc., Mesa, AZ, USA) GPS satellite/VHF radio collars which recorded a GPS fix five times/day. Collars were also programmed with two geofences acting as electronic boundaries of GPS points separating the study area into 3 areas: predominantly wildlife lands, communal grazing lands, and village lands. When a collared lion crossed one of the geofences, our research team was alerted via text message and could then provide villagers with an early warning of potential lion attacks (Chapter 4, this document).

Lion movement data and home range estimation were analyzed using kernel density estimation (KDE) with the *adehabitatHR* package (Calenge 2006) in R statistical software (R Development Core Team 2016). KDE was adapted for use in home range analyses by Worton (1989), is readily used in wildlife ecology studies, and has been shown to be the most reliable contouring method (Powell 2000). KDE has been shown to have advantages over other methods of home range estimation (e.g., minimum convex polygons) because it 1) can accommodate multiple centers of activity, 2) does not rely on outlying points to anchor corners, and 3) is less influenced by distant points (Hemson et al. 2005). Given this, we centered our efforts on KDE home range analyses and estimated home ranges at 95% and 50% isopleths denoting full home ranges and core areas of use, respectively. Lion relocations were analyzed seasonally to capture the effects of the dynamic Delta environment. Male and female home range sizes were compared via two-sided *t*-test and seasonal comparisons in home range size were made via analysis of variance (ANOVA) in R statistical software (R Development Core Team 2016).

We investigated both static and dynamic interactions between collared individuals by season. Static interaction refers to the joint space-use between two individuals without

consideration of temporal information associated with spatial fixes (Kernohan et al. 2001). Dynamic interaction accounts for both the spatial and temporal movements between two individuals and refers to the relatedness or interdependence of the two individual's movements (Macdonald et al. 1980, Doncaster 1990). To understand static interactions, we quantified two-dimensional spatial overlap in 95% and 50% KDE home ranges and calculated percent overlap in relation to each individual's home range. We also calculated the Utilization Distribution Overlap Index (UDOI; Fieberg and Kochanny 2005) to determine the extent of shared space use at the three-dimensional utilization distribution (UD) level. UDOI is a metric used to examine joint space use between two individuals as a function of the product of their individual UDs, under the assumption that their space use is independent of one another. The metric typically ranges from 0-1, with 0 values resulting from two home ranges that do not overlap, and values at 1 for two UDs that are uniformly distributed and have 100% overlap. Values >1 can result if two UDs are nonuniformly distributed but have a high degree of overlap. UDOI was calculated with the *adehabitatHR* package (Calenge 2006) in R as:

$$UDOI = A_{i,j} \int \int UD_i(x,y) \times UD_j(x,y)$$

where  $A_{i,j}$  is the area of the intersection between the two home ranges, and  $UD_i$  (resp.  $UD_j$ ) are the value of the utilization distribution of the associated animal  $i$  (resp.  $j$ ) at point  $(x,y)$ ; Fieberg and Kochanny 2005).

Cole's (1949) coefficient of association ( $Ca$ ) was used to measure dynamic interaction between collared individuals (Baumen 1998). Utilizing the *wildlifeDI* R package (Long et al. 2014), we calculated the coefficient of association as:

$$Ca = (2ST_{\alpha\beta}) / (n_{\alpha} + n_{\beta})$$

where  $ST_{\alpha\beta}$  are the spatially proximal and temporally simultaneous fixes based on user defined spatial and temporal thresholds (in this case 200m and 15min), and  $n_{\alpha}$  (resp.  $\beta$ ) is the total number of all fixes for individual  $\alpha$  (resp.  $\beta$ ) (Long et al. 2014).  $Ca$  measures the rate of all fixes within the defined thresholds and is measured on a scale of 0-1.  $Ca > 0.5$  indicates association, while  $Ca < 0.5$  indicates no association (Kernohan et al. 2001).  $Ca$  is a useful metric of attraction or association, as defined by the set thresholds, however, it is therefore subject to the manner in which the spatial and temporal thresholds were determined.

### **3.4. Results**

#### 3.4.1. Demographics & Monitoring

Between October 2014 and December 2016, we identified and monitored individuals from 5 prides and 5 coalitions in our study area (Tables 3.1-3.3). Pride sizes were small with the number of adult females ranging from 1-4 and all but one pride having  $\leq 2$  adult females. Adult male coalitions ranged from 1-2 individuals and a coalition of young dispersing males contained 3 individuals. The Airstrip Pride (AP) and Coalition (AC), Cut-tail Pride (CP), Kubu Pride (KP) and Coalition (KC), and Xamaga Coalition (XmC) were present in the study area for the full duration of the study. Other groups (i.e., Xakampa Pride [XkP] and Coalition [XkC], Hyena Den Pride [HDP], Left-eye Male [LM]) were believed to have immigrated into the area over the course of the study.

The three main prides (AP, CP and KP) raised young successfully during the study with numbers of young reaching the subadult age group ranging from 2-6 per pride (Tables 3.1-3.3). The two AP females birthed 6 cubs in January 2015, though only two

female cubs survived to sub-adulthood at the end of the study. During the same time frame, the Airstrip Dispersers (AD) left their natal pride and were seen periodically in the study area as they began life as a young coalition on their own. The CP also reared two young, though it was not known how many young were first born into the litter. Over the course of the study, the CP lost the second adult female, though her fate was not known. Two different aged male cubs were seen with the cut-tailed female, and it was believed the cut-tail female was raising the offspring from the other female's litter, though only two remained from both litters as the study progressed. The fates of the AP and CP young were not known as the study period concluded, as both pride's females were observed denning towards the end of 2016 without the young present. The larger KP reared six young males, two of which dispersed from their natal pride towards the end of our study, while the remaining four were seen on their own more frequently but still in close proximity to their natal pride.

The AP was controlled by a lone male (Airstrip Coalition [AC]) for the majority of the study period (Tables 3.1-3.3). We believe the AC formerly was comprised of 2 males and are unsure of the fate of the second male. The AC male lost pride tenure in the early dry season of 2016. Another lone male, the Xamaga Coalition (XmC), was believed to be in a coalition of three males prior to the start of the study, based on information shared by local guides. Guides believed the two coalition mates were killed by local villagers over the years, but this was not confirmed. The lone AC and XmC males formed a coalition (PiOP Coalition [PC]) of unrelated males during the early dry season 2016. They were believed to be unrelated as they had not previously associated. Additionally, we identified a pride of 2 females (Xakampa Pride [XkP]) believed to have immigrated to

the area from Duba which is deeper into the Delta to the southwest. The XkP was loosely associated with the Xakampa Coalition (XkC) which consisted of 2 males and was also believed to have immigrated from Duba.

Between August 2015 and December 2016, five lions were tracked using GPS satellite collars (Table 3.4 & Fig. 3.2). Information about lion groupings was regularly discussed with local villagers at Kgotla (community) meetings and collared individuals were assigned local names by community members. The collared AP female was named Mayenga Nyambi (“Decorated by the Gods”) while the CP female, who was already known to villagers as a cattle killer, was named Maleherehere (“The Sneaky One”). The collared AC male was named Multwankanda (“The Forager”), the lone male of the XmC was named Nduraghumbo (“The Head of the Household”), and the XkC male was named after one of the area villages, Eretsha.

### 3.4.2. Home Range Size

The 95% KDE home range sizes from the entire study period varied among the sexes (Table 3.5 & Figs. 3.3-3.4) and ranged from 421-846 km<sup>2</sup> ( $\bar{x}$  = 584 km<sup>2</sup>) for males and 270-368 km<sup>2</sup> ( $\bar{x}$  = 319 km<sup>2</sup>) for females, but were not statistically different ( $t = 1.87$ ,  $df = 2.49$ ,  $p = 0.176$ ). The 50% KDE core home ranges (Table 3.6) spanned 86-180 km<sup>2</sup> for males ( $\bar{x}$  = 122 km<sup>2</sup>) and 59-81 km<sup>2</sup> ( $\bar{x}$  = 70 km<sup>2</sup>) for females ( $t = 1.66$ ,  $df = 2.51$ ,  $p = 0.213$ ). Lion 95% KDE home ranges were smallest during the wet season (Table 3.5; males 179-296 km<sup>2</sup>,  $\bar{x}$  = 238 km<sup>2</sup>; females 65-201 km<sup>2</sup>,  $\bar{x}$  = 133 km<sup>2</sup>), as were 50% KDE core areas (Table 3.6; males 46-54 km<sup>2</sup>,  $\bar{x}$  = 50 km<sup>2</sup>; females 15-55 km<sup>2</sup>,  $\bar{x}$  = 35 km<sup>2</sup>). All collared individuals utilized larger areas during the early and late dry seasons for both 95% KDE home ranges and 50% KDE core areas (Table 3.5 & 3.6). The 95% KDE home

ranges for males ranged from 371-717 km<sup>2</sup> ( $\bar{x} = 529$  km<sup>2</sup>) and females ranged from 160-458 km<sup>2</sup> ( $\bar{x} = 250$  km<sup>2</sup>); 50% KDE core areas ranged from 76-214 km<sup>2</sup> ( $\bar{x} = 125$  km<sup>2</sup>) for males and 29-130 km<sup>2</sup> ( $\bar{x} = 61$  km<sup>2</sup>) for females. Variation in 95% KDE home range size and 50% core area size across the seasons was not significantly different ( $F = 2.07$ ,  $df = 3$ ,  $p = 0.157$ ;  $F = 1.75$ ,  $df = 3$ ,  $p = 0.211$ ).

### 3.4.3. Static Interactions

With five lions collared over the course of the study, the number of possible dyads was ten ( $n*(n-1)/2$ ); however, two individuals were never collared at the same time, therefore the number of possible dyads was nine. All nine dyads had static interactions at the 95% home range contour, meaning they utilized shared space, over the full study duration (Table 3.7, Fig. 3.5). Females utilized 152 km<sup>2</sup> of shared space, representing 41-56% of their respective home ranges. Males utilized between 125-434 km<sup>2</sup> of shared space, representing 16-90% of their respective home ranges. Male home ranges regularly overlapped with female home ranges and shared space ranged from 117-365 km<sup>2</sup>, representing 43-99% of female home ranges and 28-65% of male home ranges. Six of the possible nine dyads had static interaction at 50% core home ranges over the full study duration (Table 3.8, Fig. 3.5), two of which were for individuals known to associate with each other, one M-F dyad and one M-M. Females shared 11 km<sup>2</sup> which represented 14-19% of their core home ranges. One male dyad shared 61 km<sup>2</sup> which represented 34-71% of their core home ranges, and these individuals were known to associate for part of the study period. Male and female core home ranges regularly overlapped with 24-43 km<sup>2</sup> shared space representing 41-68% of female core home ranges and 13-50% of male core home ranges.

Seasonal static interactions were prevalent in the highly dynamic Delta ecosystem (Tables 3.9-3.16 & Figs. 3.6-3.13). Seasonal static interactions between the two non-associating collared females at the 95% KDE isopleth ranged from 22-100 km<sup>2</sup> representing 22-75% of one individual's home range (Tables 3.12, 3.14, 3.16 & Figs. 3.8, 3.10, 3.12). Static interactions were the highest for both individuals during the wet and early dry seasons when the study area is inundated with flood waters (Table 3.12 & Fig 3.8). While spatial overlap at the 95% home range isopleth was perpetual for females, their 50% core home ranges overlapped during the wet season and early dry season (2-24 km<sup>2</sup>, 4-60%; Tables 3.11, 3.13 & Figs. 3.9, 3.11). Seasonal static interactions between non-associating males at the 95% home range isopleth ranged from 90-269 km<sup>2</sup> representing 22-40% of individual ranges (Tables 3.10, 3.12, 3.14, 3.16 & Figs. 3.6, 3.8, 3.10, 3.12). Two previously non-associating males (M2 & M3) began associating in June 2016 during the early dry season and remained as such for the duration of the study. As a result, their static interactions increased substantially during this period. At the 95% home range isopleth, these males utilized 451 km<sup>2</sup> (63-86%) of shared space during the early dry season 2016 and 457 km<sup>2</sup> (96%) during the late dry season 2016 (Tables 3.14, 3.16 & Fig. 3.10, 3.12). At the 50% core home range level, this newly formed coalition shared 37 km<sup>2</sup> (17-39%) of space during the early dry season 2016 and 113 km<sup>2</sup> (86-88%) during the late dry season 2016 (Tables 3.13, 3.15 & Fig. 3.11, 3.13). Seasonal static interactions at the 50% core home range isopleth for non-associating males were limited, ranging from 0-19 km<sup>2</sup> (0-25%) of individual core home ranges (Tables 3.9, 3.11, 3.13, 3.15 & Figs. 3.7, 3.9, 3.11, 3.13). Seasonal static interactions between males and females at the 95% isopleth varied widely and ranged from 20-410 km<sup>2</sup> (31-100% of

female home ranges; 7-92% of males; Tables 3.10, 3.12, 3.14, 3.16 & Figs. 3.6, 3.8, 3.10, 3.12), with the highest amount of overlap reserved for dyads where individuals were known to associate. At the 50% core home range level, males and females shared 0-59 km<sup>2</sup> (0-98% of female home ranges; 0-76% of males; Tables 3.9, 3.11, 3.13, 3.15 & Figs. 3.7, 3.9, 3.11, 3.13), again with the highest amount of overlap reserved for dyads where individuals associated. In M-F dyads where there was no known association, static interaction was limited at the 50% core home range level (0-10 km<sup>2</sup>; 0-23% for both sexes).

Given the broad range in home range overlap at the two-dimensional level over the course of the study, we calculated three-dimensional space use overlap using UDOI to quantify the extent of shared space use between individuals. While percentages of space use were variable, at the 95% contour UDOIs for non-associating lion dyads were low (<0.30) over the course of the whole study (Table 3.17). Seasonally, OUDIs for non-associating individuals ranged from <0.01-0.40. UDOIs for associating individuals ranged from 0.57-0.87 over the course of the whole study and 0.51-1.23 seasonally. The highest UDOI registered was for the newly formed PiOP coalition males (M2 & M3). Other high UDOIs were found between males and females who were known to associate and likely mated with each other (UDOIs 0.51-1.05). At the 50% core area contour (Table 3.18), UDOIs were low for all lion dyads throughout the study (0.00-0.13), with the highest of these values resulting from dyads where there was known association. At the seasonal level, non-associating individuals showed low UDOIs (0.00-0.07), and associating individuals also had little overlap of their UD's (0.06-0.30), though highest levels were found only in individuals known to associate.

#### 3.4.4. Dynamic Interactions

While static interactions were present at both 50% and 95% home range levels for non-associating females throughout the study, seasonal *Ca* was 0.00 (Tables 3.19-3.20). Unrelated females did not associate at all during the study. Likewise, for unrelated males, seasonal *Ca* was extremely low (0.00-0.04). However, over the course of the study, the newly formed PiOP coalition led to *Ca* increasing (from 0.01 to 0.47) between males who were believed to be unrelated. *Ca* among male-female dyads were low (0.00-0.08) between individuals not observed associating, and *Ca* for male-female dyads known to associate during the study ranged from 0.00-0.47. M2 (Multwankanda) was the overlapping individual in known associations described above.

#### 3.4.5. Proximity to Risk

All collared individuals spent <9% of their time within 3 km of human settlements over the course of the whole study (Table 3.21, Fig. 3.1). The XkC male (Eretsha) had a median distance to the zone of human habitation of 3.7 km and likely had the highest chance of an encounter with humans. Other individuals had higher median distances to the zone of human habitation (8-10.9 km) and lower risk of encountering humans. The XmC male (Nduraghumbo) did venture closer to humans than usual during the early dry season 2016 (mdn dist. = 4.9 km) and 15% of relocations were within the zone of human habitation. The CP female (Maleherehere) was consistently in livestock grazing areas (30-46% of all relocations) over the course of the study (Table 3.22). All other individuals were in livestock grazing areas most often in the late dry season (30-81% of all relocations) when livestock ranged farther south into the delta (Fig. 3.1), with

median distances ranging from 0.0-1.8 km for all individuals. Both the XkC male and CP female were known cattle killers (LeFlore, unpublished data).

### **3.5. Discussion**

These results represent the most thorough assessment to date of lion home ranges, joint space use, and movements in the human-dominated Eastern Panhandle of the Okavango Delta. Lion home ranges in the Eastern Panhandle of the Okavango Delta were considerably smaller than those found in the more arid Central Kalahari region of Botswana where 95% contour home ranges averaged  $>2,700 \text{ km}^2$  (Funston 2001, Zehnder et al. 2018) and 50% core areas averaged  $\sim 560 \text{ km}^2$  (Zehnder et al. 2018). In East Africa, lion home range sizes vary dramatically (4-450  $\text{km}^2$ ; Schaller 1972, Gittleman and Harvey 1982, Van Orsdol et al. 1985, Valeix et al. 2012, Ngwenya et al. 2013, Tuqa et al. 2014, Bouley et al. 2018, Mbizah et al. 2019). Variation in home range size is site specific (Tumenta et al. 2013) but is negatively correlated with population density (Loveridge et al. 2009) and prey abundance (Van Orsdol et al. 1985, Bauer and De Iongh 2005, Loveridge et al. 2009). Average pride sizes were small for collared prides, which could be caused by numerous factors including the flooding of the region, high levels of intraspecific competition, low prey densities, and high levels of human-lion conflict in the region (Stander 1997, Hemson 2003, Kotze et al. 2018). Given high levels of retaliatory killings in this human-lion conflict zone (LeFlore et al. 2019), lion densities were likely lower than could be sustained by wild prey availability and additional domestic prey, leading to larger home ranges than comparable systems. Additional research focused on prey densities (wild and domestic) should be conducted in this area to further illuminate this point.

With reasonably large home ranges, unrelated collared individuals shared extensive amounts of their 95% and 50% core home range. Static overlap was highest during the wet season and early dry season when the area was inundated with flood waters. Our research aligns with published literature showing spatial overlap among unrelated lion groups (Schaller 1972, Van Orsdol et al. 1985, Spong 2002, Bauer and De Iongh 2005, Davidson et al. 2011, Tumenta et al. 2013, Benhamou et al. 2014, Kotze et al. 2018), and provides additional evidence that unrelated males occasionally form coalitions later in life (Schaller 1972, Bygott et al. 1979, Packer and Pusey 1982, Benhamou et al. 2014). Overlap at the two-dimensional core home range level was higher in our study than reported elsewhere (Spong 2002), but core home range overlap was low when compared via three-dimensional utilization distribution overlap index. While static interactions were prevalent in our study, dynamic interactions were reserved for associating individuals, suggesting unrelated individuals share space but vary their use of shared space temporally to avoid potentially hostile interactions. While Benhamou et al. (2014) found that dynamic avoidance (spatiotemporal movement to minimize interactions) between unrelated lions was rare, avoidance can be facilitated by nonaggressive territorial behaviors (scent marking, Schaller 1972; roaring, McComb et al. 1993, McComb et al. 1994). Additionally, individuals may operate in an existing dominance hierarchy and move independently when they are navigating shared space (Benhamou et al. 2014). We suggest that the dynamic Delta landscape and potential interactions with humans likely restrict lion movements in the Eastern Panhandle and contribute to spatial overlap in home ranges. Additionally, there are ecological factors

(e.g., conspecifics holding neighboring territories, vegetation structure, prey availability, water access) that may also restrict lion movements in the area (Dures et al. 2020).

Both anthropogenic and ecological factors are understood to impact lion movements and intraspecific interactions (Spong 2002, Hemson 2003, Davidson et al. 2010, Kotze et al. 2018, Dures et al. 2020). Most studies involving lion movements and proximity to anthropogenic threats focus on lions who spend most of their time within protected area boundaries but may range outside protected areas and encounter people (e.g., Loveridge et al. 2010, Tumenta et al. 2013, Zehnder et al. 2018). Findings presented here are one of the few examples where monitored lions ranged entirely beyond protected area boundaries in areas of high conflict potential. While most lions exist within protected areas, anthropogenic impacts beyond protected area boundaries can impact populations within protected areas (Woodroffe and Ginsberg 1998, Loveridge et al. 2010). Studying systems beyond park boundaries with high levels of human lion conflict and establishing conservation programs accounting for both ecological and sociocultural dimensions will better aid lion conservation efforts moving forward (Chapter 4 this document, Decker et al. 2012, Weise et al. 2019, LeFlore et al. 2020).

### 3.6. Literature Cited

- Bauer, H. and H.H. De Iongh. 2005. Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology* 43: 208-214.
- Bauer, H. and S. Van der Merwe. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38: 26-31.
- Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. Hunter, D. 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*: doi: 10.1073/pnas.1500664112.
- Bauer, H., C. Packer, P. Funston, P. Henschel, and K. Nowell. 2016. *Panthera leo* in the IUCN Red List of Threatened Species. Available at <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en> Accessed October 8, 2016.
- Bauman, P.J. 1998. *The Wind Cave National Park Elk Herd: Home Ranges, Seasonal Movements, and Alternative Control Methods*. South Dakota State University, Brookings, SD, USA.
- Benhamou, S., M. Valeix, S. Chameillé-Jammes, D.W. Macdonald, and A.J. Loveridge. 2014. Movement-based analysis of interactions in African lions. *Animal Behavior* 90:171-180.
- Bertram, B.C.R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology* 177: 463-482.
- Bertram, B.C.R. 1976. Kin selection in lions and in evolution. In *growing points in ethology* pp281-301. P. Bateson and R.A. Hinde. Eds. Cambridge University Press.
- Botswana Population and Housing Census. 2011. Available at [www.catalog.ihnsn.org/index.php/catalog/4243/download/55990](http://www.catalog.ihnsn.org/index.php/catalog/4243/download/55990). Accessed on October 15, 2015.
- Bouley, P., P. Michael, R. Branco, and N.H. Carter. 2018. Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biological Conservation* 227: 233-242.
- Bygott, J. D., B.C. Bertram, and J.P. Hanby. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282: 839-841.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516-519.
- Chardonnet, P. 2002. *Conservation of the African Lion: Contribution to a Status Survey*. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA, Paris, France.

- Cole, L.C. .1949. The measurement of interspecific association. *Ecology* 30: 411–424.
- Davidson, Z., M. Valeix, A.J. Loveridge, H. Madzikanda, and D.W. Macdonald. 2011. Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation* 144: 114-121.
- Decker, D.J., S.J. Riley, and W.F. Siemer eds. 2012. *Human Dimensions of Wildlife Management*. Johns Hopkins University Press, Baltimore, Maryland.
- Doncaster, C.P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* 143: 431-443.
- Dures, S.G., C. Carbone, V. Savolainen, G. Maude, and D. Gottelli. Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation* 23: 502-515.
- Elliot, N., M. Valeix, D.W. Macdonald, and A.J. Loveridge. 2014. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos* 123: 1049-1056.
- Estes, R.D. 1991. *The behavior guide to African Mammals: including hoofed mammals, carnivores, primates*. University of California Press. Berkeley and Los Angeles, California.
- Fieberg, J. and C.O. Kochanny. 2005. Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management* 69:1346-1359.
- Funston, P. 2014. The Kavango-Zambezi Transfrontier Conservation Area – critical for African lions. *Cat News* 60: 4-7.
- Funston, P. 2001. *Kalahari Transfrontier Lion Project: Final Report*. Endangered Wildlife Trust, South Africa.
- Fynn, R.W.S., M. Murray-Hudson, M. Dhliwayo, and P. Scholte. 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management* 23: 559-581.
- Gittleman, J.L. and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Social Biology* 10: 57-63.
- Hayward, M.W. and G.I.H. Kerley. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology* 267: 309-322.
- Hemson, G. 2003. *The ecology and conservation of lions: human-wildlife conflict in semi-arid Botswana*. University of Oxford, UK (Dissertation Thesis).
- Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. Macdonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74: 455-463.

- Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements. *Radio Tracking and Animal Populations* (eds J. Millspaugh and J.M. Marzluff), pp. 125-166. Academic Press, New York.
- Kgathi, D.L., D. Kniveton, S. Ringrose, A.R. Turton, C.H.M. Vanderpost, J. Lundqvist, and M. Seely. 2006. The Okavango; a river supporting its people, environment and economic development. *Journal of Hydrology* 331: 3-17.
- Kotze, R., M. Keith, C. Winterbach, H. Winterbach, and J.P. Marshal. 2018. The influence of social and environmental factors on organization of African lion (*Panthera leo*) prides in the Okavango Delta. *Journal of Mammalogy* 99: 845-858
- LeFlore, E.G., T.K. Fuller, M. Tomeletso, and A.B Stein. 2019. Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation* 18: e00592.
- LeFlore E.G., T.K. Fuller, M. Tomeletso, T.C. Dimbindo, and A.B Stein 2020 Human dimensions of human–lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana. *Environmental Conservation* 47: 182-189.
- Liberg, O., C. Chapron, P. Wabakken, H.C. Pedersen, N.T. Hobbs, and H. Sand. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society, Series B*, 279: 910-915.
- Long, J.A., T.A. Nelson, S.L. Webb, and K.L. Gee. 2014. A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology* 83: 1216-1233.
- Loveridge, A.J., G. Hemson, Z. Davidson, and D.W. Macdonald. 2010. African lions on the edge: reserve boundaries as ‘attractive sinks’. *Biology and Conservation of Wild Felids* (eds D.W. Macdonald and A.J. Loveridge), pp. 283-304. Oxford University Press, Oxford, UK.
- Loveridge, A.J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz, and D.W. Macdonald. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32: 953-962.
- Macdonald, D.W., F.G. Ball, and N.G. Hough. 1980. The evaluation of home range size and configuration using radio tracking data. *A Handbook on Biotelemetry and Radio Tracking: Proceedings of an International Conference on Telemetry and Radio Tracking in Biology and Medicine* (eds C.J. Amlaner and D.W. Macdonald), pp. 405-424. Pergamon Press, Oxford, UK.
- Mbaiwa, J.E. 2018. Effects of the safari hunting tourism ban on rural livelihoods and wildlife conservation in Northern Botswana. *South African Geographical Journal* 100: 41-61.
- Mbizah, M.M., M. Valeix, D.W. Macdonald, and A.J. Loveridge. 2019. Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution* 9: 9111-9119.

- McCarthy, J.M., T. Gumbrecht, T. McCarthy, P. Frost, K. Wessels, and F. Seidel. 2003. Flooding Patterns of the Okavango Wetland in Botswana between 1972 and 2000. *Journal of the Human Environment* 32: 453-457.
- McCarthy, T.S., G.R.J. Cooper, P.D. Tyson, and W.N. Ellery. 2000. Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *South African Journal of Science* 96: 25-33.
- McComb, K., C. Packer, and A. Pusey. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour* 47: 379-387.
- McComb, K., A. Pusey, C. Packer, and J. Grinnell. 1993. Female lions can identify potentially infanticidal males from their roars. *Proceedings of the Royal Society B: Biological Sciences*, 252: 59-64.
- Mweze, M. 2014. Botswana Department of Wildlife and National Parks. Personal Communication. October 2014, Seronga, Ngamiland, Botswana.
- Ngwenya, M.M., N.M. Mkandhla, and J.V. Muzvondiwa. 2013. A Comparison of Lion Home Range Sizes in Two Management Blocks in a Semi-Arid Savannah National Park of Zimbabwe. *International Journal of Science and Research* 2: 388-396.
- Packer, C. and A.E. Pusey. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 286: 740-742.
- Packer, C., H. Brink, B.M. Kissui, H. Maliti, H. Kushnir, and T. Caro. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology* 25: 142-153.
- Packer, C., D. Scheel, and A.E. Pusey. 1990. Why lions form groups: food is not enough. *American Naturalist* 136: 1-19.
- Powell, R.A. 2000. Animal home ranges and territories and home range estimators. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani and T.K. Fuller), pp. 65-110. Columbia University, New York.
- R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <<http://www.r-project.org>>.
- Ramberg, L., P. Hancock, M. Lindholm, T. Meyer, S. Ringrose, J. Sliva, J. Van As, and C. VanderPost. 2006. Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences* 8: 310-337.
- Riggio, J., A. Jacobson, L. Dollar, H. Bauer, A. Dickman, P. Funston, P. Henschel, H. de Iongh, L. Lichtenfeld, C. Packer, and S. Pimm. 2013. The size of savannah Africa: a lion's 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.
- Scheel, D. and C. Packer 1991. Group hunting behavior of lions: a search for cooperation. *Animal Behaviour* 41: 697-709.
- Spong, G. 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: Social and ecological factors. *Behavioral Ecology and Sociobiology* 52: 303-307.
- Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology* 29: 445-454.
- Treves, A. and K.U. Karanth. 2003 Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491-1499.
- Tumenta, P.N., M. van't Zelfde, B.M. Croes, R. Buij, P.J. Funston, H.A. Udo De Haes, and H.H. De Iongh. 2013. Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology* 78: 461-469.
- Tuqa, J.H., P. Funston, C. Musyoki, G.O. Ojwang, N.N. Gichuki, H. Bauer, W. Tamis, S. Dolrenry, M. Van't Zelfde, G.R. de Snoo, and H.H. de Iongh. 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation* 2: 1-10.
- Valeix, M., A.J. Loveridge, and D.W. Macdonald. 2012. Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. *Ecology* 93: 2490-2496.
- Valeix, M., S. Chamaillé-Jammes, A.J. Loveridge, Z. Davidson, J.E. Hunt, H. Madzikanda, and D.W. Macdonald. 2011. Understanding Patch Departure Rules for Large Carnivores: Lion Movements Support a Patch-Disturbance Hypothesis. *The American Naturalist* 178: 269-275.
- Van Orsdol, K. G. 1981. Lion Predation in Rwenzori National Park, Uganda. PhD Thesis, University of Cambridge.
- Van Orsdol, K. G., J.P. Hanby, and J.D. Bygott. 1985. Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*. 206: 97-112.
- Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution* 6: 242.
- Winterbach, H.E.K., C.W. Winterbach, and M.J. Somers. 2014. Landscape Suitability in Botswana for the Conservation of Its Six Large African Carnivores. *PLOS One* 9: e100202.

- Wittemyer, G., P. Elsen, W.T. Bean, A.C.O. Burton, and J.S. Brashares. 2008. Accelerated human population growth at protected area edges. *Science* 321: 123-126.
- Wolski, P. and H.H.G. Savenije. 2006. Dynamics of floodplain-island groundwater flow in the Okavango Delta, Botswana. *Journal of Hydrology*. 320: 283-301.
- Woodroffe, R. and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164-168.
- Zehnder, A., S. Henley, and R. Weibel. 2018. Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability. *Zoology* 128: 46-54.

### 3.7. Tables and Figures

Table 3.1. Lion prides monitored in the northern Botswana study area from October-December 2014.

Vernacular ID	Total no. of individuals	Adult males	Adult females	Sub-adult males	Sub-adult females	Cubs	Reproduction/Notes
Airstrip Pride	5	0	2	3	0	0	Both females pregnant in Dec.
Cut-tail Pride	2	0	2	0	0	?	Unknown litter sizes, both females seen with swollen mammae in Nov.
Kubu Pride	10	0	4	0	0	6	Cubs estimated ~6 months in Dec.
Airstrip Coalition	2	2	0	0	0	0	Seen with Airstrip pride females
Kubu Coalition	2	2	0	0	0	0	Assumed to father Kubu cubs.
<b>Total</b>	<b>21</b>	<b>4</b>	<b>8</b>	<b>3</b>	<b>0</b>	<b>6 (?)</b>	

Table 3.2. Lion prides monitored on the northern Botswana study area from January-December 2015.

Vernacular ID	Total no. of individuals	Adult males	Adult females	Sub-adult males	Sub-adult females	Cubs	Reproduction/Notes
Airstrip Pride*	8	0	2	0	0	6	Cubs estimated born ~Jan. 2015.
Kubu Pride	13	0	4	6	0	3	Largest stable pride.
Cut-tail Pride	5	0	2	0	0	3	3 cubs seen by guides end of 2015. Females loosely associate.
Xakampa Pride	2	0	2	0	0	0	Believed to emigrate from Duba.
Airstrip Coalition*	2	2	0	0	0	0	Fathered Airstrip cubs.
Airstrip Dispersers	3	3	0	0	0	0	Dispersed from Airstrip ~Jan 2015.
Kubu Coalition	2	2	0	0	0	0	Fathered Kubu cubs.
Xakampa Coalition*	2	2	0	0	0	0	Believed to emigrate from Duba.
Xamaga Coalition*	1	1	0	0	0	0	Believed previously in coalition of 3.
<b>Total</b>	<b>38</b>	<b>10</b>	<b>10</b>	<b>6</b>	<b>0</b>	<b>12</b>	

\* Denotes a lion group with an individual collared in August 2015.

Table 3.3. Lion prides monitored in the northern Botswana study area from January-December 2016.

Vernacular ID	Total no. of individuals	Adult males	Adult females	Sub-adult males	Sub-adult females	Cubs	Reproduction/Notes
Airstrip Pride*	4	0	2	0	2	?	Both females denning in Dec.
Hyena Den Pride	2	0	1	0	1	0	Unknown reproduction.
Kubu Pride	7	0	3	4	0	0	4 cubs from 2014 remain.
Cut-tail Pride*	5	0	1	2	0	2+?	Denning Dec 2016 - 2 cubs seen, likely more.
Xakampa Pride	2	0	2	0	0	?	One female seen with swollen mammae in Aug.
Kubu Coalition	1	1	0	0	0	0	Unknown.
Left-Eye Male	1	1	0	0	0	0	Mated with both females of Airstrip Pride.
PiOP Coalition*	2	2	0	0	0	0	Previous Airstrip male and Xamaga male formed PiOP Coalition. Strong association with Maleherehere Pride, including possible mating. Regular re-visit to female and den sites after litter was born end of 2016.

Xakampa Coalition	2	2	0	0	0	0	Unknown. Male slipped collar Dec 2015, but observed Nov 2016.
-------------------	---	---	---	---	---	---	---

---

Total	26	6	9	6	3	2+?	
-------	----	---	---	---	---	-----	--

---

\* Denotes a lion group that has an individual collared, Cut-tail pride female collared in February 2016.

Table 3.4. GPS satellite collar data for 5 collared lions in the northern Botswana study area between August 2015 and December 2016.

Vernacular ID		Date collar deployed	Date collar retrieved	No. of attempted fixes	No. of successful fixes	Percent successful
Airstrip Pride <i>Mayenga Nyambi</i>	F	Aug 2015	Dec 2016	2,399	2,285	95
Cut-tail Pride <i>Maleherehere</i>	F	Feb 2016	Dec 2016	1,681	1,583	94
PiOP Coalition*						
<i>Multwankanda</i>	M	Aug 2015	Dec 2016	2,475	1,777	72
<i>Nduraghumbo</i>	M	Aug 2015	Dec 2016	2,531	2,273	90
Xakampa Coalition <i>Eretsha</i>	M	Aug 2015	Dec 2016	609	565	93

\*PiOP Coalition formed after collar deployment; Airstrip Male and Xamaga male joined to form PiOP coalition.

Table 3.5. Seasonal 95% lion home range size estimates based on kernel density estimation (*href*) methods for 5 collared lions in the northern Botswana study area between August 2015 and December 2016.

Vernacular ID <i>Villager given name</i>	All km <sup>2</sup>	Late Dry 2015 km <sup>2</sup>	Wet 2016 km <sup>2</sup>	Early Dry 2016 km <sup>2</sup>	Late Dry 2016 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	270	251	201	175	208
Cut-tail Pride <i>Maleherehere</i>	368	N/A	65	458	160
PiOP Coalition*					
<i>Multwankanda</i>	484	371	179	526	478
<i>Nduraghumbo</i>	846	717	296	711	477
Xakampa Coalition <i>Eretsha</i>	421	421	N/A	N/A	N/A

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.6. Seasonal 50% lion home range size estimates based on kernel density estimation (*href*) methods for 5 collared lions in the northern Botswana study area between August 2015 and December 2016.

Vernacular ID <i>Villager given name</i>	All km <sup>2</sup>	Late Dry 2015 km <sup>2</sup>	Wet 2016 km <sup>2</sup>	Early Dry 2016 km <sup>2</sup>	Late Dry 2016 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	59	69	55	40	38
Cut-tail Pride <i>Maleherehere</i>	81	N/A	15	130	29
PiOP Coalition*					
<i>Multwankanda</i>	86	76	46	96	131
<i>Nduragumbo</i>	180	132	54	214	128
Xakampa Coalition <i>Eretsha</i>	100	100	N/A	N/A	N/A

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.7. During the entire study period (Aug 2015-Dec 2016), 95% core home range estimates, and percent overlap (area of overlap), based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana. Percent overlap with home range corresponds to the lions on top of contingency table. Lions that were not collared during the same timeframe and thus had no record of overlap are noted as “NR.”

Vernacular ID <i>Villager Given Name</i> 95% home range	Airstrip Pride <i>Mayenga Nyambi</i> 270 km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 368 km <sup>2</sup>	Xakampa Coalition <i>Eretsha</i> 421 km <sup>2</sup>	PiOP Coalition <i>Multwankanda</i> 484 km <sup>2</sup>	PiOP Coalition <i>Nduraghumbo</i> 846 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	41% (152 km <sup>2</sup> )	28% (117 km <sup>2</sup> )	51% (248 km <sup>2</sup> )	29% (242 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	56% (152 km <sup>2</sup> )	- (-)	NR	65% (315 km <sup>2</sup> )	43% (365 km <sup>2</sup> )
Xakampa Coalition <i>Eretsha</i>	43% (117 km <sup>2</sup> )	NR	- (-)	26% (125 km <sup>2</sup> )	16% (132 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	92% (248 km <sup>2</sup> )	86% (315 km <sup>2</sup> )	30% (125 km <sup>2</sup> )	- (-)	51% (434 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	90% (242 km <sup>2</sup> )	99% (365 km <sup>2</sup> )	31% (132 km <sup>2</sup> )	90% (434 km <sup>2</sup> )	- (-)

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.8. During the entire study period (Aug 2015-Dec 2016), 50% core home range estimates, and percent overlap (area of overlap), based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana. Percent overlap with home range corresponds to the lions on top of contingency table. Lions that were not collared during the same timeframe and thus had no record of overlap are noted as “NR.”

Vernacular ID <i>Villager Given Name</i> 50% home range	Airstrip Pride <i>Mayenga Nyambi</i> 59 km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 81 km <sup>2</sup>	Xakampa Coalition <i>Eretsha</i> 100 km <sup>2</sup>	PiOP Coalition <i>Multwankanda</i> 86 km <sup>2</sup>	PiOP Coalition <i>Nduraghumbo</i> 180 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	14% (11 km <sup>2</sup> )	0% (0 km <sup>2</sup> )	47% (40 km <sup>2</sup> )	13% (24 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	19% (11 km <sup>2</sup> )	- (-)	NR	50% (43 km <sup>2</sup> )	23% (41 km <sup>2</sup> )
Xakampa Coalition <i>Eretsha</i>	0% (0 km <sup>2</sup> )	NR	- (-)	0% (0 km <sup>2</sup> )	0% (0 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	68% (40 km <sup>2</sup> )	53% (43 km <sup>2</sup> )	0% (0 km <sup>2</sup> )	- (-)	34% (61 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	41% (24 km <sup>2</sup> )	51% (41 km <sup>2</sup> )	0% (0 km <sup>2</sup> )	71% (61 km <sup>2</sup> )	- (-)

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.9. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2015-Dec 2015. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 50% home range	Airstrip Pride <i>Mayenga Nyambi</i> 69 km <sup>2</sup>	Xakampa Coalition <i>Eretsha</i> 100 km <sup>2</sup>	Airstrip Coalition <i>Multwankanda</i> 76 km <sup>2</sup>	Xamaga Coalition <i>Nduraghumbo</i> 132 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	0% (0 km <sup>2</sup> )	76% (58 km <sup>2</sup> )	8% (10 km <sup>2</sup> )
Xakampa Coalition <i>Eretsha</i>	0% (0 km <sup>2</sup> )	- (-)	0% (0 km <sup>2</sup> )	1% (1 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	84% (58 km <sup>2</sup> )	0% (0 km <sup>2</sup> )	- (-)	14% (19 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	15% (10 km <sup>2</sup> )	1% (1 km <sup>2</sup> )	25% (19 km <sup>2</sup> )	- (-)

Table 3.10. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2015-Dec 2015. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 95% home range	Airstrip Pride <i>Mayenga Nyambi</i> 251 km <sup>2</sup>	Xakampa Coalition <i>Eretsha</i> 421 km <sup>2</sup>	Airstrip Coalition <i>Multwankanda</i> 371 km <sup>2</sup>	Xamaga Coalition <i>Nduraghumbo</i> 717 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	23% (97 km <sup>2</sup> )	65% (242 km <sup>2</sup> )	27% (191 km <sup>2</sup> )
Xakampa Coalition <i>Eretsha</i>	39% (97 km <sup>2</sup> )	- (-)	40% (149 km <sup>2</sup> )	22% (155 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	96% (242 km <sup>2</sup> )	35% (149 km <sup>2</sup> )	- (-)	38% (269 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	76% (191 km <sup>2</sup> )	37% (155 km <sup>2</sup> )	73% (269 km <sup>2</sup> )	- (-)

Table 3.11. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the wet season Jan 2016-Mar 2016. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 50% home range	Airstrip Pride <i>Mayenga Nyambi</i> 55km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 15 km <sup>2</sup>	Airstrip Coalition <i>Multwankanda</i> 46 km <sup>2</sup>	Xamaga Coalition <i>Nduraghumbo</i> 54 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	13% (2 km <sup>2</sup> )	72% (33 km <sup>2</sup> )	0% (0 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	4% (2 km <sup>2</sup> )	- (-)	9% (4 km <sup>2</sup> )	0% (0 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	60% (33 km <sup>2</sup> )	31% (4 km <sup>2</sup> )	- (-)	0% (0 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	0% (0 km <sup>2</sup> )	0% (0 km <sup>2</sup> )	0% (0 km <sup>2</sup> )	- (-)

Table 3.12. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the wet season Jan 2016-Mar 2016. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 95% home range	Airstrip Pride <i>Mayenga Nyambi</i> 201 km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 65 km <sup>2</sup>	Airstrip Coalition <i>Multwankanda</i> 179 km <sup>2</sup>	Xamaga Coalition <i>Nduraghumbo</i> 296 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	75% (49 km <sup>2</sup> )	92% (165 km <sup>2</sup> )	28% (82 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	24% (49 km <sup>2</sup> )	- (-)	29% (51 km <sup>2</sup> )	7% (20 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	82% (165 km <sup>2</sup> )	79% (51 km <sup>2</sup> )	- (-)	30% (90 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	41% (82 km <sup>2</sup> )	31% (20 km <sup>2</sup> )	50% (90 km <sup>2</sup> )	- (-)

Table 3.13. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the early dry season Apr 2016-Jul 2016. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 50% home range	Airstrip Pride <i>Mayenga Nyambi</i> 40km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 130 km <sup>2</sup>	Airstrip Coalition <i>Multwankanda</i> 96 km <sup>2</sup>	Xamaga Coalition <i>Nduraghumbo</i> 214 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	19% (24 km <sup>2</sup> )	41% (39 km <sup>2</sup> )	4% (9 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	60% (24 km <sup>2</sup> )	- (-)	59% (57 km <sup>2</sup> )	28% (60 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	98% (39 km <sup>2</sup> )	44% (57 km <sup>2</sup> )	- (-)	17% (37 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	23% (9 km <sup>2</sup> )	46% (60 km <sup>2</sup> )	39% (37 km <sup>2</sup> )	- (-)

Table 3.14. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the early dry season Apr 2016-Jul 2016. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 95% home range	Airstrip Pride <i>Mayenga Nyambi</i> 175 km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 458 km <sup>2</sup>	Airstrip Coalition <i>Multwankanda</i> 526 km <sup>2</sup>	Xamaga Coalition <i>Nduraghumbo</i> 711 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	22% (100 km <sup>2</sup> )	29% (151 km <sup>2</sup> )	15% (109 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	57% (100 km <sup>2</sup> )	- (-)	73% (386 km <sup>2</sup> )	58% (410 km <sup>2</sup> )
Airstrip Coalition <i>Multwankanda</i>	86% (151 km <sup>2</sup> )	84% (386 km <sup>2</sup> )	- (-)	63% (451 km <sup>2</sup> )
Xamaga Coalition <i>Nduraghumbo</i>	62% (109 km <sup>2</sup> )	90% (410 km <sup>2</sup> )	86% (451 km <sup>2</sup> )	- (-)

Table 3.15. 50% core home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2016-Dec 2016. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 50% home range	Airstrip Pride <i>Mayenga Nyambi</i> 38 km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 29 km <sup>2</sup>	PiOP Coalition* <i>Multwankanda</i> 131 km <sup>2</sup>	PiOP Coalition* <i>Nduraghumbo</i> 128 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	0% (0 km <sup>2</sup> )	2% (3 km <sup>2</sup> )	3% (4 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	0% (0 km <sup>2</sup> )	- (-)	18% (24 km <sup>2</sup> )	19% (24 km <sup>2</sup> )
PiOP Coalition* <i>Multwankanda</i>	8% (3 km <sup>2</sup> )	83% (24 km <sup>2</sup> )	- (-)	88% (113 km <sup>2</sup> )
PiOP Coalition* <i>Nduraghumbo</i>	11% (4 km <sup>2</sup> )	83% (24 km <sup>2</sup> )	86% (113 km <sup>2</sup> )	- (-)

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.16. 95% home range estimates, area of overlap, and percent overlap based on kernel density estimation (href) for simultaneously collared lions in the northern Botswana study area during the late dry season Aug 2016-Dec 2016. Home ranges and overlap values presented in parentheses shown in km<sup>2</sup>, percent overlap with full home range extent corresponds to the lions on top of contingency table.

Vernacular ID <i>Villager Given Name</i> 95% home range	Airstrip Pride <i>Mayenga Nyambi</i> 208 km <sup>2</sup>	Cut-tail Pride <i>Maleherehere</i> 160 km <sup>2</sup>	PiOP Coalition* <i>Multwankanda</i> 478 km <sup>2</sup>	PiOP Coalition* <i>Nduraghumbo</i> 477 km <sup>2</sup>
Airstrip Pride <i>Mayenga Nyambi</i>	- (-)	14% (22 km <sup>2</sup> )	25% (120 km <sup>2</sup> )	24% (116 km <sup>2</sup> )
Cut-tail Pride <i>Maleherehere</i>	11% (22 km <sup>2</sup> )	- (-)	34% (160 km <sup>2</sup> )	34% (160 km <sup>2</sup> )
PiOP Coalition* <i>Multwankanda</i>	58% (120 km <sup>2</sup> )	100% (160 km <sup>2</sup> )	- (-)	96% (457 km <sup>2</sup> )
PiOP Coalition* <i>Nduraghumbo</i>	56% (116 km <sup>2</sup> )	100% (160 km <sup>2</sup> )	96% (457 km <sup>2</sup> )	- (-)

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.17. 95% contour Utilization Distribution Overlap Index (UDOI) for lion dyads having static interaction during the study. UDOI is a metric of static interaction that is a function of the product of the two individual's utilization distributions (UD). UDOI equals 0 when two home ranges do not overlap and 1 if two UD's are uniformly distributed with 100% overlap. Values >1 can occur if two UD's are nonuniformly distributed but have a high degree of overlap. Dyads without concurrent data noted as "NR."

Dyad ----- Vernacular ID <i>Villager Given Name</i>	Season -----				
	All	Late Dry 2015	Wet 2016	Early Dry 2016	Late Dry 2016
Airstrip Pride : Cut-tail Pride <i>Mayenga Nyambi : Maleherehere</i>	0.28	NR	0.17	0.21	<0.01
Airstrip Pride : Xakampa Coalition <i>Mayenga Nyambi : Eretsha</i>	0.08	0.05	NR	NR	NR
Airstrip Pride : PiOP Coalition* <i>Mayenga Nyambi : Multwankanda</i>	0.82	1.05	1.02	0.65	0.14
Airstrip Pride : PiOP Coalition* <i>Mayenga Nyambi : Nduraghumbo</i>	0.30	0.26	0.07	0.10	0.14
Cut-tail Pride : Xakampa Coalition <i>Maleherehere : Eretsha</i>	NR	NR	NR	NR	NR
Cut-tail Pride : PiOP Coalition* <i>Maleherehere : Multwankanda</i>	0.87	NR	0.30	0.88	0.51

Cut-tail Pride : PiOP Coalition* <i>Maleherehere : Nduraghumbo</i>	0.57	NR	<0.01	0.55	0.51
Xakampa Coalition : PiOP Coalition* <i>Eretsha : Multwankanda</i>	0.03	0.08	NR	NR	NR
Xakampa Coalition : PiOP Coalition* <i>Eretsha : Nduraghumbo</i>	0.03	0.07	NR	NR	NR
PiOP Coalition* : PiOP Coalition* <i>Multwankanda : Nduraghumbo</i>	0.76	0.40	0.11	0.58	1.23

---

\*PiOP Coalition formed after collar deployment, Airstrip male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.18. 50% contour Utilization Distribution Overlap Index (UDOI) for lion dyads having static interaction over the course of the study. UDOI is a metric of static interaction that is a function of the product of the two individual's utilization distributions (UD). UDOI equals 0 when two home ranges do not overlap and 1 if two UD's are uniformly distributed with 100% overlap. Values >1 can occur if two UD's are nonuniformly distributed but have a high degree of overlap. Dyads without concurrent data noted as "NR."

Dyad ----- Vernacular ID <i>Villager Given Name</i>	Season -----				
	All	Late Dry 2015	Wet 2016	Early Dry 2016	Late Dry 2016
Airstrip Pride : Cut-tail Pride <i>Mayenga Nyambi : Maleherehere</i>	0.00	NR	0.02	0.07	0.00
Airstrip Pride : Xakampa Coalition <i>Mayenga Nyambi : Eretsha</i>	0.00	0.00	NR	NR	NR
Airstrip Pride : PiOP Coalition* <i>Mayenga Nyambi : Multwankanda</i>	0.13	0.25	0.20	0.17	0.00
Airstrip Pride : PiOP Coalition* <i>Mayenga Nyambi : Nduraghumbo</i>	0.03	0.02	0.00	0.01	0.00
Cut-tail Pride : Xakampa Coalition <i>Maleherehere : Eretsha</i>	NR	NR	NR	NR	NR
Cut-tail Pride : PiOP Coalition* <i>Maleherehere : Multwankanda</i>	0.10	NR	0.04	0.14	0.07

Cut-tail Pride : PiOP Coalition* <i>Maleherehere : Nduraghumbo</i>	0.06	NR	0.00	0.09	0.07
Xakampa Coalition : PiOP Coalition* <i>Eretsha : Multwankanda</i>	0.00	0.00	NR	NR	NR
Xakampa Coalition : PiOP Coalition* <i>Eretsha : Nduraghumbo</i>	0.00	<0.01	NR	NR	NR
PiOP Coalition* : PiOP Coalition* <i>Multwankanda : Nduraghumbo</i>	0.12	0.02	0.00	0.06	0.30

---

\*PiOP Coalition formed after collar deployment, Airstrip male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.19. Coefficients of association (Ca) for lion dyads having static interaction during the late dry season 2015 (top of contingency table) and wet season 2016 (bottom). Ca is a metric of dynamic interaction generated from the relationship between the number of relocations for both individuals within specified time/distance thresholds and the sum of n relocations for both individuals. Coefficients range from 0 to 1 with strong associations generally considered as >0.5 and weaker/no associations as <0.5. Individuals without relocations for the specified time period noted with “NR.”

Vernacular ID <i>Villager Given Name</i>	Airstrip Pride <i>Mayenga Nyambi</i>	Cut-tail Pride <i>Maleherehere</i>	Xakampa Coalition <i>Eretsha</i>	PiOP Coalition* <i>Multwankanda</i>	PiOP Coalition* <i>Nduraghumbo</i>
Airstrip Pride <i>Mayenga Nyambi</i>	--	NR	0.00	0.35	0.00
Cut-tail Pride <i>Maleherehere</i>	0.00	--	NR	NR	NR
Xakampa Coalition <i>Eretsha</i>	NR	NR	--	0.00	0.00
PiOP Coalition* <i>Multwankanda</i>	0.47	0.08	NR	--	0.04
PiOP Coalition* <i>Nduraghumbo</i>	0.00	0.00	NR	0.01	--

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.20. Coefficients of association (Ca) for lion dyads having static interaction during the early dry season 2016 (top of contingency table) and late dry season 2016 (bottom). Ca is a metric of dynamic interaction generated from the relationship between the number of relocations for both individuals within specified time/distance thresholds and the sum of n relocations for both individuals. Coefficients range from 0 to 1 with strong associations generally considered as >0.5 and weaker/no associations as <0.5. Individuals without relocations for the specified time period noted with “NR.”

Vernacular ID <i>Villager Given Name</i>	Airstrip Pride <i>Mayenga Nyambi</i>	Cut-tail Pride <i>Maleherehere</i>	Xakampa Coalition <i>Eretsha</i>	PiOP Coalition* <i>Multwankanda</i>	PiOP Coalition* <i>Nduraghumbo</i>
Airstrip Pride <i>Mayenga Nyambi</i>	--	0.00	NR	0.15	0.00
Cut-tail Pride <i>Maleherehere</i>	0.00	--	NR	0.01	0.02
Xakampa Coalition <i>Eretsha</i>	NR	NR	--	NR	NR
PiOP Coalition* <i>Multwankanda</i>	0.00	0.02	NR	--	0.15
PiOP Coalition* <i>Nduraghumbo</i>	0.00	0.03	NR	0.47	--

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.21. Lion proximity to human habitation across seasons (All = all relocations, LD15 = Late dry season 2015, W16 = Wet season 2016, ED16 = Early dry season 2016, LD16 = Late dry season 2016). Percentage (PCT) of individual lion's relocations within 3 km of human habitation, median (Mdn) distance of all relocations to nearest point that is within 3 km of human habitation, and standard deviation (SD) of each lion's distances to nearest point that is within 3 km of human habitation for the given season.

Vernacular ID <i>Villager Given Name</i>	All			LD15			W16			ED16			LD16		
	PCT	Mdn	SD	PCT	Mdn	SD	PCT	Mdn	SD	PCT	Mdn	SD	PCT	Mdn	SD
Airstrip Pride <i>Mayenga Nyambi</i>	0	8.1	2.3	0	7.9	1.5	0	7.0	2.3	0	9.0	2.4	0	8.1	2.4
Cut-tail Pride <i>Maleherehere</i>	1	8.0	4.0	--	--	--	2	5.0	0.22	<1	8.1	5.4	0	8.7	2.1
Xakampa Coalition <i>Eretsha</i>	9	3.7	5.7	9	3.7	5.7	--	--	--	--	--	--	--	--	--
PiOP Coalition* <i>Multwankanda</i>	<1	8.0	3.3	<1	8.1	3.7	0	7.6	2.4	<1	8.7	3.7	0	8.0	2.9
PiOP Coalition* <i>Nduraghumbo</i>	4	10.9	6.7	0	14.0	7.0	0	15.2	4.0	15	4.9	5.9	<1	7.9	3.2

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

Table 3.22. Lion proximity to cattle grazing areas across seasons (Wet, Early Dry, and Late Dry). Percentage (PCT) of individual lion's relocations within cattle grazing areas, median (Mdn) distance of all relocations to nearest cattle grazing area, and standard deviation (SD) of each lion's distances to nearest cattle grazing area for the given season.

Vernacular ID <i>Villager Given Name</i>	Wet			Early Dry			Late Dry		
	PCT	Mdn	SD	PCT	Mdn	SD	PCT	Mdn	SD
Airstrip Pride <i>Mayenga Nyambi</i>	18	2.1	1.9	0	5.4	2.5	81	0.0	0.8
Cut-tail Pride <i>Maleherehere</i>	45	0.2	1.5	30	4.7	4.9	46	0.5	1.7
Xakampa Coalition <i>Eretsha</i>	--	--	--	--	--	--	67	0.0	2.4
PiOP Coalition* <i>Multwankanda</i>	11	3.1	2.2	12	5.1	3.5	68	0.0	2.5
PiOP Coalition* <i>Nduraghumbo</i>	<1	10.7	3.9	44	1.6	4.9	30	1.8	6.1

\*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition during late dry season 2016.

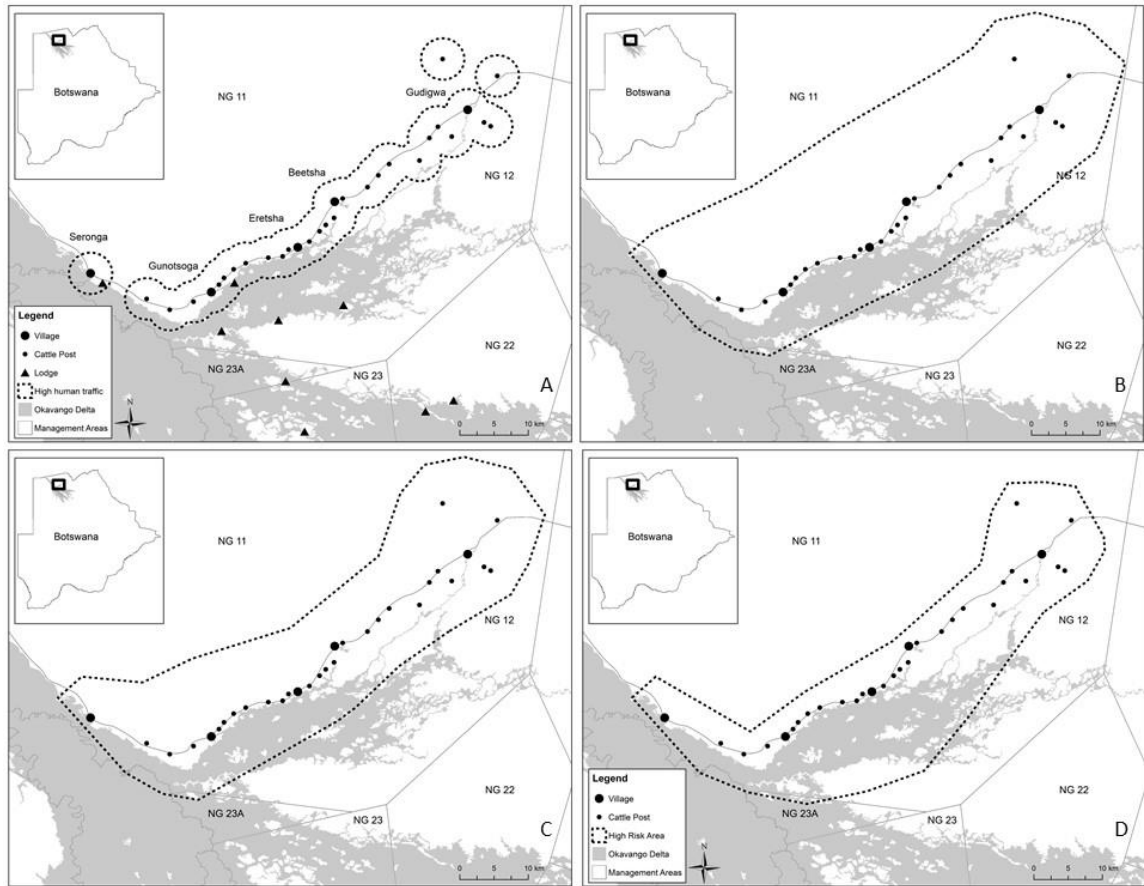


Figure 3.1. Map of the northern Botswana study area showing villages, cattle posts, safari lodges, government-defined management area (NG = Ngamiland) boundaries, and high risk areas for lions where they may encounter people or livestock. A: High human traffic areas (within 3 km of human habitation); B: Cattle grazing area during the wet season; C: Cattle grazing area during the early dry season; D: Cattle grazing area during the late dry season. Cattle grazing areas estimated based on field observations, expert elicitation, and data presented in Weise et al. (2019).

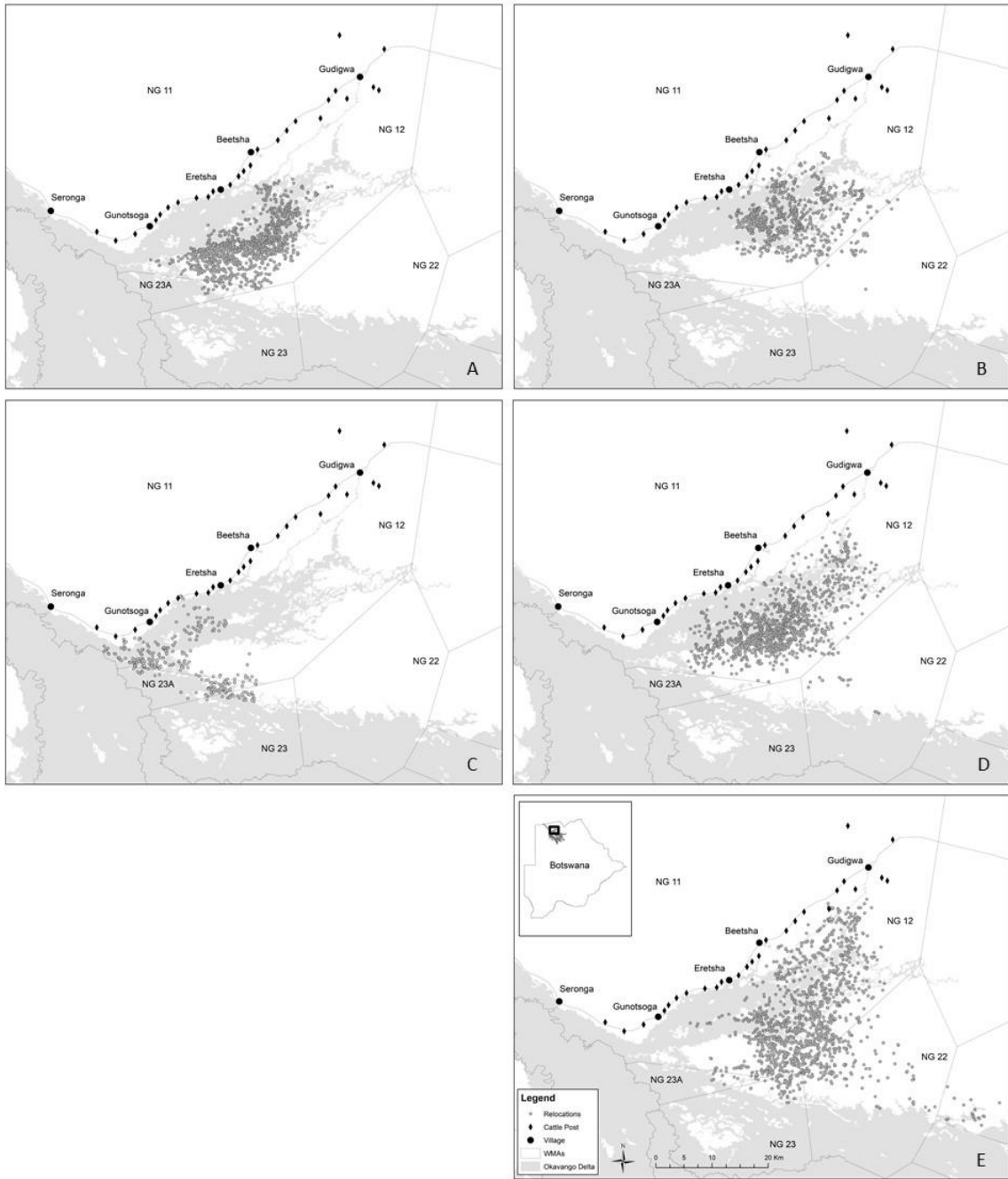


Figure 3.2. All locations for collared lions in the northern Botswana study area between August 2015 and December 2016. A: Female 1 (Airstrip Pride); B: Female 2 (Cut-tail Pride); C: Male 1 (Xakampa Coalition); D: Male 2 (Airstrip Coalition); E: Male 3 (Xamaga Coalition).

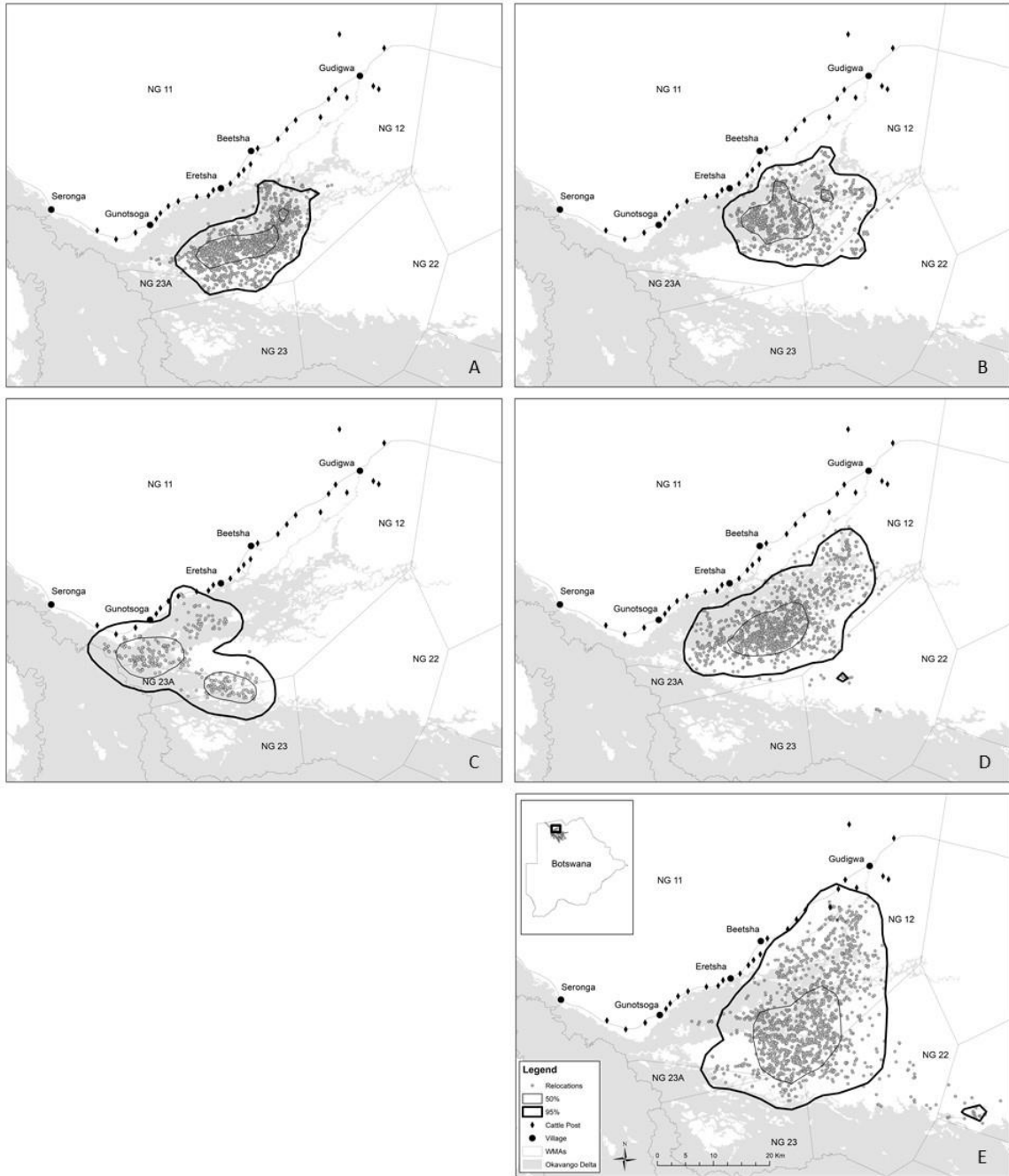


Figure 3.3. All locations and 50% and 95% contours from kernel density estimation (href) for collared lions in the northern Botswana study area between August 2015 and December 2016. A: Female 1 (Airstrip Pride); B: Female 2 (Cut-tail Pride); C: Male 1 (Xakampa Coalition); D: Male 2 (Airstrip Coalition); E: Male 3 (Xamaga Coalition).

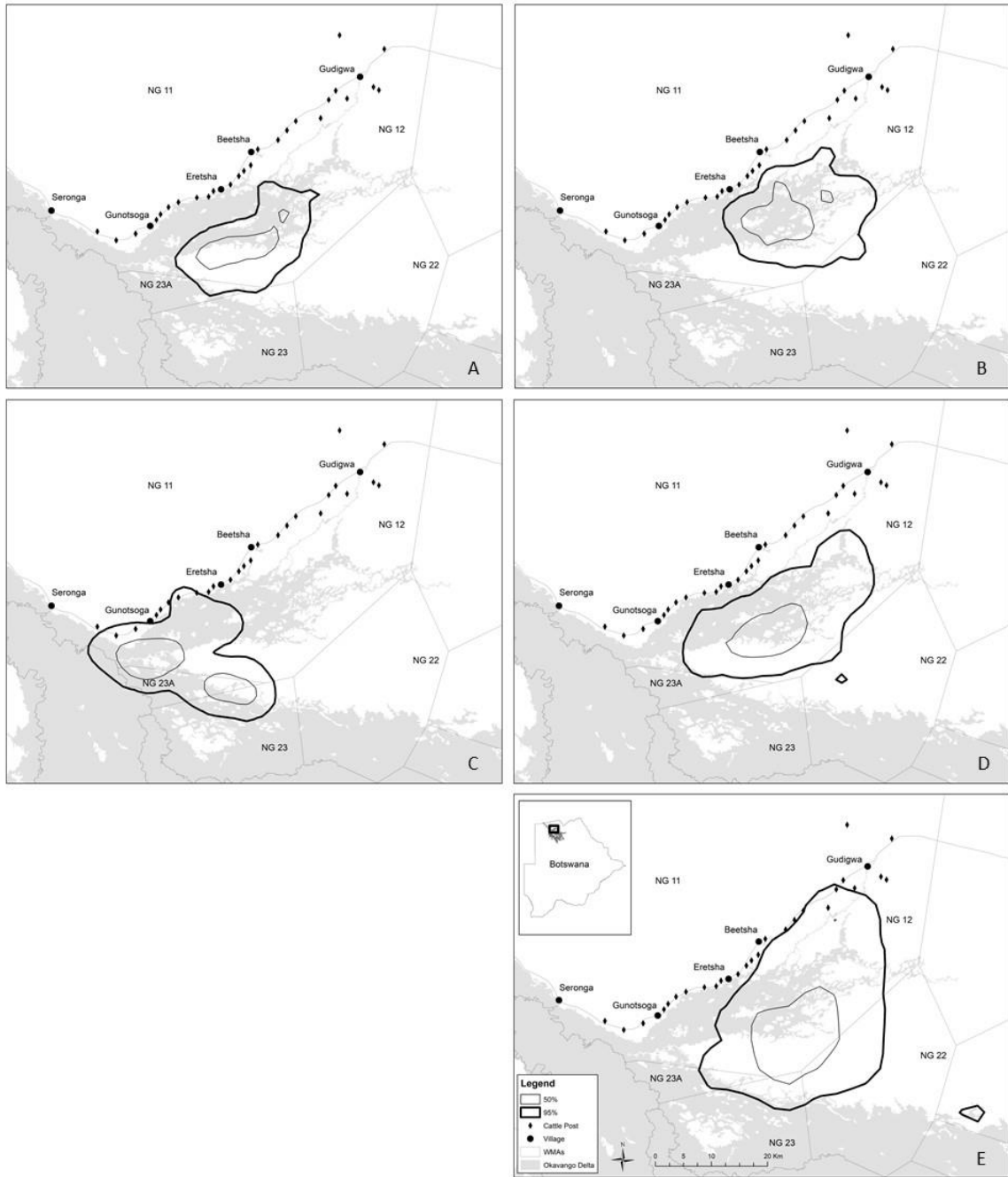


Figure 3.4. 50% and 95% contours from kernel density estimation (href) for collared lions in the northern Botswana study area between August 2015 and December 2016. A: Female 1 (Airstrip Pride); B: Female 2 (Cut-tail Pride); C: Male 1 (Xakampa Coalition); D: Male 2 (Airstrip Coalition); E: Male 3 (Xamaga Coalition).

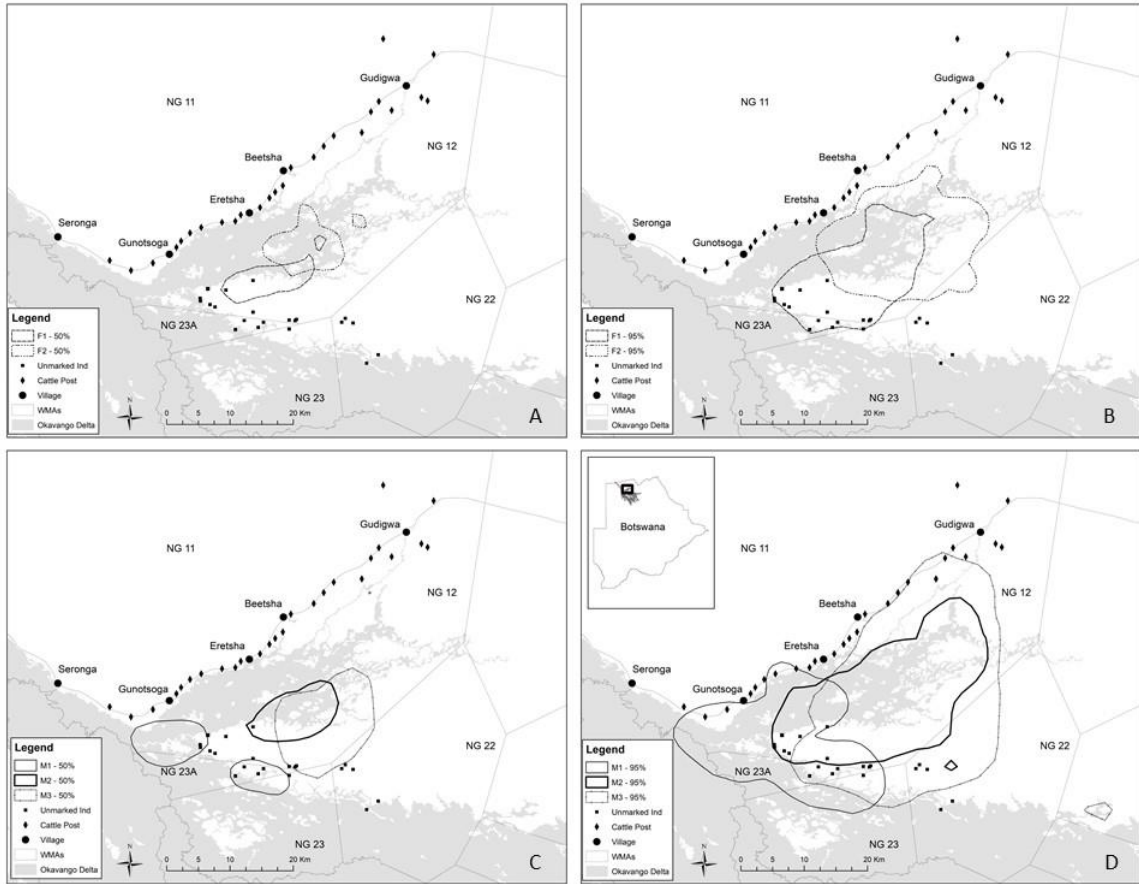


Figure 3.5. 50% and 95% contours from kernel density estimation (href) for collared female and male lions with unmarked individual sightings in the northern Botswana study area between August 2015 and December 2016. A: Females 50% (Female 1 - Airstrip Pride, Female 2 - Cut-tail Pride); B: Females 95% (Female 1 - Airstrip Pride, Female 2 - Cut-tail Pride); C: Males 50% (Male 1 - Xakampa Coalition, Male 2 - Airstrip Coalition, Male 3 - Xamaga Coalition). D: Males 95% (Male 1 - Xakampa Coalition, Male 2 - Airstrip Coalition, Male 3 - Xamaga Coalition).

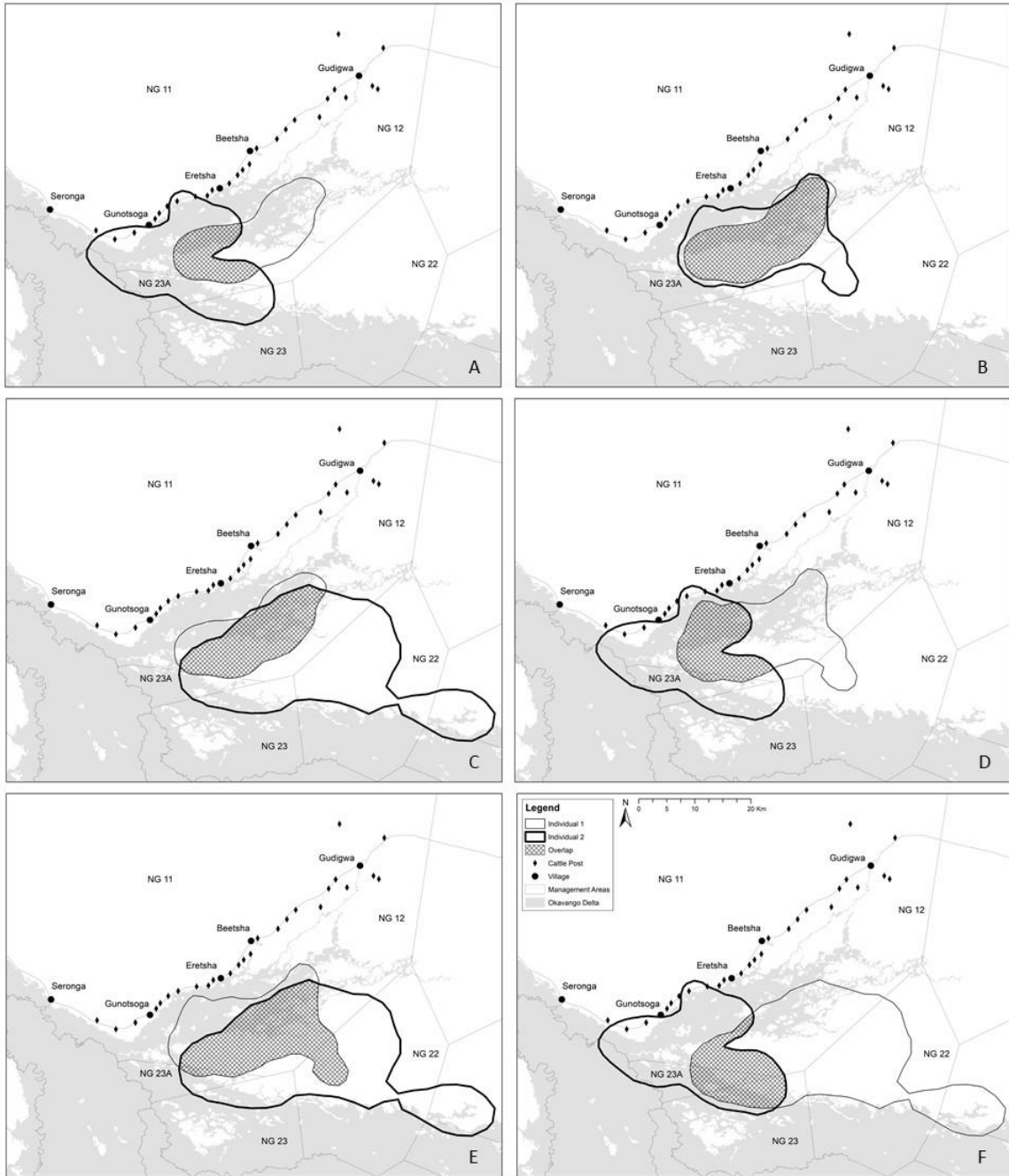


Figure 3.6. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2015. A: dyad 1 = Female 1(Airstrip Pride) : Male 1 (Xakampa Coalition); B: dyad 2 = F1(Airstrip Pride) : M2 (Airstrip Coalition); C: dyad 3 = F1 (Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : M1 (Xakampa Coalition); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : M1 (Xakampa Coalition).

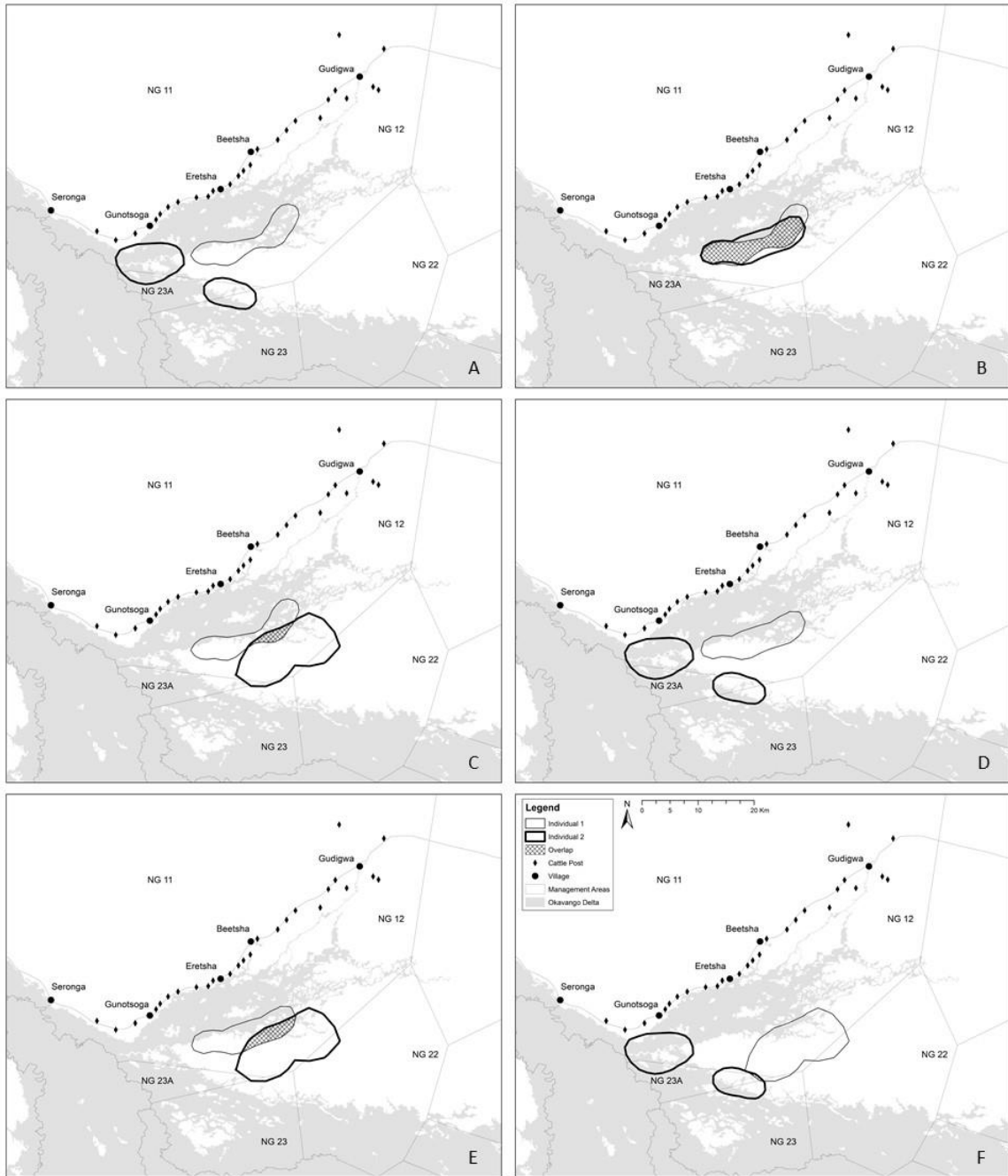


Figure 3.7. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2015. A: dyad 1 = Female 1(Airstrip Pride) : Male 1 (Xakampa Coalition); B: dyad 2 = F1(Airstrip Pride) : M2 (Airstrip Coalition); C: dyad 3 = F1 (Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : M1 (Xakampa Coalition); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : M1 (Xakampa Coalition).

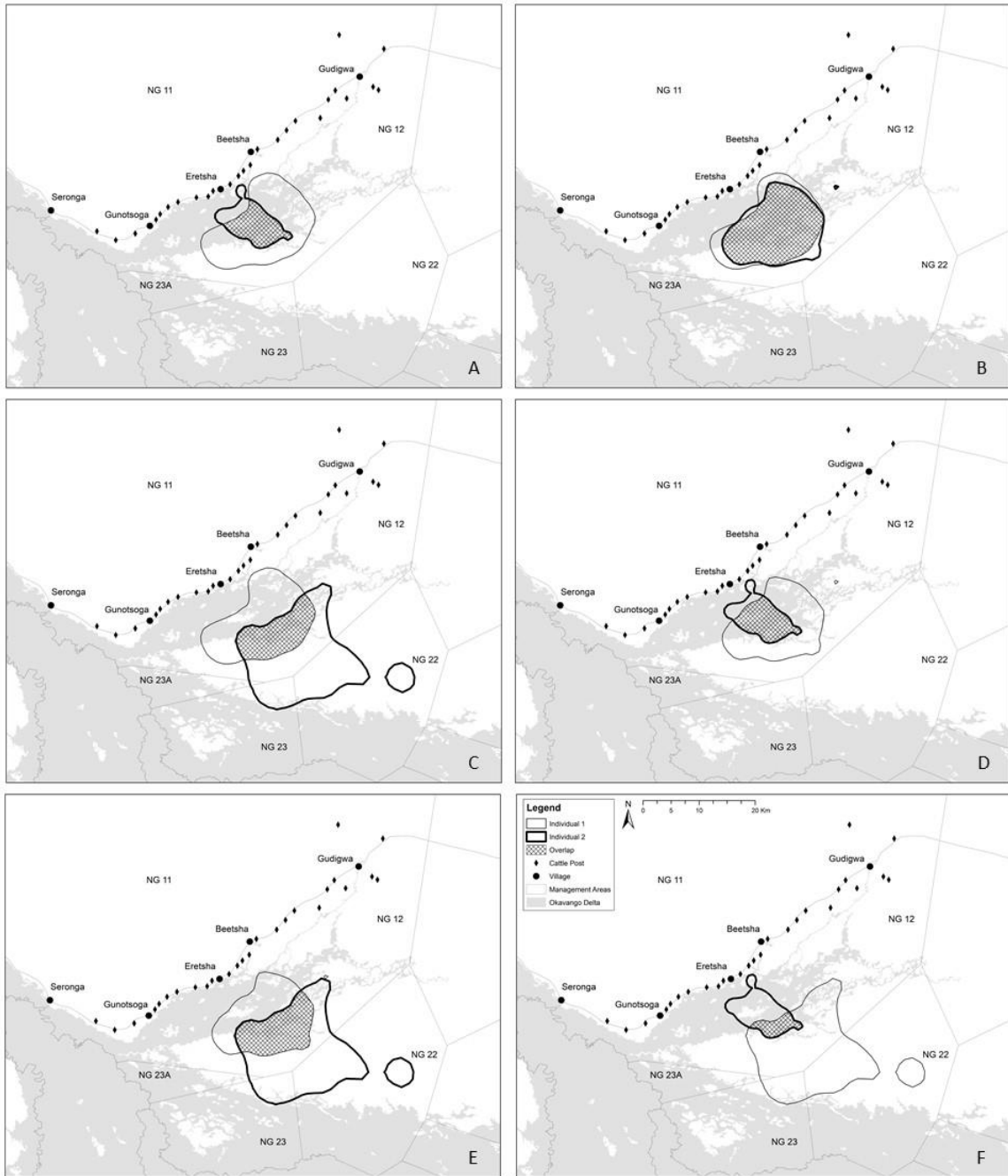


Figure 3.8. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the wet season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).

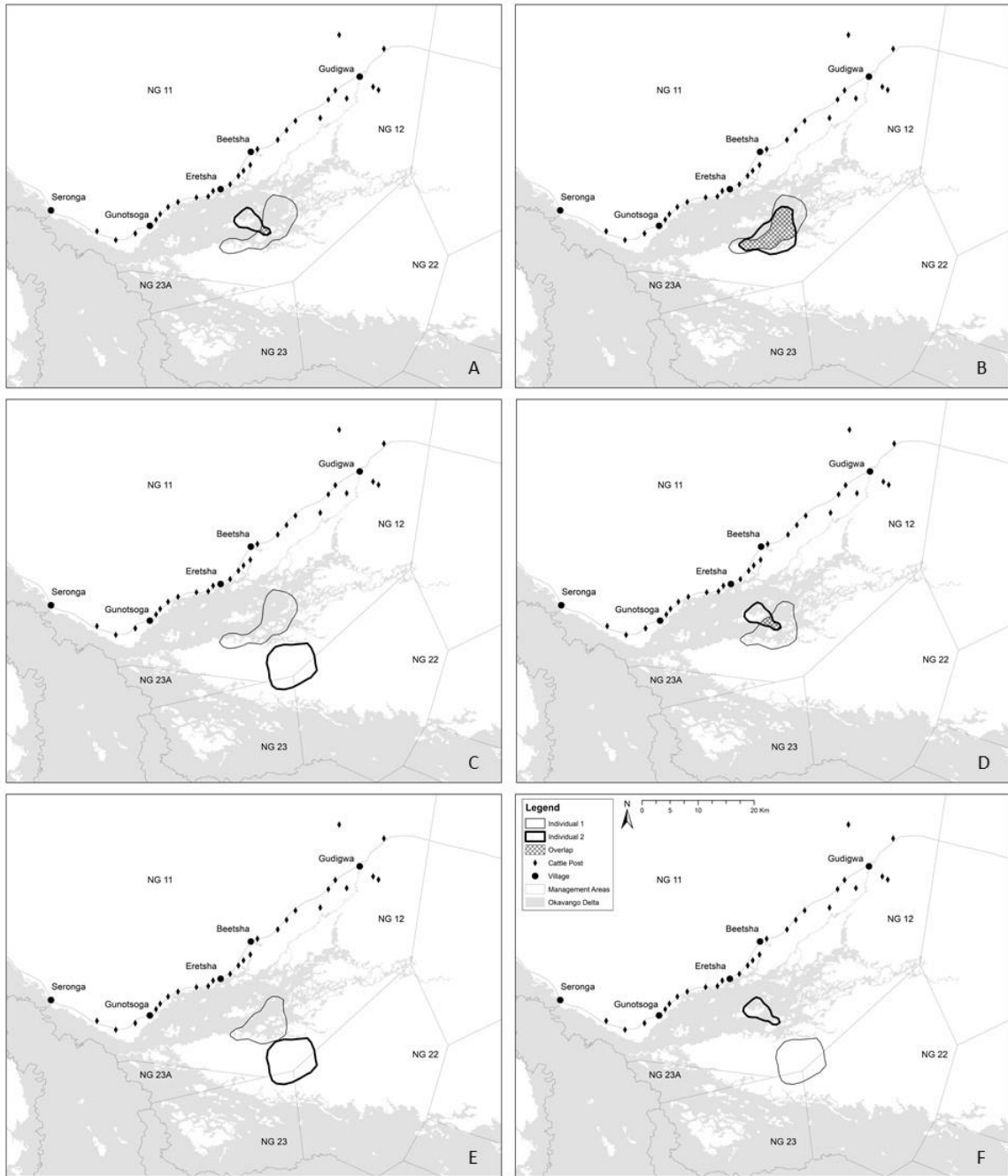


Figure 3.9. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the wet season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).

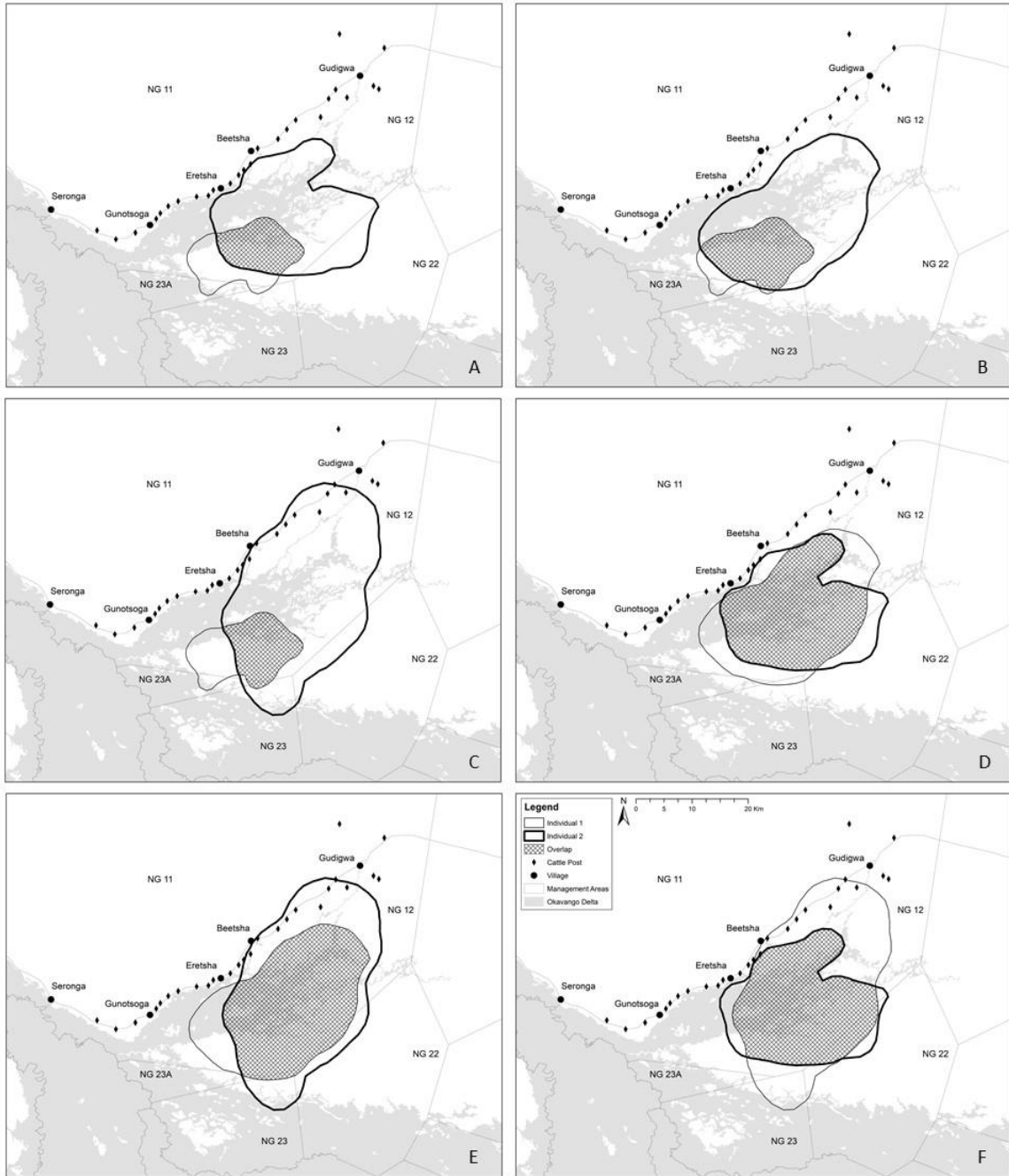


Figure 3.10. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the early dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).

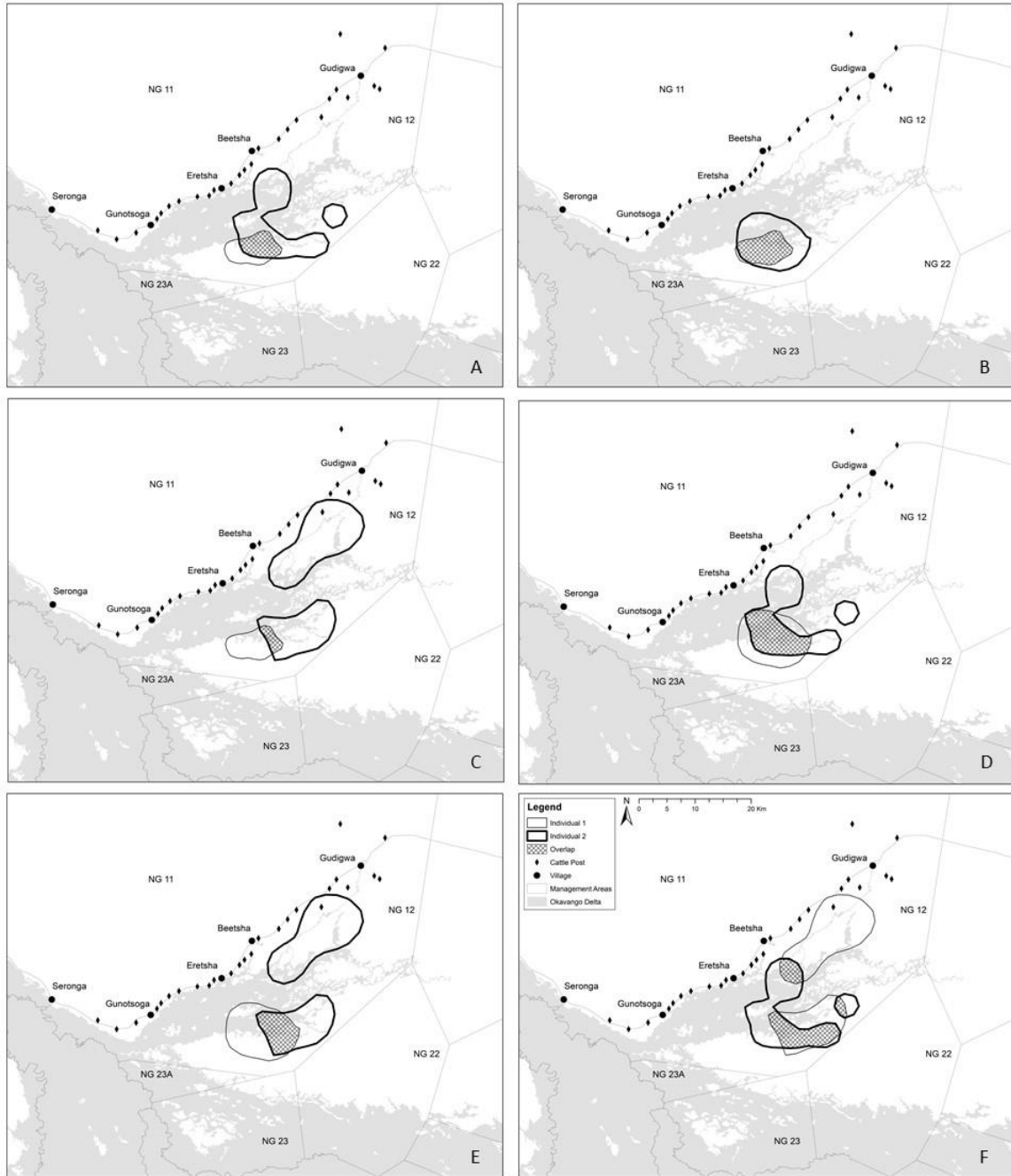


Figure 3.11. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the early dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).

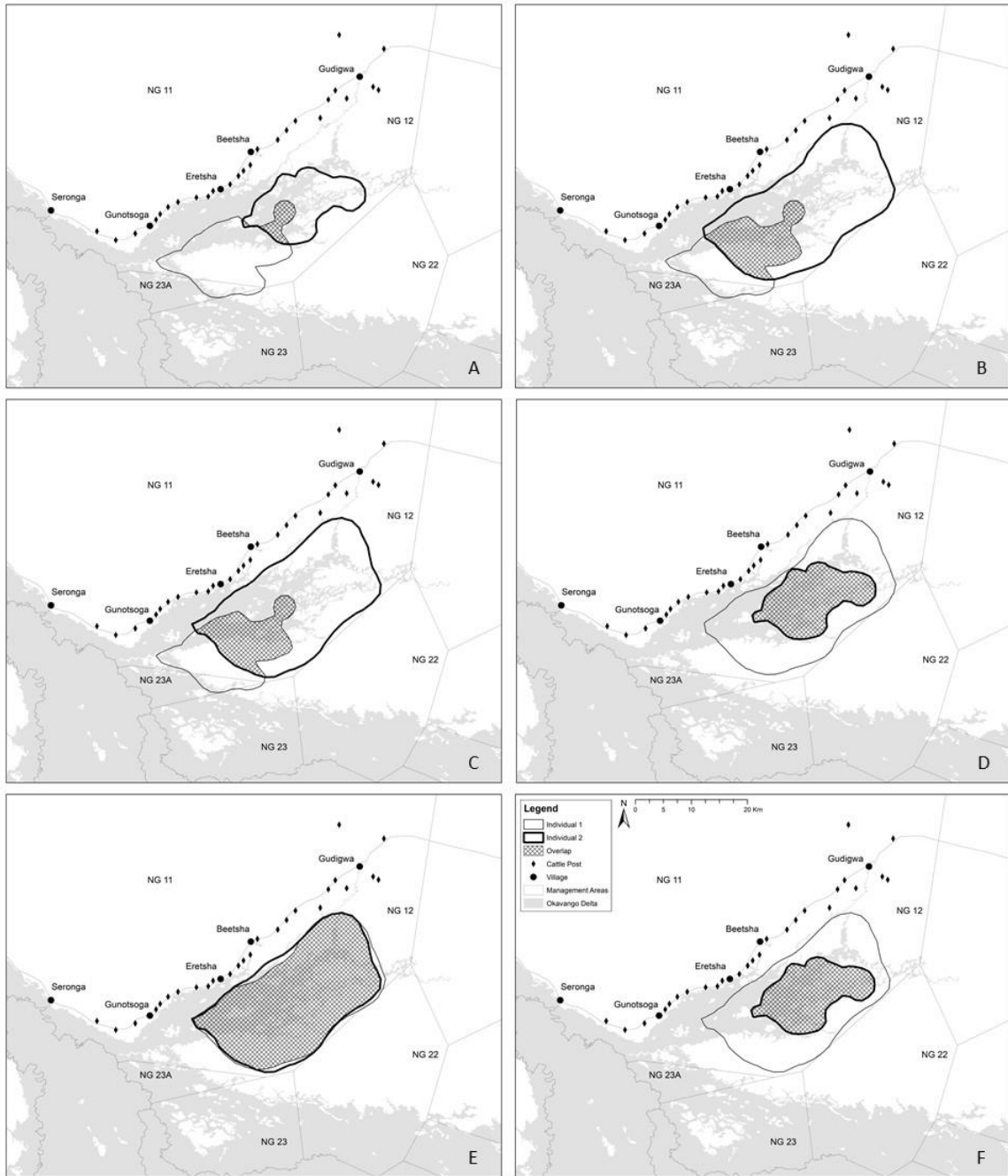


Figure 3.12. Area of overlap (static interaction) at 95% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).

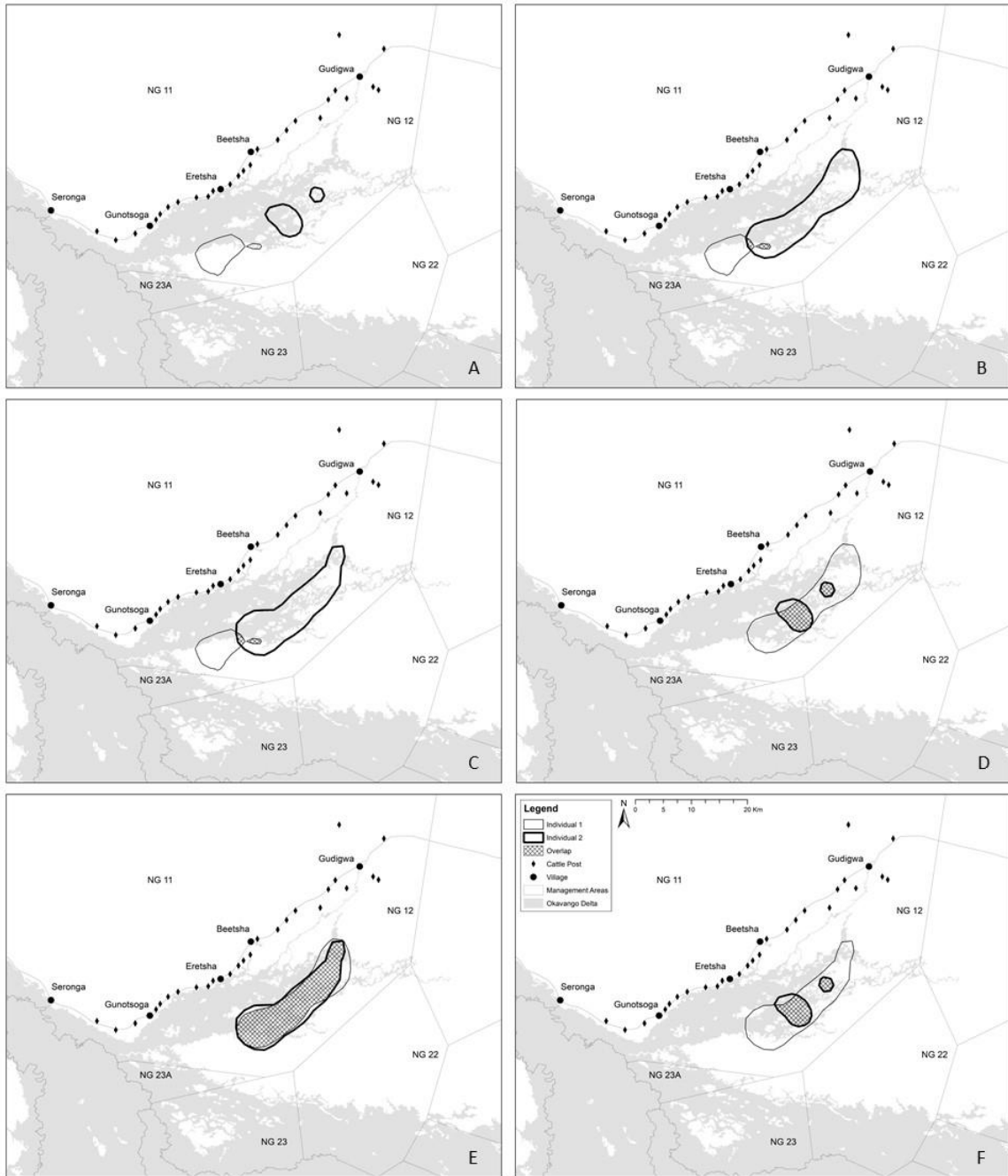


Figure 3.13. Area of overlap (static interaction) at 50% contour home ranges for collared lions based on kernel density estimation (href) in the northern Botswana study area during the late dry season 2016. A: dyad 1 = Female 1(Airstrip Pride) : Female 2 (Cut-tail Pride); B: dyad 2 = F1(Airstrip Pride) : Male 2 (Airstrip Coalition); C: dyad 3 = F1(Airstrip Pride) : M3 (Xamaga Coalition); D: dyad 4 = M2(Airstrip Coalition) : F2 (Cut-tail Pride); E: dyad 5 = M2(Airstrip Coalition) : M3 (Xamaga Coalition); F: dyad 6 = M3 (Xamaga Coalition) : F2 (Cut-tail Pride).

## CHAPTER 4

### LION ALERTS: STRATEGIES FOR MITIGATING HUMAN-LION CONFLICTS IN NORTHERN BOTSWANA

**Abstract** - Large carnivore populations are in decline globally due to conflicts with people as they are killed by people who see them as a threat to their livestock, livelihoods, or themselves. African lions (*Panthera leo*) are an acute example, and their numbers have declined precipitously over the last ~50 years primarily due to human-lion conflict. In addition to the resultant negative trends in lion populations, human-lion conflicts negatively impact local stakeholders who bear the costs of living among lions. Despite numerous studies and applied management programs, coexistence between local stakeholders and lions remains elusive. In the Okavango Delta of northern Botswana between October 2014 and December 2016, we developed a multilevel approach to address lion conservation and minimize human-lion conflicts designed specifically for rural Botswana and focused on the needs of the local people (i.e., a desire to protect their livestock) as a way to protect biodiversity. As a part of our community-based conflict management program (Pride in Our Prides) we investigated livestock losses to wild carnivores, monitored the local lion population, established conflict mitigation strategies including a locally-sourced livestock enclosure building program and an early-warning system linked to lion GPS satellite collars, and investigated local stakeholder attitudes towards lions and their perceptions of the established program. Here, we describe the efficacy of the livestock enclosure building and the early-warning system aspects of the conflict mitigation program. Twelve predator-proof livestock enclosures (“kraals”) made

from locally-sourced mopane (*Colophospermum mopane*) trees were built across the study area in areas of high human-lion conflict. Kraals were given to farmers through a multistep lottery process and villagers were shown how to construct them for themselves. While they received strong reviews from villagers, only 66% of constructed kraals were regularly used to protect livestock overnight. Lion alert early-warning messages were dispersed throughout the villages when GPS satellite collared lions moved into areas of high livestock or human use. Collars were programmed with two “nested” electronic geofences denoting livestock grazing lands and village lands, enabling an email and text message notification to program staff. Upon receiving a notification of a geofence breach, program staff initiated a lion alert to affected local stakeholders (within 5-8km of the breach location) but did not share the GPS coordinates of the encroaching lion. Eighty-seven lion alerts (out of 101 geofence breaches) were dispersed to village headmen and elders and then passed throughout the community via a branching phone tree. The automated collar breach notification system was often delayed ( $\bar{x} = 8$  hours), thus inhibiting the distribution of lion alert messages to villagers. Villagers responded favorably to the lion alert program, though only 36% of surveyed farmers had actually received an alert by the end of 2016. Over the course of the study, villagers noted an increase in their tolerance of lions and an increase in the belief that coexistence with lions is possible. Modifications making the early-warning system more autonomous, dynamic, and real-time would likely increase its efficacy. Despite the challenges encountered here, community-based, multileveled conservation management programs with an early-warning alert system provide an exciting opportunity to address human-lion conflict (and other human-wildlife conflicts) moving forward.

#### 4.1. Introduction

Many large carnivore species are facing declines that are almost completely the result of human actions (Ogada et al. 2003, Ripple et al. 2014). Outside protected areas, large carnivores are at risk of being shot (Woodroffe and Frank 2005, Treves et al. 2016) and poisoned (Márquez et al. 2013, Aryal et al. 2014) by local people who see them as a threat to themselves, their livestock, and livelihoods. The African lion (*Panthera leo*) is a prime example of this storyline as human-carnivore conflicts are now a main driver of widespread lion declines throughout Africa (Nowell and Jackson 1996, Woodroffe and Ginsberg 1998, Linnell et al. 1999, Hazzah et al. 2014, Bauer et al. 2016). Lion population estimates suggest a decline of >90% within the last ~40 years, and current levels now stand around 20,000 individuals (Myers 1975, Nowell and Jackson 1996, Bauer and Van Der Merwe 2004, Chardonnet 2002). Successful conservation efforts require reducing the amount of human-caused lion mortality events. Lowering the number of livestock losses to lions should, in turn, help to conserve lions (Ogada et al. 2003, Lichtenfeld et al. 2015). However, this requires site-specific management based on both biological and social data (Treves and Karanth 2003, Inskip and Zimmerman 2009).

Throughout Africa, many different structural techniques have been used to contain and protect livestock at night. Traditionally, thorn branch and wooden structures have been used but in recent years, various organizations have tried to adapt and improve upon existing structures. Begg and Kushnir (2010) compiled the Human-Lion Conflict Toolkit that cited many different types of livestock enclosures ranging from traditional thorn branch enclosures to manufactured structures composed of chain link and cement. While thorn branch enclosures are inexpensive, they require extensive maintenance to

maintain their functionality. Stone corrals are also inexpensive, but similarly require substantial labor to maintain. An additional drawback for both structures, is they are only applicable in areas where the materials are present. Chain link enclosures are expensive to build and cannot be widely utilized unless materials are brought to villages that are often quite isolated and rural. Mobile, manufactured fences have the positive feature that they can be moved to where the farmer needs them throughout the year but have similar downsides as chain link enclosures. Living wall style enclosures incorporate both native tree species and manufactured fences and have been shown to be effective (Lichtenfeld et al. 2015). These structures can be costly to implement. Wooden pole corrals are inexpensive to build but only able to be constructed in areas with sufficient materials. While there are a lot of options for livestock enclosures, each location and system will lend itself to a certain type of structure, and identifying the proper technique is integral (Begg and Kushnir 2010).

Other methods of dealing with livestock depredation by lions include compensation and insurance programs to help minimize the financial burden felt by farmers when livestock are killed by predators (Pettigrew et al. 2012). Compensation programs have been shown to be effective tools for reducing human-wildlife conflicts (Dickman et al. 2011) but have also been criticized for not meeting conservation goals (Pettigrew et al. 2012). In many cases they are unable to disburse funds in a timely manner, accurately verify claims, identify false reports, and they can be mired in government corruption (Nyhus et al. 2005). In Botswana, the Department of Wildlife and National Parks (DWNP) compensation scheme (DWNP 2013) is underfunded and slow to disburse funds (LeFlore et al. 2019, 2020). Additionally, it does not reimburse farmers

for losses to all predators. Notably, the program only focuses on the economic aspect of the conflict which Pettigrew et al. (2012) argues should be linked with land-use practices that are conservation minded. Insurance programs are an alternative to compensation programs but can encounter the same challenges as compensation programs (Pettigrew et al. 2012). Localized, self-funded insurance programs have been shown as a viable method for funding compensation of livestock losses caused by snow leopard (*Panthera uncia*) in Pakistan and India (Hussain 2000, Mishra et al. 2003), though in northern Botswana they do not seem to be a viable option (LeFlore et al. 2020). Generally, however, compensation and insurance programs do not eliminate losses to carnivores and thus do not address the social psychological and sociological dimensions (Decker et al. 2012) associated with the conflict. These programs merely reimburse the affected individual, addressing the economic dimensions of the conflict.

Despite a plethora of research and applied conservation programs (Hazzah et al. 2014, Trinkel and Angelici 2016, van Eeden et al. 2018), widespread human-lion coexistence has yet to be realized (Bauer et al. 2015). We developed a multilevel approach to address lion conservation and minimize human-lion conflicts designed specifically for rural Botswana that focused on the needs of the local people (i.e., a desire to protect their livestock) as a way to protect biodiversity. If livestock are more protected and people become more tolerant of predators, the need to kill carnivores to protect their herds should be diminished (Ogada et al. 2003, Lichtenfeld et al. 2015). Through the establishment of a community-based conservation program (Pride in Our Prides, hereafter PiOP), we investigated livestock losses to wild carnivores (LeFlore et al. 2019), monitored the local lion population (Chapter 3, this document), assessed and strived to

minimize negative feelings towards lions and other carnivores (LeFlore et al. 2020), created employment opportunities for local villagers, and established conflict mitigation strategies including a locally sourced livestock enclosure building program (Weise et al. 2018) and an early-warning system linked to lion GPS satellite collars to assist in fortifying livestock husbandry in the area (Weise et al. 2019). This chapter further describes the efficacy of the livestock enclosure building and the early-warning system aspects of the conflict mitigation program.

## **4.2. Study Area**

The eastern panhandle of the Okavango Delta of northern Botswana (Fig. 4.1) lies within the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA), an area of critical importance for lion conservation (Funston 2014). The KAZA TFCA of ~440,000 km<sup>2</sup> spans five countries, includes 36 protected areas, and is home to one of the largest lion populations in Africa (c. 3,500 lions; Funston 2014), classifying it as a lion stronghold (Riggio et al. 2013). The eastern panhandle is a corridor that connects the Delta to the rest of the KAZA TFCA and supports people, their livestock, and plentiful wildlife (Ramberg et al. 2006, Fynn et al. 2015). The Okavango Delta is a seasonally flooded inland wetland system composed of a shifting matrix of river channels, swamps and islands (McCarthy et al. 2003), fed by rains from Angola that flow into the Okavango River. The eastern panhandle study area is inundated by the early waves of flooding, when waters reach the panhandle starting in February (McCarthy et al. 2003). Waters remain high into July when they begin slowly receding from our study area and push further southeast to the rest of the Delta. The yearly cycling of the floods is not congruent with the rainy season, which runs from November to March (Wolski and Savenije 2006),

so the Delta becomes an important water source in the dry Kalahari environment (McCarthy et al. 2003). Furthermore, the delta experiences variability in seasonal flooding (Murray-Hudson 2009) which influences the socio-ecology and movements of lions (Kotze et al. 2018; Chapter 3, this document). We defined three seasons: the wet season ran from January to March and was characterized by warm days, heavy rainfall, and rising flood waters in the Delta, the early dry season spanned April to July when the flood waters reached their peak and began receding, little to no rain, and cool winter temperatures, and the late dry season spanned August to December and was characterized by the drying of the Delta to its lowest levels where water only remained in permanent channels and hot summer days with temperatures regularly  $>30^{\circ}\text{C}$ . This study was conducted in government-defined management areas slated for uses ranging from human habitation and natural resource consumption (Ngamiland [NG] 11 and 12) to wildlife management and community/internationally run ecotourism (NG 22, 23 and 23A) (Fig. 4.1). A national hunting ban in Botswana outlawed both safari and subsistence hunting in 2014 (Mbaiwa 2018), though retaliatory lion killings still occur in the study area (pers. comm. Mweze 2014). The area is one of the most sought-after wildlife viewing areas in Africa.

Local villagers (population c. 5,000; Botswana Population and Housing Census 2011) are agropastoralists, keeping livestock (cattle, *Bos taurus/Bos indicus*; goat, *Capra hircus*; horse, *Equus caballus*; and donkey, *Equus asinus*) and tending crops (e.g., sorghum [*Sorghum sp.*], millet [*Pennisetum sp.*], and watermelon [*Citrullus lanatus*]) during the growing season which typically runs December-April. In NG 11 and 12, people and their livestock are concentrated in five villages (Beetsha, Eretsha, Gudigwa,

Gunotsoga, and Seronga) and in smaller familial settlements called cattle posts. Livestock populations have risen dramatically in the area but average herd size in the area is approximately 12 individuals per farmer (LeFlore, unpublished data). Official government cattle counts show the population almost doubling over the previous decade (from c. 6,000 in 2006 to c. 11,000 in 2017; Department of Veterinary Services, Seronga office), though actual numbers are likely higher as one independent count estimated ~16,000 livestock in 2017 (Weise et al. 2019). Livestock are occasionally protected overnight in traditional thorn branch or wooden post enclosures, referred to locally as 'kraals' (Fig. 4.2) but roam freely during the day (Fig. 4.2; LeFlore et al. 2019, 2020). People live in villages and cattle posts (smaller familial settlements). With extensive human and livestock activity in the area, the area poses a risk to free-ranging lions. While unguarded livestock represent an easy prey option for lions, people kill lions in response to lost livestock or even the perceived threat of losing livestock (LeFlore et al. 2019, 2020).

Traditional kraals are typically round and made of thorn branches or many upright, thick branches of local hardwoods. In a third kraal style, villagers use upright branches and bailing wire to enclose livestock; however, this method is not widely used. Reasons for kraaling livestock at night include protecting livestock against theft, keeping livestock safe from predators, keeping animals centrally located for morning milking, general management, and controlling animals during the growing season (LeFlore et al. 2020, LeFlore unpublished data). Other than kraaling animals at night, there is relatively little other livestock management that occurs. Historically, there was a strong local herding culture. But as schools became more readily accessible and younger people

migrated towards larger towns and cities, that herding culture has decreased, a trend seen broadly throughout Africa (Breitenmoser et al. 2005). Furthermore, from a sociocultural perspective, herding as a profession has lost its status and professional herders are often looked down upon in the community. People usually let livestock out of the kraals in the morning, allowing them to graze unsupervised during the day. Towards the late afternoon, people will track their livestock and herd back however many individuals they can into the kraals for the night. Many livestock are left “unkraaled” (out of the kraal) around the cattle posts and villages at night, while others remain in the bush, unprotected and away from human settlements.

#### **4.3. Methods**

In May 2015, construction began on 12 wooden kraals made from locally harvested and accessible materials. Nine kraals were square and roughly 12 x 12 x 2 m while three kraals were circular with 2 m high walls and varied in size depending on the farmers herd size. Walls of the square kraals were composed of woven mophane (*Colophospermum mopane*) branches held together with additional mophane crosspieces and walls of the round kraals were comprised of horizontally stacked mophane trunks to create a strong physical and visual barrier between livestock and predators (Fig. 4.3). For all kraals, mophane tree trunks were used as upright support poles, and in square kraals paneling was secured to the frame with 8-gauge bailing wire. These structures were more substantial than traditional local livestock enclosure methods. Cattle posts were selected to receive kraals through a multistep process. First, cattle posts with the greatest number of conflicts were selected based on depredation event investigations and Department of Wildlife and National Parks’ Problem Animal Control data (Chapter 2, this document;

LeFlore et al. 2019). Next, a random selection process was used to select the individual cattle post where the kraal was to be built. At cattle posts with more than one family and where elders were unable to select an individual family to receive the kraal, an individual family was selected to own and use the kraal through a lottery process.

Beginning in August of 2015, 5 lions (3 male and 2 female) from different prides and coalitions were collared in the region under the authority of the Botswanan Department of Wildlife and National Parks (research permit number: EWT 8/36/4 XXVII (61), darting permit numbers WP/RES 15/2/2 XXVII (22) & WP/RES 15/2/2 XXVII (141)). Lions were fitted with Telonics Iridium TGW-4570-3 units (Telonics Inc., Mesa, AZ, USA) GPS satellite/VHF radio collars which recorded a GPS fix five times/day. Collars were programmed with two geofences, electronic boundaries of GPS locations, that were determined based upon the study area configuration and local expert elicitation from MT and community members (i.e., where villages and cattle posts were located, where livestock typically grazed, and where villagers believed most lions lived; Fig. 4.1). Two geofences were designated to provide a multi-leveled warning system, enabling a targeted approach to villager notification. A breach of the first geofence represented lions moving into the area where livestock spent a significant amount of time grazing (grazing lands geofence; ~5-8 km away from areas of human habitation); the second geofence delineated the village boundaries and signaled when lions were near areas of high human habitation (within ~1-5 km). A village geofence breach presupposes a grazing lands geofence breach as the two geofences are “nested” with the village area north of the grazing lands geofence. When a collared individual breached either geofence, the collar switched to record a fix every two hours until the individual was back outside geofenced

areas. Additionally, project staff were alerted via an automated email and text message from Telonics. Lion alerts were then disseminated through the affected village(s) if they were within ~8 km of a grazing lands geofence breach and ~5km of a village lands geofence breach. Lion alerts were disseminated via SMS (short-message system) text message and phone calls, initially to village elders and headmen, and then village leaders passed the message on to their community members creating a phone tree to spread the information. Community members were informed lions that were present in their vicinity, and it would be beneficial for them to ensure livestock were adequately protected. Participation in receiving lion alert messages was voluntary and individuals could do as they wished with the information, though project staff offered suggestions during community meetings and discussions with local stakeholders (e.g., ensuring livestock were kraaled, fires at kraals, noisemakers, lights/torches, etc.). Specific lion GPS locations were not shared to minimize the potential for retaliatory or preemptive lion killings.

In addition to the establishment of the kraal building program and early-warning system, six local villagers were employed by the conservation program and extensive amounts of community outreach were undertaken by program staff. Staff gave presentations at village schools, had a constant presence in the community, and attended regular community meetings where they shared conservation project updates and information about the study lions with villagers. Each village was invited to provide a local name for a collared lion as a way to connect community members with study animals. Descriptive statistics were calculated with R statistical software (R Development Core Team 2016).

#### 4.4. Results

The 12 newly constructed predator-proof mophane kraals (Figs. 4.1 & 4.3) were dispersed through the five villages with Beetsha receiving three kraals, Eretsha receiving four, Gudigwa and Gunotsoga receiving 2, and Seronga receiving one (Table 4.1). Kraals were used to secure livestock at night to a varying degree, with some used daily and others not at all. Four square kraals (one per village, excluding Seronga) were not used at all (33%), or they were used communally for various livestock husbandry activities (e.g., milking, branding, etc.). All kraals developed termite damage over the course of the study and three (25%) kraals were damaged by elephants and falling tree limbs. Though not all newly constructed kraals were regularly used, there were no depredation events inside any when they were used.

87 lion alerts were sent to villagers between October 2015 and December 2016 on 101 collared individual geofence breaches (19 village lands geofence breaches) and three instances where un-collared lions were known to be in areas of high human and livestock traffic (Tables 4.1 & 4.2). Between August collar deployments and October 2015, the geofence system was not accurately established by Telonics and breach notifications were not received. Twenty-four lion alerts (28%) were disseminated to multiple villages with “primary” villages being in closer proximity to the breach point and “secondary” villages being slightly farther away but still within ~5-8km of the breach point. Automated text messages and emails were typically received within approximately eight hours of the geofence breach, and >90% of geofence breaches occurred at night (between 18:00 and 06:00). On average, there was an eight-hour delay between the time the collars recognized the geofence breach and when program staff received the automated message

and could initiate sending the lion alert message to villagers ( $\sigma = 4$ ). On 17 breaches (17%), no alert was sent because the lion was known to already have left all geofenced areas when the incoming breach message was received. In these circumstances, the incoming and outgoing messages were often received simultaneously or in rapid succession. For 11 breaches (11%), incoming messages were not received at all, only outgoing messages were received. Lion alerts were only able to be sent to villagers if project staff had cellular phone and/or internet service, automated breach messages were received, and if lion collars were able to obtain a fix successfully. The collar on PiOP coalition male “Multwankanda” malfunctioned and missed successful fixes resulting in a 72% success rate, while other collars operated with >90% success (Table 4.2).

In five instances (5%), multiple alerts were sent on successive days for the same breach event, and on three instances (3%) a single alert was sent for multiple collared individuals who were known to associate. All five collared individuals breached the grazing lands geofence (Figs. 4.4 & 4.5) and breaches lasted for 17 hours on average ( $\sigma = 28$  hrs; Males  $n = 72$ ,  $\bar{x} = 18$ ,  $\sigma = 31$ ; females  $n = 29$ ,  $\bar{x} = 14$ ,  $\sigma = 16$ ; Table 4.2). Two males and one female breached the village lands geofence and breaches lasted between 4 and 23 hours on average (Males  $n = 18$ ,  $\bar{x} = 20$ ,  $\sigma = 26$ ; females  $n = 1$ ,  $\bar{x} = 4$ ,  $\sigma = 0$ ; Table 4.2). Breaches were not distributed evenly over the course of the study when compared monthly based on a chi-square goodness of fit test ( $\chi^2 = 44.784$ ,  $df = 16$ ,  $p < 0.001$ ), with most breaches occurring during the months of April-July and November (Fig. 4.6). Likewise, lion alerts were not sent to all villages equally as Beetsha, Gunotsoga, and Eretsha were sent the most alerts ( $\chi^2 = 41.448$ ,  $df = 4$ ,  $p < 0.001$ ). On only three occasions

were collared lions directly responsible for known livestock depredation events and one of those depredation events took place in a traditional kraal.

Villagers provided local names for each of the collared lions and the names were circulated around the community with lions becoming almost legendary. Project staff were regularly stopped in the community and asked for information about a particular lion and their pride or coalition. Local lion names, their associated English translation, and sex were as follows (Table 4.2): “Maleherehere” (“The Sneaky One” – female), “Mayenga Niambi” (“Decorated by the Gods” – female), “Eretsha” (“Eretsha” [named for village] – male), “Multwankanda” (“The Forager” – male), and “Nduraghumbo” (“Leader of the Household” – male).

#### **4.5. Discussion**

Given the complexities of human-lion conflicts and impacts (Dickman 2010), multifaceted management approaches are necessary for successful mitigation. Here, the model of protecting livestock at night in locally and naturally available formidable kraals, establishing an early-warning system linked to lion GPS satellite collars, and extensive community engagement provides a compelling management approach. Due to the relatively new technological advancements in wildlife tracking (Wall et al. 2014) facilitating geofences and resultant notifications of wildlife movements, early-warning systems hold promise as human-lion conflict mitigation tools, despite the costs (~\$5,000 per unit deployment and ~\$18 per day), if a higher percentage of the lion population was collared and efforts could be targeted to known livestock raiders (Weise et al. 2019). Further technological advancements leading to longer collar deployments could bring the cost of this approach down, especially if wider use eliminates livestock losses and

subsequent need for compensation (Weise et al. 2019). Without a targeted approach in conflict hotspots, general and widespread use of GPS satellite collars would likely be cost prohibitive (Thomas et al. 2011, Weise et al. 2019). Additionally, given the seasonality of lion socio-ecology and movements in the Delta (Kotze et al. 2018; Chapter 3, this document), livestock losses caused by lions can vary over the course of the year (LeFlore et al. 2019, Pozo et al. 2020).

Lion alerts and early-warning systems are an exciting development in managing human-lion conflicts but are not the panacea, as they have drawbacks (e.g., cost, labor intensive, malfunction, etc.) and do not fully address the issue. As designed in this initial pilot study, automated geofence breach notifications were often delayed, minimizing their effectiveness and impeding villager notification. Streamlining the alert system would be beneficial and would require a more automated, real-time, fine scale, and customized solution where local stakeholders could opt into an SMS message notification list triggered by a geofence breach. In addition to real-time lion tracking, incorporating real-time livestock movements could provide another layer of critical information to local stakeholders. These data, among other ecological factors, could be used to establish dynamic geofences which would increase the efficacy of the early warning system (Weise et al. 2019). Furthermore, lion alerts are rendered useless and ineffective without active human responses to warnings along with consistent and secure livestock husbandry practices (e.g., daytime herding, nighttime protection in enclosures, etc.), which are understood to minimize livestock losses to predators (Ogada et al. 2003, Lichtenfeld et al. 2015).

While alerts can be a helpful tool to inform local stakeholders when there was a higher potential danger of livestock loss, human actions in response to alerts and consistent, secure livestock husbandry practices remain integral in minimizing livestock losses. In surveys conducted towards the end of this study in 2016 (Chapter 5, this document; LeFlore et al. 2020), only 36% of questioned farmers had received a lion alert message, but 81% of all respondents believed that lion alerts were beneficial. All but one farmer who had received an alert noted their response to the alert was to kraal their livestock, and >90% built fires at the kraal. All farmers also noted they passed the message along to other community members. Seventy percent of respondents reported changing their livestock husbandry practices because of the conflict mitigation program with most of those respondents citing an increase in the frequency of kraaling. Herding increased significantly over the course of the study, though still strikingly low, with the percentage of farmers who always had a herder with their livestock increasing from 1% to 8% ( $\chi^2 = 5.3, p = 0.021$ ). Eighty-nine percent of all respondents noted seeing the newly constructed predator-proof kraals and 82% believed the kraals were more secure than traditional kraals. This resulted in 89% of respondents claiming they wanted a predator-proof kraal of their own, though just 63% of them were interested in building one for themselves. Targeted use of autonomous early-warning systems, coupled with more secure and consistent livestock husbandry and the appropriate management actions in response to early warnings offers an exciting avenue for addressing human-lion conflict.

Noted human behavior changes as a result of this conservation project and broad support in the community highlight the potential to minimize the negative impacts (for both humans and lions) associated with human-lion conflict moving forward. Though

changing the cultural perceptions, social psychology, and sociology around human-lion conflicts and impacts remains an arduous task and likely takes significantly more time (Manfredo 2008, Stedman 2012, Vaske and Manfredo 2012). Under the cognitive hierarchy (Manfredo 2008), human values (i.e., modes of conduct, desirable individual states, or qualities of life) are shared widely amongst community members and are slow to change. Value orientations (i.e., basic belief patterns) highlight how a value achieves meaning for an individual (Vaske and Manfredo 2012). Actions and behaviors are built upon attitudes (favorable or unfavorable evaluations of a person, object or action), value orientations, and values. While an individual's behaviors may be adjusted on a shorter time scale, lasting communal changes (e.g., community establishment of secure livestock husbandry practices or appropriate response to lion alerts) will be based on changed villager attitudes, value orientations and values. These changes are challenging to achieve and evolve over longer timeframes (Vaske and Manfredo 2012). Likewise, the ultimate goal of attaining coexistence between people and lions, effectively eliminating lion killing as an acceptable behavior in response to livestock losses, will require a large cultural shift in values. When villagers were asked about coexistence with carnivores and their tolerance of lions, over the course of the study there was an increase in number of respondents believed coexistence with carnivores is possible (18% to 28%,  $\chi^2 = 5.69$ ,  $p = 0.017$ ) and 50% of respondents say the described conflict mitigation program increased their tolerance of lions (mean tolerance scores increased from -0.79 to -0.13,  $t = -6.04$ ,  $p = <0.001$ ; Chapter 5, this document; LeFlore et al. 2020). Tools like predator-proof kraals and lion alerts provide the foundation to impact villager's attitudes, value orientations, and values. With a respectful and tailored community-centered approach, these tools can

offer a blueprint to minimize human-lion conflict moving forward. Management solutions developed in conjunction with important stakeholders and with human dimensions in mind can lead to more robust conservation (Decker et al. 2012). More broadly, the framework presented here is widely transferable and could be used as a model in other areas where conflicts with other wildlife species occur.

#### 4.6. Literature Cited

- Aryal, A., D. Brunton, W. Ji, R.K. Barraclough, and D. Raubenheimer. 2014. Human–carnivore conflict: ecological and economical sustainability of predation on livestock by snow leopard and other carnivores in the Himalaya. *Sustainability Science*: 9: 321–329.
- Bauer, H. and S. Van der Merwe. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38: 26-31.
- Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. Hunter, D. 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*: doi: 10.1073/pnas.1500664112.
- Bauer, H., C. Packer, P. Funston, P. Henschel, and K. Nowell. 2016. *Panthera leo* in the IUCN Red List of Threatened Species. Available at <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en> Accessed October 8, 2016.
- Begg, C. and H. Kushnir. 2010. eds Human-lion conflict toolkit. Ratel Trust, Cape Town, South Africa. [http://www.rateltrust.org/library\\_files/Human-Lion%20Conflict%20Toolkit.pdf](http://www.rateltrust.org/library_files/Human-Lion%20Conflict%20Toolkit.pdf). Accessed June 28 2014.
- Botswana Population and Housing Census. 2011. URL [www.catalog.ihsn.org/index.php/catalog/4243/download/55990](http://www.catalog.ihsn.org/index.php/catalog/4243/download/55990). Accessed on October 15, 2015.
- Breitenmoser U., C. Angst, J-M. Landry, C. Breitenmoser-Würsten, J.D.C. Linnell, and J-M. Weber. 2005. Non-lethal techniques for reducing depredation. *In People and Wildlife – Conflict or Coexistence?* R. Woodroffe, S. Thirgood, and A.R. Rabinowitz eds pp. 49–71. Cambridge University Press, Cambridge, UK.
- C. Márquez, C., J.M. Vargas, R. Villafuerte, and J.E. Fa. 2013. Understanding the propensity of wild predators to illegal poison baiting. *Animal Conservation* 16: 118–129.
- Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA, Paris, France.
- Decker, D.J., S.J. Riley, and W.F. Siemer. 2012. eds. Human Dimensions of Wildlife Management. John Hopkins University Press, Baltimore, Maryland, U.S.A.
- Department of Wildlife and National Parks. 2013. Compensation Guidelines for Damages Caused by Elephants and Lion. Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism.
- Dickman A.J., E.E. Macdonald, and D.W. Macdonald. 2011. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *PNAS* 108:13937–44.

- Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict: *Animal Conservation* 13: 458–466.
- Funston, P. 2014. The Kavango-Zambezi Transfrontier Conservation Area – critical for African lions. *Cat News* 60: 4-7.
- Fynn, R.W.S., M. Murray-Hudson, M. Dhliwayo, P. Scholte. 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management* 23: 559–581.
- Hazzah, L., S. Dolrenry, L. Naughton, C.T.T. Edwards, O. Mwebi, F. Kearney, and L. Frank. 2014. Efficacy of Two Lion Conservation Programs in Maasailand, Kenya. *Conservation Biology* 28: 851-860.
- Hussain, S. 2000. Protecting the snow leopard and enhancing farmers' livelihoods. *Mountain Research and Development* 20: 226-31.
- Inskip, C. and A. Zimmermann. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43:18–34.
- Kotze, R., M. Keith, C. Winterbach, H. Winterbach, and J.P. Marshal. 2018. The influence of social and environmental factors on organization of African lion (*Panthera leo*) prides in the Okavango Delta. *Journal of Mammalogy* 99: 845-858.
- LeFlore E.G., T.K. Fuller, M. Tomeletso, T.C. Dimbindo, and A.B Stein. 2020. Human dimensions of human–lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana. *Environmental Conservation* 47:182-189.
- LeFlore, E.G., T.K. Fuller, M. Tomeletso, and A.B Stein. 2019. Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation* 18:e00592.
- Lichtenfeld, L.L., C. Trout, and E.L. Kisimir. 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodivers Conserv* 24: 483-491.
- Linnell, J., J. Odden, M. Smith, R. Aanes, and J. Swenson. 1999. Large carnivores that kill livestock: do “problem individuals” really exist? *Wildlife Society Bulletin* 27, 698–705.
- Manfredo, M.J. 2008. *Who cares about wildlife?* Springer, New York, New York, U.S.A.
- Mbaiwa, J.E. 2018. Effects of the safari hunting tourism ban on rural livelihoods and wildlife conservation in Northern Botswana. *South African Geographical Journal* 100: 41–61.
- McCarthy, J.M., T. Gumbricht, T. McCarthy, P. Frost, K. Wessels, and F. Seidel. 2003. Flooding Patterns of the Okavango Wetland in Botswana between 1972 and 2000. *Journal of the Human Environment* 32: 453-457.

- Mishra, C., P. Allen, T. McCarthy, M.D. Madhusudan, A. Bayarjargal, and H.H.T. Prins. 2003. The role of incentive programs in conserving the snow leopard. *Conservation Biology* 17: 1512-1520.
- Murray-Hudson, M. 2009. Floodplain Vegetation Responses to Flood Regime in the Seasonal Okavango Delta, Botswana. University of Florida.
- Myers, N. 1975. The silent savannahs. *International Wildlife* 5: 5–10.
- Nowell, K. and P. Jackson. 1996. Wild Cats: Status Survey and Conservation Action Plan. World Conservation Union, Gland, Switzerland 5577.
- Nyhus, P.J., S.A. Osofsky, P. Ferraro, F. Madden, and H. Fischer. 2005. Bearing the cost of human-wildlife conflict: the challenges of compensation schemes. *In People and Wildlife: Conflict or Coexistence?* Woodroffe, R., S. Thirgood, and A. Rabinowitz eds pp. 107-121. Cambridge University Press, Cambridge.
- Ogada, M.O., R. Woodroffe, N.O. Oguge, and L.G. Frank. 2003. Limiting Depredation by African Carnivores: the Role of Livestock Husbandry. *Conservation Biology* 17: 1-10.
- Pettigrew, M., Y. Xie, A. Kang, M. Rao, J. Goodrich, T. Liu, and J. Berger. 2012. Human-carnivore conflict in China: a review of current approaches with recommendations for improved management. *Integrative Zoology* 7:21-226.
- Pozo, R.A., E.G. LeFlore, A.B. Duthie, N. Bunnefeld, I.L. Jones, J. Minderman, O.S. Rakotonarivo, and J.J. Cusack. 2020. A multispecies assessment of wildlife impacts on local community livelihoods. *Conservation Biology* 35: 297-306.
- Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., et al. (2006). Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences* 8: 310–337.
- 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.
- Stedman, R.C. 2012. Sociological Considerations in Wildlife Management. *In Human Dimensions of Wildlife Management* 2<sup>nd</sup> ed. D.J. Decker, S.J. Riley, and W.F. Siemer eds pp. 58-67. John Hopkins University Press, Baltimore, Maryland, U.S.A..
- Thomas, B., J.D. Holland, and E.O Minot. 2011. Wildlife tracking technology options and cost considerations. *Wildlife Research* 38: 653–663.
- Treves A., M. Krofel, and J. McManus. 2016. Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment* 14: 380-388
- Treves, A. and K.U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491–1499.

- Trinkel, M., and F.M. Angelici. 2016. The decline in the lion population in Africa and possible mitigation measures. *In Problematic Wildlife*, ed F. M. Angelici. Springer International Publishing, Switzerland. pg 45–68.
- van Eeden, L. M., A. Eklund, J.R.B. Miller, J.V. López-Bao, G. Chapron, M.R. Cejtin, et al. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16:e2005577.
- Vaske, J.J. and M.J. Manfredo. 2012. Social Psychological Considerations in Wildlife Management. *In Human Dimensions of Wildlife Management* 2nd ed. D.J. Decker, S.J. Riley, and W.F. Siemer eds pp. 43-57. John Hopkins University Press, Baltimore, Maryland, U.S.A. *Human Dimensions of Wildlife Management*.
- Wall, J., G. Wittemyer, B. Klinkenberg, and I. Douglas-Hamilton. 2014. Novel opportunities for wildlife conservation and research with real-time monitoring. *Ecological Applications* 24: 593–601.
- Weise, F. J., M.W. Hayward, R. Casillas Aguirre, M. Tomeletso, P Gadimang, M.J. Somers, et al. 2018. Size, shape and maintenance matter: a critical appraisal of a global carnivore conflict mitigation strategy – livestock protection kraals in northern Botswana. *Biological Conservation* 225: 88–97.
- Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution* 6: 242.
- Wolski, P. and H.H.G. Savenije. 2006. Dynamics of floodplain-island groundwater flow in the Okavango Delta, Botswana. *Journal of Hydrology* 320: 283-301.
- Woodroffe, R. and L.G. Frank. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* 8: 91-98.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164-168.

#### 4.7. Figures and Tables

Table 4.1. Cattle posts listed for each village (with posts that received mophane kraals bolded) in the northern Botswana study area and lion alert messages sent to each village between August 2015 and December 2016. \*Matswii 2 received both a square and round kraal.

Village	Beetsha	Eretsha	Gudigwa	Gunotsoga	Seronga	
Cattle Post	Gomoteretere 1	Kachirachira	Kopano	Ndorotsha 1	Dungu	
	Gomoteretere 2	<b>Katapa</b>	Kwisangwana	Ndorotsha 2	Kawoyo	
	<b>Matswii 1</b>	<b>Kwaga</b>	Matetere	Ndorotsha 3	Kwaxiana	
	<b>Matswii 2*</b>	<b>Jungwe</b>	Pompa	<b>Samoti</b>	Mbiroba	
	Nxeke	<b>Moyagogo</b>	Sekuku	<b>Xau 1</b>	Nxiniga	
	Samogo		Tanijo	Xau 2	Samoxuma	
	Zambia 1		<b>Xaodobe</b>		<b>Teekae</b>	
	Zambia 2		<b>Xwishoro</b>		Thinxo	
					Xamoga	
Lion Alerts						Total
Primary	25	10	5	23	0	63
Secondary	10	10	4	0	0	24
Total	35	20	9	23	0	87

Table 4.2: GPS satellite collar data for 5 collared lions and associated number of independent geofence breaches and lion alerts sent in the northern Botswana study area between August 2015 and December 2016. The average duration (in hours) and standard deviation for each lion's geofence breaches shown in parentheses ( $\bar{x}$ ,  $\sigma$ ). \*PiOP Coalition formed after collar deployment, Airstrip Male and Xamaga male joined to form PiOP coalition.

Vernacular ID (Villager given name)	Sex	Collar deployment period	Number of attempted fixes	Number of successful fixes	Percent fixes in grazing lands	Percent fixes in village lands	Number of grazing lands geofence breaches	Number of village geofence breaches	Lion alerts sent
Airstrip Pride (Mayenga Nyambi)	F	8/15-12/16	2,399	2,285	1	0	10 (5, 6)	0 (NA, NA)	4
Cut-tail Pride (Maleherehere)	F	2/16-12/16	1,681	1,583	9	<1	19 (19, 18)	1 (4, 0)	10
PiOP Coalition*									
(Multwankanda)	M	8/15-12/16	2,475	1,777	3	0	21 (8, 8)	0 (NA, NA)	8
(Nduraghumbo)	M	8/15-12/16	2,531	2,273	8	4	31 (24, 42)	12 (23, 31)	22
Xakampa Coalition (Eretsha)	M	8/15-12/15	609	565	20	5	20 (19, 24)	6 (15, 12)	17

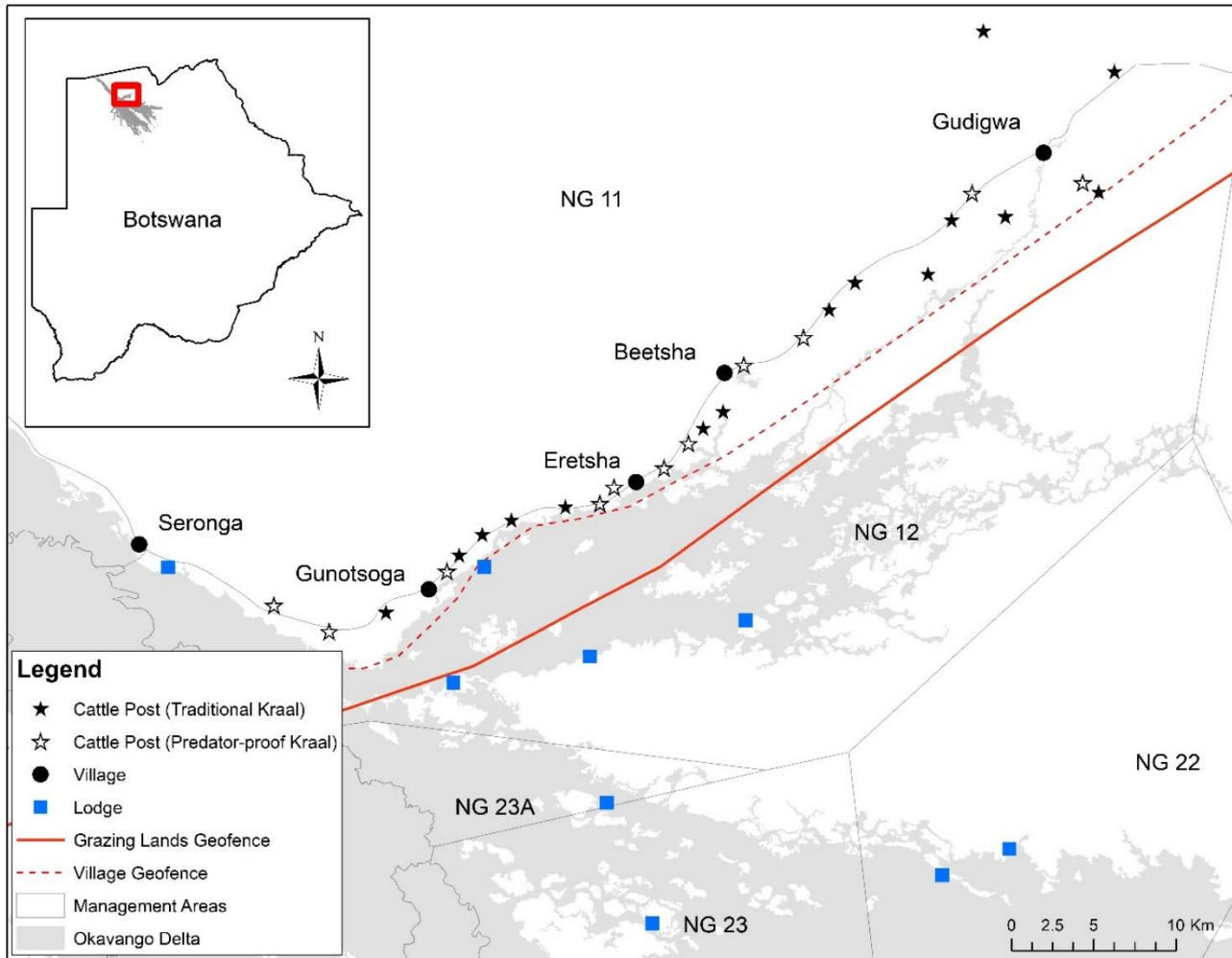


Figure 4.1. Map of the lion conflict study area in northern Botswana as well as locations of PiOP sponsored predator-proof kraals (livestock enclosures) and lion alert electronic geofence boundaries in the lion conflict study area in northern Botswana.



Figure 4.2. Traditional kraal structures in northern Botswana. Top: thorn branch style construction, Bottom: thick wooden branch construction.



Figure 4.3. Pride in Our Prides newly constructed predator-proof kraals in the lion conflict study area in northern Botswana. Top: Rectangular woven mophane branch kraal. Bottom: Portion of circular stacked mophane trunk kraal.

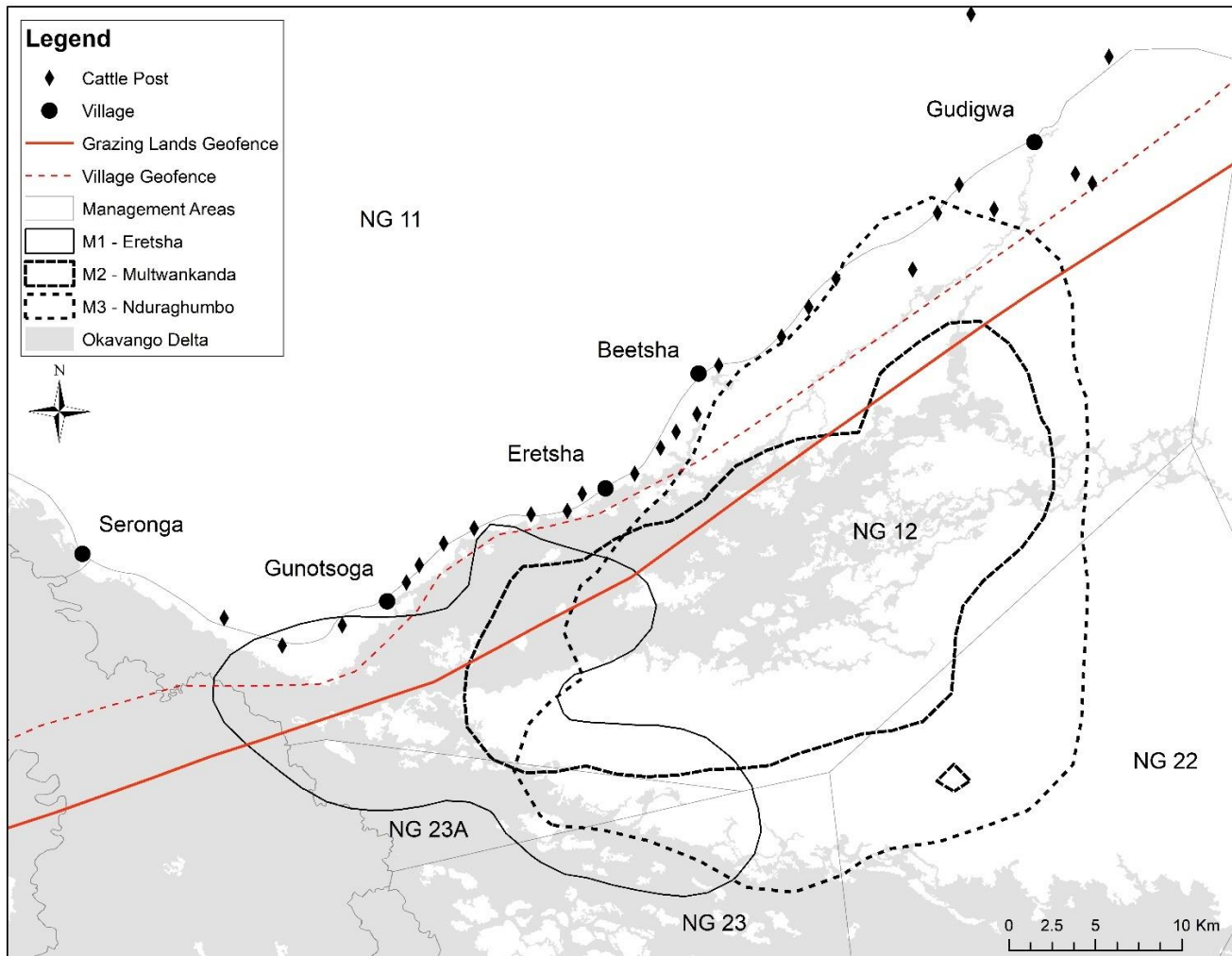


Figure 4.4. Male lion 95% kernel density estimation home ranges in the lion conflict study area in northern Botswana and lion alert electronic geofence boundaries in the lion conflict study area in northern Botswana.

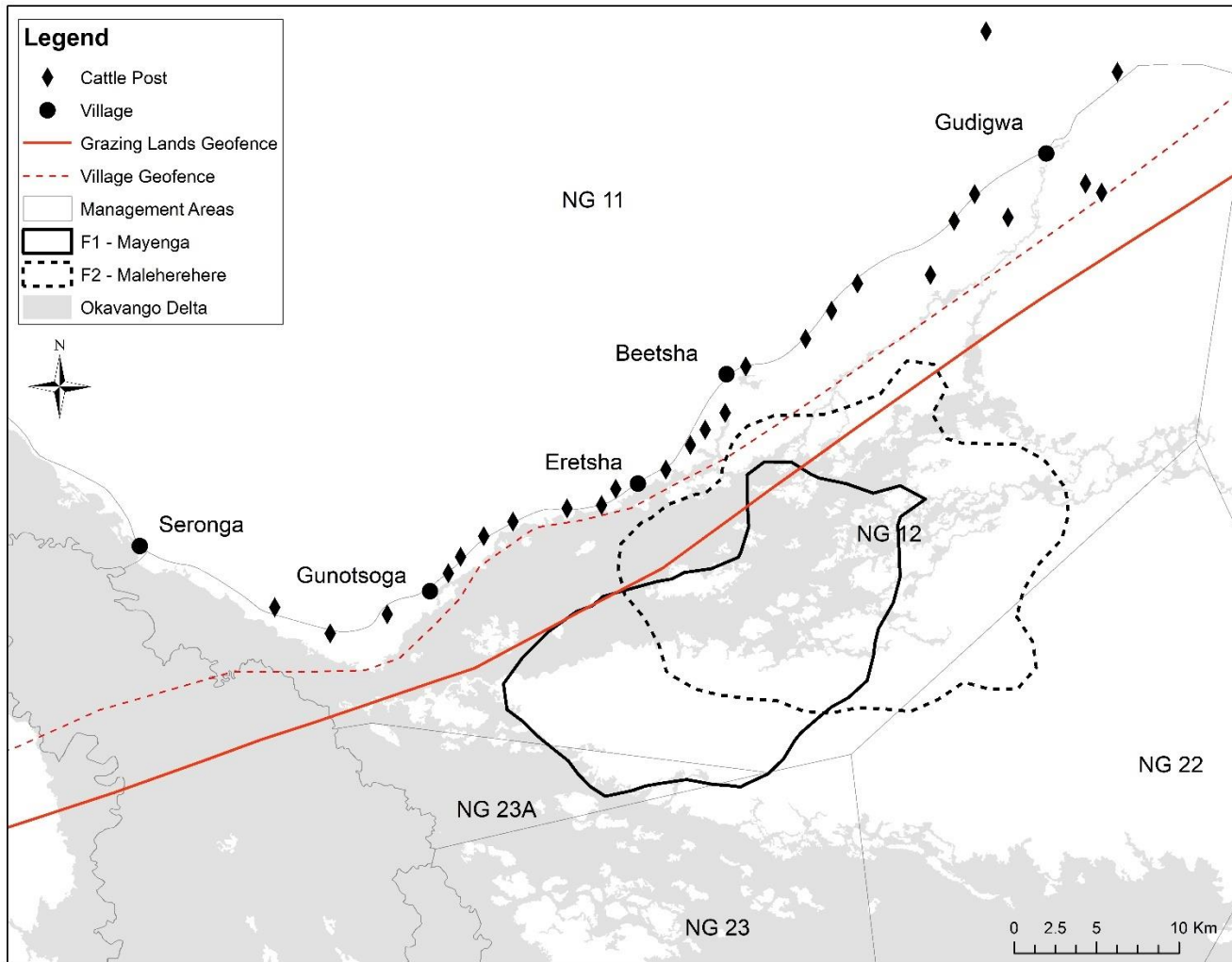


Figure 4.5. Female lioness 95% kernel density estimation home ranges in the lion conflict study area in northern Botswana and lion alert electronic geofence boundaries in the lion conflict study area in northern Botswana.

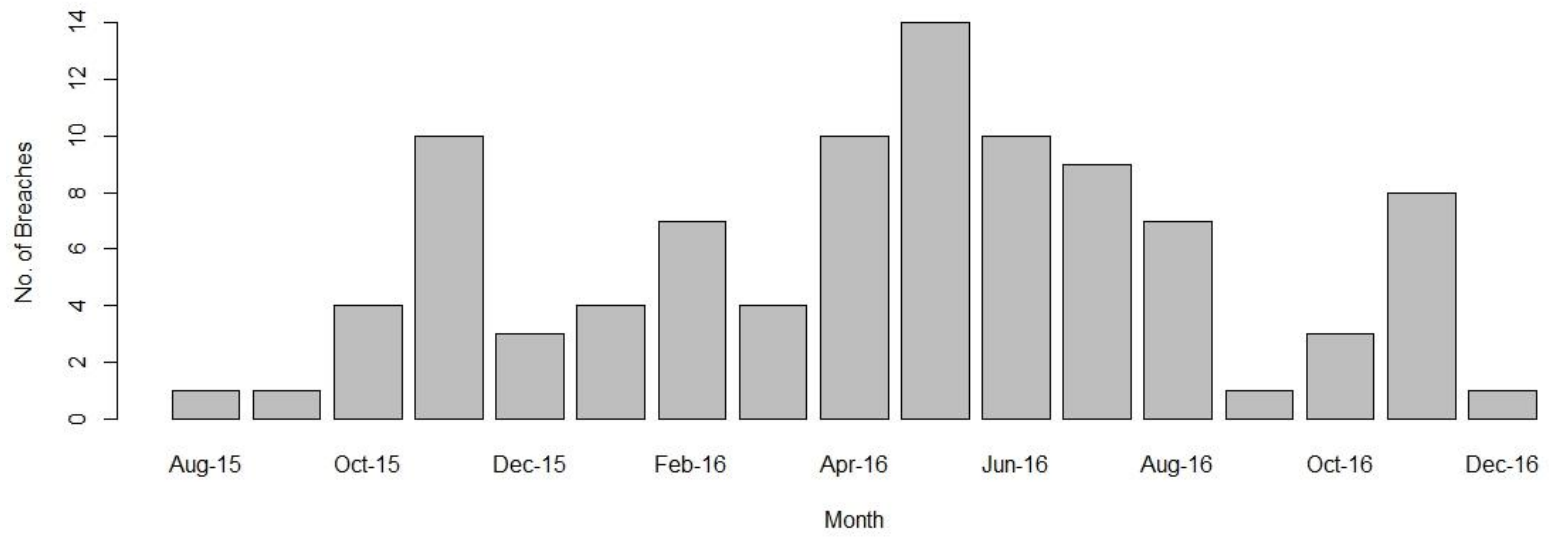


Figure 4.6. Number of geofence breaches by month over the course of the human-lion conflict study in northern Botswana.

## CHAPTER 5

### HUMAN DIMENSIONS OF HUMAN-LION CONFLICT: A PRE- AND POST-ASSESSMENT OF A CONFLICT MITIGATION PROGRAM IN THE OKAVANGO DELTA, BOTSWANA

**Abstract** - Human-carnivore conflicts are contributing to global large carnivore declines. Conservation efforts must include biological and social solutions while attempting to increase local stakeholder tolerance of carnivores. We investigated human-carnivore conflict in the Okavango Delta, Botswana between 2014 and 2016, and tested conflict mitigation strategies alongside an already established government compensation program. Our conflict mitigation program included predator-proof livestock enclosure construction, establishment of an early warning system linked to GPS satellite lion collars, depredation event investigations, and educational programming. We conducted pre- (n=201) and post- (n=208) assessments of villagers' attitudes towards carnivores, livestock husbandry, and perceptions of conflict and established mitigation programs. Husbandry levels were low as 50% of farmers lost livestock to carnivores and 5-10% of owned stock was lost. Respondents had strong negative attitudes towards lions, which kill most depredated livestock. Tolerance for large carnivores significantly increased following our conflict mitigation efforts, though tolerance for lions near villages did not. The number of respondents who believed that coexistence with carnivores was possible significantly increased. Respondents had negative attitudes towards the government-run compensation program, citing low and late payments, but were supportive of our

mitigation strategies. Our efforts show targeted, intensive conflict management can positively impact stakeholder tolerance of carnivores.

## **5.1. Introduction**

Large, terrestrial mammalian carnivores have suffered substantial population declines and range contractions as a result of human activities (Woodroffe 2001, Ripple et al. 2014). Conflicts with people continue to be a primary cause of these declines as large carnivores kill livestock and occasionally kill people (Woodroffe 2001). Sociopolitical factors significantly impact carnivore conservation, as people are responsible for substantial amounts of global predator mortality (Treves & Karanth 2003). With carnivore declines being caused by social pressures, successful conservation must incorporate both biological and social solutions (Rientjes 2001, Treves & Karanth 2003), focusing on increasing human tolerance and cultivating coexistence between people and predators in multiuse landscapes (Treves & Bruskotter 2014, van Eeden et al. 2018).

In Africa, three socio-economic factors impact large carnivore conservation, 1) people's attitudes and behavior towards large carnivores, 2) costs on people coexisting with large carnivores, and 3) large carnivore benefits that act as an incentive for people to coexist with these species (Winterbach et al. 2013). Recognizing the importance of these factors in areas where human-wildlife conflicts occur is integral in the formation of comprehensive carnivore management plans. Rural people generally determine their views and attitudes towards wildlife in terms of the wildlife's value as a resource (Lamarque et al. 2009). If a species has no concrete monetary or cultural value, people can associate it with negative feelings and attitudes, either for real or perceived losses it

causes (Mbaiwa et al. 2008, Lamarque et al. 2009). Fear and the threat of livestock losses, as well as actual losses, can adversely affect carnivore conservation and lead to lethal control of carnivores (Naughton-Treves & Treves 2005, Wang & Macdonald 2006). People whose livelihood is directly linked to livestock (e.g. food, clothing, income) are least likely to tolerate large carnivores (Mishra 1997, Patterson et al. 2004, Frank et al. 2005). Livestock also represent many rural Africans' savings and community standing, so the emotional value ascribed to them is often more important than their actual monetary worth (Loveridge 2005, Dickman 2009). Understanding the perceptions of local people is vital as negative attitudes can severely hinder conservation initiatives (Mishra et al. 2003, Naughton-Treves et al. 2003).

Local opinions towards problem carnivores vary across locations (Li et al. 2015), but typically, positive attitudes are associated with lower monetary losses due to the conflict (Dickman 2005), benefits received from local ecotourism (Lindsey et al. 2005, Hemson et al. 2009), and increased levels of education and wealth (Naughton-Treves et al. 2003, Zimmermann et al. 2005). Communication of the benefits associated with a given species, as well as ways to avoid risk, can encourage increased tolerance and more positive perceptions of carnivores (Bruskotter & Wilson 2014). Generally, however, local community members have low levels of tolerance for large carnivores (Kansky et al. 2014, Inskip et al. 2016). This intolerance, fueled by both actual and perceived conflicts, is regularly exhibited through lethal control practices and contributes to species' population declines (Naughton-Treves & Treves 2005, Woodroffe et al. 2005).

Here we focus on human-carnivore conflict in northern Botswana, where the government established a compensation program designed to reimburse farmers for

losses to carnivores of conservation concern, and thus encourage tolerance of and coexistence with carnivores (Department of Wildlife and National Parks [DWNP] 1998, DWNP 2013). In 2013 in the eastern Panhandle of the Okavango Delta, local farmers experienced high levels of livestock depredation by wild carnivores, especially lions (*Panthera leo*), and retaliated in kind by shooting problem animals and indiscriminately poisoning others (LeFlore et al. 2019). In 2014, we established a multipronged lion conservation program that independently investigated livestock losses (LeFlore et al. 2019), established a predator-proof livestock enclosure building program (Chapter 4, this document; Weise et al. 2018), created a novel early warning system linked to lion satellite-GPS collars (Chapter 4, this document; Weise et al. 2019), tracked the local lion population (Chapter 3, this document;), and shared information about lions with local villagers at village meetings and schools. Additionally, and presented here, we used questionnaires administered through in-person interviews, both before and after establishing the above mitigation efforts, to investigate local farmers' attitudes towards carnivores and conservation, perceptions of the conflict, livestock husbandry methods, and attitudes towards our and the government's conflict mitigation programs. We hypothesized that villagers and farmers would have negative attitudes towards lions and other carnivores, limited livestock husbandry practices, and would disapprove of the government's livestock compensation program, as has been seen elsewhere in Botswana (Gusset et al. 2009, Hemson et al. 2009). Furthermore, we expected villagers to be supportive of our conflict mitigation efforts but that tolerance for carnivores would only marginally increase.

## 5.2. Study Area

This study was conducted in northern Botswana within a portion of the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA), which has been identified as an area of critical importance for lion conservation (Funston 2014). The KAZA TFCA is roughly 440,000 km<sup>2</sup>, spans 5 countries (Angola, Botswana, Namibia, Zambia, and Zimbabwe), includes 36 protected areas, and is home to an estimated 3,500 lions. Our efforts focused in the eastern panhandle of the Okavango Delta (Figure 5.1), one of the largest inland deltas, or alluvial fans, in the world (McCarthy et al. 2000, McCarthy et al. 2003, Kgathi et al. 2006). Our study area connects the Okavango Delta to the rest of the KAZA TFCA and supports both people and wildlife.

Our research encompassed the concessions of NG (Ngamiland) 11, 12, 22, 23, and 23A, which are government-defined management areas slated for various uses ranging from community managed areas allowing human habitation and natural resource use (NG's 11 & 12) to wildlife management areas (WMA's) and photographic tourism areas (NG's 22, 23, and 23A; Figure 5.1). People can live, farm, and utilize natural resources in both NG's 11 and 12. NG's 22, 23, and 23A, WMA's designated for photographic wildlife tourism, incorporate community-run wildlife tourism but are also leased to various international agents for wildlife conservation and photographic tourism purposes. Hunting is not allowed in any of these WMAs as Botswana imposed a national hunting ban in 2014. NG 11 and 12 are inhabited by 4 distinct ethnic groups—Bakgaladadi, Bambukushu, Basarwa, and Bayei—speaking 4 different languages: Sekgaladi, Sembukushu, Sesarwa, and Seyei. Most people also speak Setswana, which is one of two national languages in Botswana. In addition to Setswana and at least one other

local language, some people also speak varying amounts of English, the second national language.

Villagers are agriculturists who keep livestock (cattle, *Bos taurus/indicus*; goat, *Capra hircus*; horse, *Equus caballus*; and donkey *Equus asinus*; LeFlore et al. 2019) and tend crops during the growing season, which is typically from December to April but varies with the rains. People live in concentrated villages and in smaller settlements referred to as cattle posts. Individuals living at a specific cattle post are usually related (e.g., a man and his wife/wives and children, or brothers and their wives and children). These cattle posts lie within a larger village. This study included 4 focal villages—Beetsha, Eretsha, Gudigwa, and Gunotsoga—and their associated cattle posts. These villages were chosen due to the high levels of reported carnivore conflicts and proximity to important lion habitat. Village populations, including the people living at associated cattle posts, ranged from approximately 700-1,600 people with a total population over 4,000 (Botswana Population and Housing Census 2011). The villages and cattle posts lie along a gravel road, and villagers typically reside in thatched-roof mud huts. Livestock are kept in thorn-branch or thick wooden-branch enclosures, referred to locally as “kraals”. In addition to human settlements and agriculture, there are several safari lodges in the area. They are located south of the villages in the Delta and most lie across a seasonally flooded channel of the Okavango River (Figure 5.1).

### **5.3. Methods**

We conducted 409 structured interviews across four focal villages (Beetsha, Eretsha, Gudigwa, and Gunotsoga) in two rounds of surveys between September-December 2014 and October-December 2016 (initial surveys n=201, follow-up surveys

n=208). Within each village, respondents were organized by where they live the majority of the year, either in the village center or at a surrounding cattle post. Respondents were opportunistically selected, and an attempt was made to speak with the head of the household to obtain the most influential opinions in the household; both men and women, ages 18+, were included in the study. Interviews were conducted in English and translated into a local language, depending on the respondent's preference, by local team members (MT and TD) who were native speakers of the national languages (English and Setswana) and the four local languages (Sembukushu, Seyei, Sesarwa, and Sekgaladi). When conducting follow-up interviews, we attempted to resample individuals that had previously taken part in initial interviews from 2014 (ultimately, our resample rate was 65%). When circumstances made this impossible (i.e., original respondents passed away, moved, were remotely employed, or declined to be interviewed), we opportunistically selected additional respondents, as above, to have similar sample sizes as the first survey. Major demographic characteristics (sex ratio, farmer ratio, average age, and average household size) from resampled and new respondent groupings of follow-up surveys were compared via two-tailed Pearson's  $\chi^2$  tests and two-tailed t-tests. Resampled and new respondent data were pooled as no significant differences were found between groupings (sex ratio:  $\chi^2 = 3.6$ ,  $p = 0.058$ ; farmer ratio:  $\chi^2 = 1.84$ ,  $p = 0.175$ ; average age:  $t = 0.442$ ,  $p = 0.659$ ; average household size:  $t = 0.867$ ,  $p = 0.387$ ).

All interviews were structured and comprised of both open- and close-ended questions with some questions providing space for additional explanation. Questions focused on demographics, livestock husbandry techniques, livestock losses, attitudes towards and knowledge of carnivores, knowledge and perceptions of wildlife and

conservation, human-carnivore conflict, attitudes towards the Botswanan government's livestock loss compensation program, and attitudes towards our conflict mitigation strategies (Weise et al. 2018, LeFlore 2019, Weise et al. 2019). Respondents were informed that their responses were confidential, their participation was voluntary, and that answering all questions was not mandatory. Initial interviews took an average of 47 minutes (range = 20-156 min., median = 45 min.) and follow-up interviews took an average of 27 minutes (range = 11-74 min., median = 28 min.). Results were analyzed using R statistical software (R version 3.5.1; R Core Team 2018), and a combination of tolerance scores, descriptive statistics,  $\chi^2$  and *t* tests were used in analyses.

## **5.4. Results**

### **5.4.1. Respondent Demographics**

During the initial survey in 2014, 201 interviews were conducted, and 208 interviews were conducted during the follow-up survey in 2016, across four focal villages, with the totals for each village (village center and cattle post) ranging between 47 and 56 (Tables S1 & S2 in Appendix A). In the initial survey, 100 respondents resided in the village centers while 101 resided at cattle posts; in follow-up surveys, 111 respondents resided in the village centers and 97 resided at cattle posts. In both rounds of surveys, men were interviewed more often, making up 69% (n=139) and 71% (n=148), respectively, of respondents which resulted in sex ratios of 2.24:1 and 2.46:1. The average age of respondents was 40 years old (range 19-84) in the initial round and 46 (range 20-92) in the follow-up round of surveys. Most respondents were heads of their household in both initial (65%, n=131) and follow-up (63%, n=131) surveys with an average of 7 people in their household. Based on information presented in the Botswana

Population and Housing Census (2011), projected national population growth rates from the World Bank (2016), and our respondents speaking for approximately 7 people per household, we estimate that our sample represented ~30% of the total population of individuals in these four villages for each round of surveys. The majority of respondents from both initial and follow-up surveys either received no education at all (initial 43%, n=87; follow-up 37%, n=76) or received a secondary school education (37%, n=74; 36%, n=75). Livestock owners comprised 71% (n=143) of initial and 82% (n=171) of follow-up respondents.

#### 5.4.2. Perceptions of Wildlife, Conservation, and National Parks

All initial survey respondents were asked about their general perceptions of wildlife, conservation, and national parks during initial surveys (Table 5.1). Most respondents (75%, n=151) believed that there was more wildlife than ten years before while 31% (n=62) reported having a family member who holds a job associated with wildlife. The majority of respondents believed the level of human-carnivore conflict was increasing (79%, n=159). Similarly, only 18% (n=36) of initial respondents thought coexistence with carnivores was possible, as 87% (n=174) of respondents believed that domestic livestock were a lion's top food choice. Significantly more respondents from cattle posts than village centers believed domestic prey are a lion's top food choice ( $\chi^2=4.39$ ,  $p=0.036$ ). When asked about the ways to improve coexistence with predators, respondents' top answers centered on avoiding the opportunity for interaction by keeping predators separate from people and livestock (25%, n=50), keeping predators in a national park (13%, n=27), keeping predators within fences (10%, n=21), or by removing predators altogether (8%, n=15); another 8% of respondents (n=16) believed that it was

impossible to improve coexistence. The majority of respondents (83%, n=167) claimed that they did not use lethal control of carnivores to manage human-carnivore conflict, but two individuals (1%) cited shooting predators as a means of control. While there was a consensus that respondents did not use lethal means to control predators, 50% of livestock farmers (n=67) stated that they had zero tolerance for livestock depredations (i.e., after 1 event they would retaliate and kill the offending predator).

There was a general consensus from all initial survey respondents (87%, n=174) that national parks are good, as people believed they generate money for the government (95%, n=191), protect wildlife for future generations (94%, n=189), keep wildlife away from livestock (87%, n=175), and subsequently decrease conflicts between wildlife and livestock (81%, n=163; Table 5.1). About a third of respondents believed that national parks take land away from people (37%, n=74) or livestock (35%, n=70). Half of respondents thought national parks took land away from hunting (49%, n=99).

While significantly more initial survey respondents believed that wildlife benefits them (56%, n=112,  $\chi^2=4$ ,  $p=0.046$ ) and support the national hunting ban (66%, n=132,  $\chi^2=23.59$ ,  $p<0.001$ ), respondents from village centers and cattle posts did not hold these views similarly; a significantly higher proportion of respondents from village centers than cattle posts believed wildlife benefited them (72%, n=72 vs. 40%, n=40;  $\chi^2=20.08$ ,  $p<0.001$ ) and supported the hunting ban (75%, n=75 vs. 56%, n=57;  $\chi^2=6.88$ ,  $p=0.008$ ; Table 5.1). Conversely, a significantly higher proportion of respondents from cattle posts (47%, n=47) than village centers (27%, n=27) believed that national parks take land away from people ( $\chi^2=7.42$ ,  $p=0.006$ ). Furthermore, cattle post farmers had more negative views towards carnivores; significantly more respondents from cattle posts believed that

human carnivore conflict was increasing (88%, n=89 vs. 70%, n=70;  $\chi^2=8.91$ ,  $p=0.003$ ), and significantly fewer respondents believed coexistence with carnivores was possible (10%, n=10 vs. 26%, n=26;  $\chi^2=7.8$ ,  $p=0.005$ ). There is a general understanding from all respondents that it is illegal to collect firewood from national parks (82%, n=165), though cattle post farmers seem to be more aware of this fact as a significantly higher proportion of them state so (88%, n=89 vs. 76%, n=76;  $\chi^2=4.23$ ,  $p=0.04$ ).

Similarly to initial surveys, a significantly higher proportion of follow-up survey respondents from village centers believed that wildlife benefitted them (88%, n=98 vs. 74%, n=72;  $\chi^2=5.95$ ,  $p=0.015$ ; Table 5.1). In general, significantly more respondents from follow-up surveys believed that wildlife benefits them (82%, n=170,  $\chi^2=85.45$ ,  $p<0.001$ ; Table 5.1), and this represents a significant increase from initial surveys ( $\chi^2=31.1$ ,  $p<0.001$ ; Table 5.2). The number of respondents (45%, n=94; Table 5.1) with a family member who holds a job associated with wildlife also significantly increased in the time between initial and follow-up surveys ( $\chi^2=8.32$ ,  $p=0.004$ ; Table 5.2). The number of respondents who support the national hunting ban remained relatively constant between initial and follow-up surveys (66%, n=132 vs. 64%, n=134;  $\chi^2=0.03$ ,  $p=0.872$ ), as did the number of respondents who believed that human-carnivore conflict is increasing (66%, n=132 vs. 64%, n=134;  $\chi^2=0.03$ ,  $p=0.872$ ; Table 5.2).

#### 5.4.3. Livestock Husbandry

In the initial survey, 71% (n=143) of respondents reported owning livestock. Only 6% (n=8) of them paid a herder to guard livestock, 7% (n=10) had a child herd livestock, and 1% (n=2) had a herder with livestock at all times (Table 5.2). The vast majority of livestock owners claimed to kraal their livestock at night (96%, n=137) but only 60%

(n=85) reportedly kraal their livestock *every* night. Most (76%; n=109) livestock owners were willing to modify their husbandry practices if the changes helped minimize conflicts with carnivores. Approximately half of livestock owners reported losing livestock to carnivores in the year before initial surveys (50%, n=72) were conducted in 2014 and over the course of the two-year study as reported on follow-up surveys in 2016 (46%, n=79). Initial respondents owned a total of 3,611 livestock and follow-up respondents owned a total of 3,383 livestock (Table S3 in Appendix A); cattle are the most prevalent livestock in the area. In the year leading up to initial surveys in 2014, respondents reported that 10% (n=371) of owned livestock were lost to predators. This number declined over the course of the study as respondents reported losing 5% (n=181) of owned livestock in follow-up surveys with lions being responsible for 75% of killed livestock. According to government valuation of livestock via nationally averaged market value (DWNP 2013), the sum of livestock reported killed by predators in the 12 months prior to initial surveys was US\$~97,000, and over the course of the study livestock lost to predators was valued at US\$~47,000 (Table S4 in Appendix A).

While the percentage of respondents who reported kraaling their livestock at night significantly declined over the course of the study (88% [n=150], down from 96% [n=137];  $\chi^2=5.49$ ,  $p=0.02$ ), the percentage who kraal their livestock *every* night increased, though not significantly, from 60% (n=85) to 69% (n=116;  $\chi^2=2.03$ ,  $p=0.154$ ). The percentage of respondents who paid a herder remained constant at 6% (n=10); respondents who had a child herd livestock increased from 7% to 14% (n=24), but not significantly ( $\chi^2=3.3$ ,  $p=0.069$ ), and the percentage that always had a herder with livestock significantly increased from 1% to 8% (n=13,  $\chi^2=5.3$ ,  $p=0.021$ ).

#### 5.4.4. Tolerance/Approval Scores

Respondents were asked about their attitudes towards lions, other predators, and the established government-run compensation program on a five-point scale in both initial and follow-up surveys. Tolerance/approval scores were obtained by assigning scores, ranging from -2 to +2, to responses with most negative answers receiving -2, slightly negative receiving -1, neutral receiving a 0, slightly positive receiving +1, and most positive receiving +2. Initial surveys yielded a mean tolerance score for lions of -0.79 ( $\sigma=1.03$ ; Table 5.3), with 61% (n=123) of respondents having strong and moderate negative attitudes towards lions. Respondents from the initial survey were less tolerant of having lions close to the village resulting in a mean tolerance score of -1.53 ( $\sigma=0.67$ ), with 94% of respondents having strong and moderately negative attitudes towards lions being near villages. When asked about attitudes towards predators in general, respondents were slightly more tolerant, with 48% (n=96) having strong and moderately negative attitudes, resulting in a mean tolerance score of -0.45 ( $\sigma=1.11$ ). For all three of these tolerance metrics, respondents from cattle posts had significantly more negative attitudes than respondents from village centers.

Overall, 59% (n=118) of respondents had strong and moderately negative attitudes towards the government run compensation program, yielding a mean approval score of -0.09 ( $\sigma=1.34$ ; Table 5.3); 84% of those respondents (n=99) cited low payments as the reason for their dissatisfaction. There was no significant difference in mean approval scores between respondents from village centers and cattle posts. We also asked initial survey respondents about their interest in a potential livestock insurance program that would run separately from the government compensation program, and 90% of

livestock owners (n=129) were interested in participating. Of those interested in participating, 86% (n=111) were willing to pay to participate; however, they were not willing to pay enough to make the program viable, with 69% (n=76) willing to pay only US\$~25 (BWP250; US\$1 = BWP10 , July 2015) or less annually.

During the follow-up survey, respondents were significantly more tolerant of both lions ( $t=-6.04$ ,  $p<0.001$ ) and predators ( $t=-3.7$ ,  $p<0.001$ ), with increases in mean tolerance scores to -0.13 ( $\sigma=1.16$ ) for lions and -0.03 ( $\sigma=1.08$ ; Table 5.3) for predators. With a mean tolerance score of -1.45 ( $\sigma=0.98$ ), there was not a significant difference ( $t=-0.97$ ,  $p=0.333$ ) in respondents' tolerance towards having lions close to the village. Respondents from cattle posts continued to have significantly stronger negative attitudes towards lions ( $t=3.1$ ,  $p=0.002$ ) and having lions close to villages ( $t=1.99$ ,  $p=0.048$ ) than respondents from village centers.

#### 5.4.5. Perceptions of Conflict Mitigation Program

To assess the efficacy our conflict mitigation program, we asked follow-up survey respondents about their impressions of the predator-proof livestock enclosures, lion alert system, and human-lion conflict in general (Table 5.1). Respondents had positive views of our conflict mitigation program. Most respondents had seen the predator-proof kraals (89%, n=186) and believe they were more secure than traditional kraals (82%, n=171). Most livestock owners (89%, n=152) wanted to have their own predator-proof kraal, while 63% (n=107) were interested in building one for themselves, citing limited time and resources as impediments. Only 36% of farmers (n=62) had received a lion alert when follow-up surveys were conducted, but respondents in general believed that lion alerts are beneficial (81%, n=168). Some 42% of respondents (n=87) knew the local

name of at least one collared lion. Half of respondents (49%, n=102) believe our project efforts had increased their tolerance of lions, with significantly more of an increase occurring with respondents from cattle posts ( $\chi^2=11.01, p<0.001$ ). The majority of livestock owners (70%, n=119) reported changing their husbandry practices as a result of the conflict mitigation program, citing an increase in their frequency of “kraaling.” Despite these positive trends, 80% of respondents (n=167) still perceived lions to be a problem.

## **5.5. Discussion**

### **5.5.1. Livestock Husbandry and Losses**

Limited livestock husbandry practices substantially contribute to the loss of livestock in northern Botswana and are likely a result of the decline in the previously strong herding culture and complacency following the establishment of government funded compensation program (Breitenmoser et al. 2005, Dickman et al. 2011). As has been seen elsewhere in Africa, both North and South America, and western Europe, herding has largely been eliminated (Breitenmoser et al. 2005). Here in Botswana, children attend school and are unable to tend to livestock, villagers freely state that herding is looked down upon as an inferior position, and farmers do not have the resources to pay a herder’s salary. These circumstances, along with growing populations of both people and livestock, have led to increased human-carnivore conflict (Messmer 2000, Krafte Holland et al. 2019). Improved livestock husbandry methods minimize losses to carnivores (Ogada et al. 2003, Treves & Karanth 2003, Woodroffe et al. 2007) which, in turn, could help to decrease the number of retaliatory killings carried out against carnivores. With 76% of initial respondents stating that they were willing to

modify their livestock husbandry methods to minimize losses to carnivores, there is potential to increase the levels of livestock management. Here and elsewhere, future conflict mitigation efforts should focus on increasing livestock husbandry standards and educating local farmers about the benefits of strong husbandry practices (Eklund et al. 2017, Krafte Holland et al. 2018).

Initial reports from 2014 that 10% of owned livestock were lost to predators in one year were high compared to published literature where depredation levels ranged from 0.02% to 5.5% (Kruuk 1981, Karani 1994, Frank 1998, Patterson et al. 2004, Graham et al. 2005, Kolowski & Holekamp 2006, Hemson et al. 2009). This is likely due to unusually high levels of conflict prior to survey implementation (LeFlore et al. 2019), an overstatement of the actual conflict levels by respondents, and/or a misguided understanding of the conflict due to negative attitudes and perceptions of carnivores (Dickman 2010, Tumenta et al. 2013, Dickman et al. 2014). Depredation levels in our study area over the two-year span between surveys (5%) were in line with the general trends presented in other areas. This decline over the course of the study could be caused by increased awareness and stronger husbandry practices as a result of our project, a decline in the local lion population as a result of numerous retaliatory killings in 2013, or trends toward more realistic representation of information from respondents. As a part of our conflict mitigation program, we independently investigated 102 depredation events affecting 129 livestock in this same timeframe (see LeFlore et al. 2019). Data presented above are likely biased high for reasons previously discussed, and/or our efforts to investigate depredation events were not able to effectively cover the area, as discussed in LeFlore et al. (2019). While losses claimed here were reported through an unverified

interview process, and thus may be inaccurate, they represent the attitudes and perceptions of local stakeholders and directly affect conflict mitigation and conservation efforts (Dickman & Hazzah 2016). Though overall levels of loss may have been exaggerated, our independent depredation investigations confirmed what villagers reported here – lions were responsible for 75% of livestock losses (LeFlore et al. 2019).

### 5.5.2. Attitudes Towards Carnivores

People who live at cattle posts had more negative attitudes towards wildlife and conservation, and perceptions of human-wildlife conflict, than people who live in village centers. Cattle post farmers typically have fewer resources and less access to education than villagers, leading them to generally have more negative attitudes towards carnivores (Roskaft et al. 2007, Lagendijk & Gusset 2008, Gebresenbet et al. 2018). Additionally, respondents from cattle posts live more remotely and own more livestock than people in villages. They are more likely to encounter carnivores and have negative interactions, which can contribute to negative attitudes (Zimmerman et al. 2005).

Even though respondents had strong negative attitudes towards and low tolerance of predators, only two initial survey respondents (1%) said that they kill problem carnivores in response to depredation events. This figure is lower than a similar study in Botswana where ~12% of respondents said that they had attempted to kill a lion (Hemson et al. 2009; Hemson et al. asked if respondents had ever attempted to kill a lion while we asked how respondents deal with problem carnivores). Initial interviews were conducted as a first step in understanding the human-lion conflict in the study area, so a strong relationship with community members had not yet been solidified. This could have biased results and caused respondents to be apprehensive when discussing illegal

activities like killing problem carnivores. Moreover, due to previous poisoning events and lions that were shot in retaliation to increased livestock depredation events in 2013 (30-50% lion population reduction; LeFlore et al. 2019), this reportedly low level of lethal control is unlikely. While the effects and frequency of indiscriminate killings of large carnivores in northern Botswana are still largely unknown (Gusset et al. 2009), their effects in East Africa were shown to be significant (Woodroffe & Frank 2005), with 19 out of 20 collared lions being killed by humans in response to livestock losses. Further investigation of lethal control of lions and other predators in the eastern panhandle of the Okavango Delta is required.

Both actual losses to, and perceived costs caused by, predators contribute to local stakeholder's negative attitudes (Naughton-Treves 1997, Naughton-Treves et al. 2003). While around 50% of livestock owners reported losing livestock to predators, almost 90% of all respondents believed that a lion's top prey choice is domestic livestock. These real losses and perceived costs lead most people to believe that coexistence with lions and other predators is impossible. We suggest the government run compensation program alone has not effectively changed villagers' willingness to coexist with large carnivores, or even their belief that coexistence is possible (Gusset et al. 2009). The program requires modifications to achieve the desired goals of conflict mitigation and adjusting local people's attitudes towards carnivores, as respondents disapproved of the current system.

### 5.5.3. Conflict Mitigation Program Efficacy

Our proposed livestock insurance program, a potential alternative to the governmental compensation program for providing economic relief for losses to predators, proved financially infeasible (Nyhus et al. 2003, Nyhus et al. 2005, Dickman et

al. 2011). While farmers were willing to participate, most were only willing to pay less than US\$25 per year for a premium, eliminating the potential for a sustainable independent livestock insurance program. Significant external funds would be required to initiate and maintain a livestock insurance program (Nyhus et al. 2003, Nyhus et al. 2005, Dickman et al. 2011). Conflict mitigation strategies are likely only popular and effective if costs to the community are kept to a minimum. Our results suggest that intensive human-carnivore conflict mitigation programs, in this case established alongside government compensation, can positively impact tolerance towards predators. Tolerance scores significantly increased even though respondents continued to have negative attitudes towards carnivores. While response bias may have influenced respondents into providing more positive answers regarding their attitudes towards predators, we argue this was unlikely as there was a disparity between attitudes towards lions in general and lions in close proximity to the village. Respondents maintained strong negative attitudes towards having lions near their village, while attitudes towards lions in general significantly improved. Conservation efforts encouraging human-carnivore coexistence typically target reducing predation on livestock, providing economic incentives for coexistence, and/or creating tolerance for carnivores through conservation education (Western et al. 2019). Our efforts (building predator-proof enclosures, establishing an early warning system, sharing information about lion ecology and encouraging community engagement around carnivore conservation, and investigating depredation events), alongside the government compensation program, address all three targets mentioned above and further support the effectiveness of a multi-pronged approach to promote coexistence with carnivores (Western et al. 2019). Future carnivore conservation

efforts should aim to increase human tolerance for, and encourage coexistence with, carnivores through interdisciplinary and locally tailored approaches (Dickman 2010, Dickman et al. 2011, Treves & Bruskotter 2014).

## **5.6. Conclusion**

While tolerance levels increased over the course of our study, negative attitudes towards carnivores persist in the community and likely impede coexistence with carnivores in the Okavango Delta and KAZA TFCA in general (Mishra et al. 2003, Naughton-Treves et al. 2003, Naughton-Treves & Treves 2005, Funston 2014). Both real and perceived costs of carnivores contribute to these negative attitudes and addressing these negative attitudes should be a focus of future carnivore conservation efforts. Our work also reinforces the notion that a solid comprehension of site-specific human-carnivore conflict is necessary before implementing conflict mitigation strategies (Woodroffe et al. 2007, Dickman et al. 2011). Similarly, the structure of the governmental livestock compensation program requires revision if it is to positively impact the conflict and people's attitudes towards carnivores, as compensation alone does not accomplish these goals (Dickman et al. 2011). Quantifying and understanding the viewpoints of people affected by conflicts with carnivores, as presented here, is an integral step in the development and assessment of conflict mitigation strategies established by governments and conservation organizations.

## 5.7. Literature Cited

- Botswana Population and Housing Census. 2011. URL [www.catalog.ihsn.org/index.php/catalog/4243/download/55990](http://www.catalog.ihsn.org/index.php/catalog/4243/download/55990). Accessed on October 15, 2015.
- Breitenmoser U., C. Angst, J-M. Landry, C. Breitenmoser-Würsten, J.D.C. Linnell, and J-M. Weber. 2005. Non-lethal techniques for reducing depredation. *In People and Wildlife – Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz pp. 49–71. Cambridge University Press, Cambridge, UK.
- Bruskotter, J.T., and R.S. Wilson. 2014. Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. *Conservation Letters* 7: 158-165.
- Dickman, A. 2005. An assessment of pastoralist attitudes and wildlife conflict in the Rungwa-Ruaha region, Tanzania, with particular reference to large carnivores. M.Sc. Thesis, University of Oxford, Oxford, United Kingdom.
- Dickman, A.J. 2009. Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania. Ph.D. Thesis, University College London, London, United Kingdom.
- Dickman A.J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation* 13: 458-66.
- Dickman, A.J. and L. Hazzah. 2016. Money, myths and man-eaters: Complexities of human-wildlife conflict. *In Problematic wildlife: A cross-disciplinary approach*, ed F.M. Angelici, pp. 339-56. Switzerland: Springer International Publishing.
- Dickman, A.J., L. Hazzah, C. Carbone, and S.M. Durant. 2014. Carnivores, culture and ‘contagious conflict’: Multiple factors influence perceived problems with carnivores in Tanzania’s Ruaha landscape. *Biological Conservation* 178: 19-27.
- Dickman, A.J., E.A. Macdonald, and D.W. Macdonald DW. 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.
- Department of Wildlife and National Parks. 1998. Guidelines for Compensation. Department of Wildlife and National Parks, Gaborone.
- Department of Wildlife and National Parks. 2013. Compensation Guidelines for Damages Caused by Elephants and Lion. Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism. Government of Botswana, Gaborone, Botswana.
- Eklund, A., J.V. Lopez-Bao, M. Tourani, G. Chapron, and J. Frank. 2017. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific Reports* 7: 2097.

- Frank, L.G., R. Woodroffe, and M.O. Ogada. 2005. People and predators in Laikipia District, Kenya. *In* People and Wildlife: Conflict or Coexistence? eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 286-304. Cambridge, UK: Cambridge University Press.
- Funston, P. 2014. The Kavango-Zambezi Transfrontier Conservation Area – critical for African lions. *Cat News* 60: 4-7.
- Gebresenbet, F., H. Bauer, J.M. Vadjunec, and M. Papeş. 2018. Beyond the numbers: Human attitudes and conflict with lions (*Panthera leo*) in and around Gambella National Park, Ethiopia. *PLoS ONE* 13: e0204320.
- Graham, K., A.P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159-171.
- Gusset, M., M.J. Swarner, L. Mponwane, K. Keletile, and J.W. McNutt. 2009. Human-wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. *Oryx* 43: 67-72.
- Hemson, G., S. Maclellan, G. Mills, P. Johnson, and D. Macdonald. 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.
- Inskip, C., N. Carter, S. Riley, T. Roberts, and D. MacMillan. 2016. Toward Human-Carnivore Coexistence: Understanding Tolerance for Tigers in Bangladesh. *PLoS ONE* 11: e0145913.
- Kansky, R., M. Kidd, and A.T. Knight. 2014. Meta-analysis of attitudes toward damage-causing mammalian wildlife. *Conservation Biology* 28: 924-938.
- Karani, I.W. 1994. An Assessment of Depredation by Lions and other Predators in the Group Ranches Adjacent to Masai Mara National Reserve. M.Sc. Thesis, Moi University, Eldoret, Kenya.
- Kgathi, D.L., D. Kniveton, S. Ringrose, A.R. Turton, C.H.M. Vanderpost, J. Lundqvist, and M. Seely M. 2006. The Okavango; a river supporting its people, environment and economic development. *Journal of Hydrology* 331: 3-17.
- Kolowski, J.M., and K.E. Holekamp. 2006. Spatial and temporal variation in livestock depredation by large carnivores along a Kenyan reserve border. *Biological Conservation* 128: 529-541.
- Krafte Holland, K., L.R. Larson, and R.B. Powell. 2018. Characterizing conflict between humans and big cats *Panthera* spp: A systematic review of research trends and management opportunities. *PLoS ONE* 13: e0203877.
- Kruuk, H. 1981. The Effects of Large Carnivores on Livestock and Animal Husbandry in Marsabit District, Kenya. IPAL Technical Report E-4, UNEP-MAB integrated project in arid lands.

- Lagendijk, D.D.G. and M. Gusset. 2008. Human–Carnivore Coexistence on Communal Land Bordering the Greater Kruger Area, South Africa. *Environmental Management* 42: 971-6.
- Lamarque, F., J. Anderson, R. Fergusson, M. Lagrange, Y. Osei-Owusu, and L. Bakker. 2009. Human-Wildlife Conflict in Africa. Causes, Consequences and Management Strategies. Food and Agriculture Organization of the United Nations Forestry, Rome, Italy.
- LeFlore, E.G., T.K. Fuller, M. Tomeletso, and A.B. Stein. 2019. Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation* 18: e00592.
- Li, C., Z. Jiang, C. Li, S. Tang, F. Li, Z. Luo, X. Ping, et al. 2015. Livestock depredations and attitudes of local pastoralists toward carnivores in the Qinghai Lake Region, China. *Wildlife Biology* 21: 204-212.
- Lindsey, P.A., J.T. duToit, and M.G.L. Mills. 2005. Attitudes of ranchers towards African wild dogs *Lycaon pictus*: conservation implications on private land. *Biological Conservation*. 125: 113-121.
- Loveridge, A.J. 2005. Conflict synthesis. *In* Lion Conservation Research: From Conflict to Socioecology. Workshop 3 & 4, eds A.J. Loveridge, T. Lynam, and D.W. Macdonald, Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.
- Marker, L.L., M.G.L. Mills, D.W. Macdonald. 2003. Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology* 17: 1290-1298.
- Mbaiwa, J.E., B.N. Ngwenya, and D.L. Kgathi. 2008. Contending with unequal and privileged access to natural resources and land in the Okavango Delta, Botswana. *Singapore Journal of Tropical Geography* 29: 155-172.
- McCarthy, T.S., G.R.J. Cooper, P.D. Tyson, and W.N. Ellery. 2000. Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *South African Journal of Science* 96: 25-33.
- McCarthy, J.M., T. Gumbricht, T. McCarthy, P. Frost, K. Wessels, and F. Seidel. 2003. Flooding Patterns of the Okavango Wetland in Botswana between 1972 and 2000. *Journal of the Human Environment* 32: 453-457.
- Messmer, T.A. 2000. Emergence of human–wildlife conflict management: turning challenges into opportunities. *International Biodeterioration and Biodegradation* 45: 97-102.
- Mishra, C. 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24: 338-343.

- Mishra, C., P. Allen, T. McCarthy, M.D. Madhusudan, A. Bayarjargal, and H.H.T. Prins. 2003. The role of incentive programs in conserving the snow leopard. *Conservation Biology* 17: 1512-1520.
- Naughton-Treves, L. 1997. Farming the forest edge: vulnerable places and people around Kibale National Park, Uganda. *The Geographical Review* 87: 27-47.
- Naughton-Treves, L. and A. Treves. 2005. Socio-ecological factors shaping local support for wildlife: crop raiding by elephants and other wildlife in Africa. *In People and Wildlife: Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 252-277. Cambridge, UK: Cambridge University Press.
- Naughton-Treves, L., R. Grossberg, and A. Treves. 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology* 17: 1500-1511.
- Nyhus, P., H. Fischer, F. Madden, and S. Osofsky. 2003. Taking the bite out of wildlife damage: the challenges of wildlife compensation schemes. *Conservation in Practice* 4: 37-43.
- Nyhus, P.J., S.A. Osofsky, P. Ferraro, F. Madden, H. Fischer. 2005. Bearing the cost of human-wildlife conflict: the challenges of compensation schemes. *In People and Wildlife: Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 107-121. Cambridge, UK: Cambridge University Press.
- Ogada, M.O., R. Woodroffe, N.O. Oguge, and L.G. Frank. 2003. Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. *Conservation Biology* 17: 1-10.
- Patterson, B.D., S.M. Kasiki, E. Selempo, and R.W. Kays. 2004 Livestock depredation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119: 507-516.
- R Core Team. 2018 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rientjes, S. 2001. Nature conservation: much more than an exercise in applied ecology. *European Nature* 6: 5-7.
- Ripple, W.J., J.A. Estes, R.L. Beschta, C.C. Wilmers, E.G. Ritchie, M. Hebblewhite, J. Berger, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484.
- Roskaft, E., B. Handel, T. Bjerke, and B.P. Kaltenborn. 2007. Human attitudes towards large carnivores in Norway. *Wildlife Biology* 13: 172-85.
- Treves, A. and J. Bruskotter. 2014. Tolerance for predatory wildlife. *Science* 344: 476-477.
- Treves, A. and K.U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491-1499.

- Tumenta, P.N., H.H. de Iongh, P.J. Funston, and H.A. Udo de Haes. 2013. Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx* 47: 237-242.
- van Eeden, L. M., A. Eklund, J.R.B. Miller, J.V. López-Bao, G. Chapron, M.R. Cejtin, et al. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16:e2005577.
- Wang, S. and D. Macdonald. 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation* 129: 558-565.
- Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. Lions at the Gates: Transdisciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution* 6: 242.
- Weise, F. J., M.W. Hayward, R. Casillas Aguirre, M. Tomeletso, P Gadimang, M.J. Somers, et al. 2018. Size, shape and maintenance matter: a critical appraisal of a global carnivore conflict mitigation strategy – livestock protection kraals in northern Botswana. *Biological Conservation* 225: 88–97.
- Western, G., D.W. Macdonald, A.J. Loveridge, and A.J. Dickman. 2019. Creating Landscapes of Coexistence: Do Conservation Interventions Promote Tolerance of Lions in Human-dominated Landscapes? *Conservation and Society* 17: 204-217.
- Winterbach, H.E.K., C.W. Winterbach, M.J. Somers, and M.W. Hayward. 2013. Key factors and related principles in the conservation of large African carnivores. *Mammal Review* 43: 89-110.
- Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. *In* Carnivore Conservation, eds J.L. Gittleman, R.K. Wayne, D.W. Macdonald, and S.M. Funk, pp. 61-92. Cambridge, UK: Cambridge University Press.
- Woodroffe, R. and L.G. Frank. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* 8: 91-98.
- Woodroffe, R., L.G. Frank, P.A. Lindsey, S.M.K. ole Ranah, and S. Romañach. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity Conservation* 16: 1245-1260.
- Woodroffe, R., S. Thirgood, and A. Rabinowitz. 2005. The impact of human-wildlife conflict on natural systems. *In* People and Wildlife: Conflict or Coexistence? eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 1-12. Cambridge, UK: Cambridge University Press.
- World Bank. 2016. Botswana Population Rate. World Development Indicators, The World Bank. URL <http://data.worldbank.org/indicator/SP.POP.GROW?locations=BW> Accessed November 25, 2016.

Zimmermann, A., M.J. Walpole, and N. Leader-Williams. 2005. Cattle ranchers' attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. *Oryx* 39: 406-412.

## 5.8. Tables and Figures:

Table 5.1: Percent “yes” responses (no. of respondents in parentheses) to questions of conservation importance from initial surveys in 2014 (Village Center “VC” n=100, Cattle Post “CP” n=101, total n=201) and follow-up surveys in 2016 (VC n=111, CP n=97, total n=208) by location with associated  $\chi^2$  tests for homogeneity. Follow-up surveys also included questions regarding the established management interventions. Total percent “yes” responses (number of respondents in parentheses) and associated  $\chi^2$  goodness of fit tests also shown. Significant  $p$ -values denoted with an “\*.”

Question	VC	CP	$\chi^2$	$p$ -value	Total	$\chi^2$	$p$ -value
2014							
Is there more wildlife now than 10 years ago?	77 (77)	73 (74)	0.20	0.654	75 (151)	66.02	<0.001*
Do you have a family member who has a job associated with wildlife?	35 (35)	27 (27)	1.25	0.262	31 (62)	28.26	<0.001*
Believe level of human-carnivore impact is increasing	70 (70)	88 (89)	8.91	0.003*	79 (159)	203.94	<0.001*
Believe coexistence with carnivores is possible	26 (26)	10 (10)	7.8	0.005*	18 (36)	81.92	<0.001*
Believe domestic prey are a lion’s top food choice	81 (81)	93 (92)	4.39	0.036	87 (174)	117.88	<0.001*
Do you believe that national parks are good?	87 (87)	86 (87)	<0.001	1	87 (174)	124.48	<0.001*
Do you think national parks generate money for the government?	95 (95)	95 (96)	<0.001	1	95 (191)	182.19	<0.001*
Do national parks protect wildlife for future generations?	95 (95)	93 (94)	0.08	0.78	94 (189)	171.74	<0.001*
Do national parks keep wildlife away from livestock?	84 (84)	90 (91)	1.16	0.281	87 (175)	123.21	<0.001*
Do national parks decrease interactions between livestock & wildlife?	82 (82)	80 (81)	0.02	0.884	81 (163)	91.65	<0.001*
Do national parks take land away from people?	27 (27)	47 (47)	7.42	0.006*	37 (74)	10.91	<0.001*
Do national parks take land away from livestock?	29 (29)	41 (41)	2.49	0.115	35 (70)	14.55	<0.001*
Do national parks take land away from hunting?	44 (44)	54 (55)	1.8	0.18	49 (99)	0.13	0.719
Does wildlife benefit you?	72 (72)	40 (40)	20.08	<0.001*	56 (112)	4	0.046*
Do you support the national hunting ban?	75 (75)	56 (57)	6.88	0.008*	66 (132)	23.59	<0.001*
It is illegal to collect firewood in national parks?	76 (76)	88 (89)	4.23	0.04*	82 (165)	95.34	<0.001*
2016							
Believe level of human-carnivore impact is increasing	70 (78)	78 (76)	1.36	0.243	74 (154)	155.81	<0.001*
Believe coexistence with carnivores is possible	31 (34)	26 (25)	0.39	0.535	28 (59)	36.92	<0.001*
Do you have a family member who has a job associated with wildlife?	51 (56)	39 (38)	2.22	0.136	45 (94)	1.92	0.166
Does wildlife benefit you?	88 (98)	74 (72)	5.95	0.015*	82 (170)	85.45	<0.001*
Do you support the national hunting ban?	67 (74)	62 (60)	0.33	0.563	64 (134)	17.31	<0.001*
Seen predator-proof kraals	99 (89)	90 (87)	2.9	0.088	89 (186)	129.31	<0.001*

Believe predator-proof kraals are more secure than traditional kraals	81 (90)	84 (81)	0.08	0.784	82 (171)	126.15	<0.001*
Farmers who want a predator-proof kraal	90 (73)	88 (79)	0.06	0.808	89 (152)	127.01	<0.001*
Farmers interested in building a predator-proof kraal for themselves	62 (50)	63 (57)	<0.01	0.954	63 (107)	16.69	<0.001*
Farmers who received a lion alert	32 (26)	40 (36)	0.84	0.361	36 (62)	12.92	<0.001*
Believe lion alerts are beneficial	79 (88)	82 (80)	0.17	0.684	81 (168)	145.45	<0.001*
Know at least one lion's given local name	44 (49)	39 (38)	0.34	0.559	42 (87)	5.26	0.022*
Claim project efforts have increased their tolerance of lions	38 (42)	62 (60)	11.01	<0.001*	49 (102)	0.89	0.347
Farmers who have changed their husbandry practices	68 (55)	71 (64)	0.08	0.773	70 (119)	34.51	<0.001*
Perceive lions as a problem	80 (74)	88 (85)	10.2	0.001*	80 (167)	77.92	<0.001*

---

Table 5.2: Comparison by  $\chi^2$  tests for homogeneity for key questions involving wildlife, conservation, and livestock management from initial surveys in 2014 and follow-up surveys in 2016. Percent of respondents who answered “yes” shown (number of respondents in parentheses). All respondents answered questions about wildlife and conservation (2014 n=201, 2016 n=208) while only livestock owners answered questions about livestock management (2014 n=143, 2016 n=171). Significant *p*-values denoted with an “\*.”

Question	2014	2016	$\chi^2$	<i>p</i> -value
<b>ALL RESPONDENTS</b>				
Believe wildlife benefits them	56 (112)	82 (170)	31.1	<0.001*
Have family member who has a job associated with wildlife	31 (62)	45 (94)	8.32	0.004*
Support the hunting ban	66 (132)	64 (134)	0.03	0.872
Believe level of human-carnivore impact is increasing	79 (159)	74 (154)	1.19	0.275
Believe coexistence with carnivores is possible	18 (36)	28 (59)	5.69	0.017*
<b>LIVESTOCK OWNERS</b>				
Kraal livestock at night	96 (137)	88 (150)	5.49	0.02*
Kraal livestock every night	60 (85)	69 (116)	2.03	0.154
Pay a livestock herder	6 (8)	6 (10)	<0.01	1
Have a child herd livestock	7 (10)	14 (24)	3.3	0.069
Always have herder with livestock	1 (2)	8 (13)	5.3	0.021*
Lost livestock to carnivores	50 (72)	46 (79)	0.38	0.535

Table 5.3: Mean tolerance/approval scores by location (village center “VC” and cattle post “CP”) for initial and follow-up surveys along with associated  $t$ -statistic. Further comparison by  $t$ -statistic of total mean tolerance scores between initial and follow-up surveys also shown. Significant  $p$ -values denoted with an “\*.”

Question	Initial						Follow-up						Comparison	
	VC	CP	$t$	$p$ -value	Total	$\sigma$	VC	CP	$t$	$p$ -value	Total	$\sigma$	$t$	$p$ -value
Tolerance of lions	-0.6	-0.97	2.57	0.011*	-0.79	1.03	0.1	-0.39	3.1	0.002*	-0.13	1.16	-6.04	<0.001*
Tolerance of lions being close to villages	-1.37	-1.69	3.46	<0.001*	-1.53	0.67	-1.32	-1.59	1.99	0.048*	-1.45	0.98	-0.97	0.333
Tolerance of predators	-0.09	-0.77	4.54	<0.001*	-0.45	1.11	0.07	-0.15	1.45	0.15	-0.03	1.08	-3.7	<0.001*
Approval of compensation program	-0.01	-0.17	0.82	0.413	-0.09	1.34	N/A							

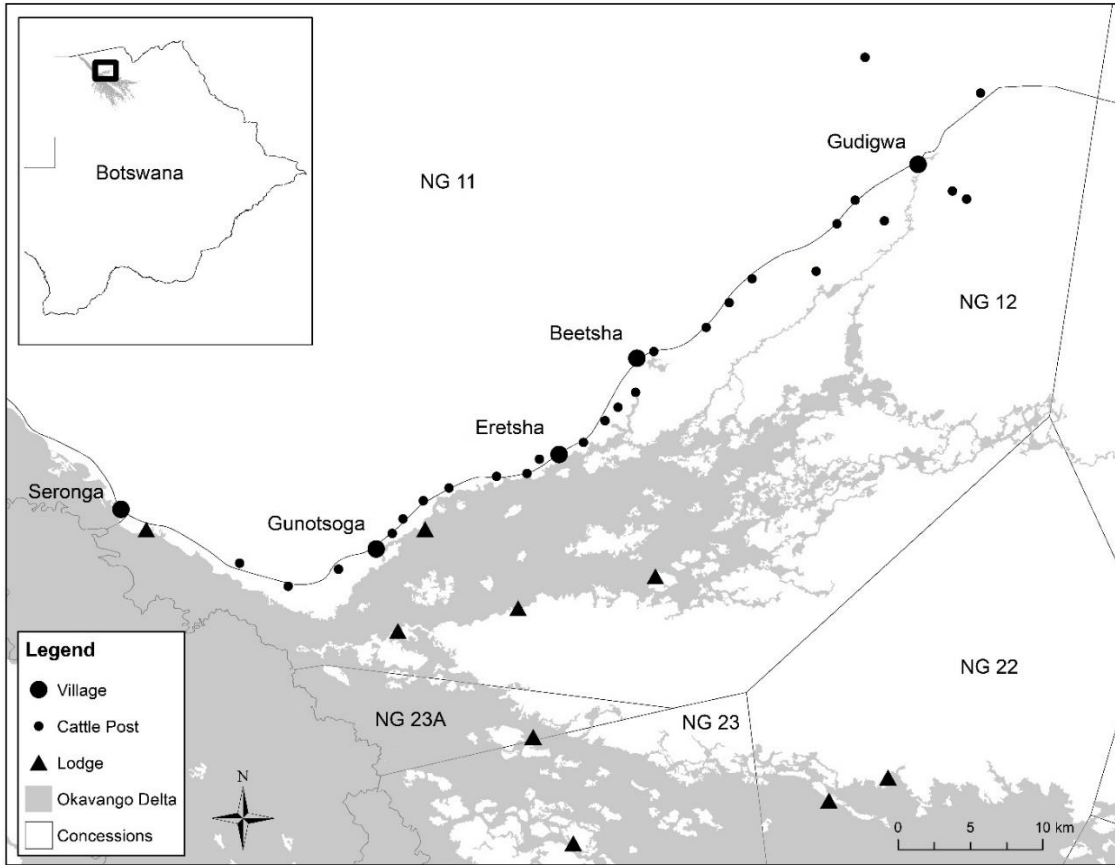


Figure 5.1: Study area map showing villages, cattle posts, safari lodges, and concession boundaries.

## CHAPTER 6

### CONCLUSION: THE FUTURE OF LION CONSERVATION IN AFRICA

#### 6.1. Dissertation Summary

An overarching goal for this dissertation research was to investigate human-lion conflict in the eastern panhandle of the Okavango Delta, Botswana. The conflict in the area had not yet been researched but was broadly understood to be quite severe as villagers regularly claimed to lose livestock to lions and would then retaliate and resort to lethal control measures to minimize their losses. To assess the levels of human-lion conflict, I investigated livestock depredation events when they occurred to determine the wildlife species responsible and determine the numbers of livestock lost over time. This information was then compared to governmental problem animal control data which are used to compensate farmers for lost livestock. These efforts were documented above in Chapter 2. Most livestock losses (>90%) occurred while livestock were grazing unguarded, and lions were responsible for ~75% of investigated livestock depredation events. Annualized average losses across the study area based on our independent depredation investigations were ~\$14,000 and ~\$25,000 based on governmental data (~\$25-45/household/year). Though the loss of even one animal could have major implications for a farmer and their family as one animal can be valued at over \$550. In its current form, the government run compensation program does not have enough funding to compensate all reported livestock losses that qualify for reimbursement.

In addition to assessing levels of livestock loss in the area, I tracked and monitored the local lion population to learn how they navigate a multi-use, highly

dynamic habitat matrix and to better inform future management interventions. Chapter 3 highlighted these efforts and documented one of the only ecological studies of lions existing entirely outside protected area boundaries in communal land. Lions were tracked using GPS satellite/VHF radio collars and there was considerable amount of shared space use among neighboring individuals who were believed to be unrelated. While neighboring individuals utilized shared space, shared space use was varied temporally to avoid potentially costly conspecific interactions. The highest levels of home range overlap occurred during the wet and early dry seasons when the study area is inundated with Okavango Delta flood waters, restricting available habitat. Lions minimized time spent in close proximity to humans but were able to utilize areas where livestock are known to graze. Both ecological and anthropogenic factors likely impact lion movements in this highly dynamic and human-dominated landscape.

Another major aspect to this dissertation research was the development of a conflict mitigation program that was informed by conflict investigations and lion movements (Chapter 4). Twelve predator-proof livestock enclosures (“kraals”) were built across the study area and were made from locally available mopane (*Colophospermum mopane*) branches and trunks. These kraals received varying levels of use as villagers employ relatively unsecure livestock husbandry practices. While one-third of the predator-proof kraals went unused, there was widespread interest in the kraals as villagers noted they wished they had one of their own. No depredation events took place at these newly constructed predator-proof kraals. Another aspect of the conflict mitigation program was the novel development of an early-warning system linked to lion satellite/GPS collars. As lions moved into electronically geofenced areas of high

livestock or human activity, I could disperse a lion alert to villagers who were potentially at risk of a livestock attack. This study was the first time any such technology had been used for the purposes of warning local stakeholders about potential danger from lions. In practice, as the collars were programmed in this iteration of the pilot study, there were often delays between when the lion crossed the geofence and when I was notified about the geofence breach, delaying the transmission of the lion alert to at-risk stakeholders. Despite the technical challenges, there was widespread support for the early-warning lion alerts. Though only about one-third of survey respondents recalled receiving a lion alert, >80% of respondents believed that lion alert messages were beneficial.

In Chapter 5, I examined the attitudes of local villagers towards predators and the established conflict mitigation program. I conducted 201 initial baseline surveys in 2014 to uncover the perspectives, beliefs, and practices of local stakeholders and then conducted 208 follow-up surveys at the end of the study in 2016 to determine if sentiments or practices had changed and how stakeholders viewed the conflict mitigation program. Respondents admitted having pretty unsecure livestock husbandry practices and 50% of farmers lost livestock to wild predators with 5-10% of owned livestock lost. Linked to the livestock losses, respondents had strong negative attitudes towards lions. Towards the end of the study, however, respondents noted an increase in lion tolerance and the potential for coexistence with carnivores.

On the whole, this project serves as a model for future human-lion conflict mitigation programs. The tactics and technology used here are highly transferrable and could be implemented in areas where there are high levels of human-wildlife conflict. Though, the efficacy of a new system would be improved with technological advances

and a more autonomous, streamlined, and efficient alerting system. It should be clearly stated however, that early-warning systems are likely not cost effective on their own, but coupled with additional conflict mitigation strategies, they can be a useful and well-received management tool. Moving toward a more holistic approach to manage carnivore populations and their impacts is critical for future conservation efforts.

## **6.2. Future Directions**

This initial human-lion conflict mitigation attempt yielded intriguing results and with some modifications, the program could be improved upon here in northern Botswana and adapted to fit different human-wildlife interfaces around the globe. Next iterations of this early-warning system should incorporate a more real-time interface that eliminates the cumbersome drawbacks of the system utilized here (Weise et al. 2019). Additionally, the establishment of dynamic geofences informed by ecological parameters could better represent the regularly shifting ecological system. The inclusion of parameters like livestock movements, flooding regimes, vegetative habitat structure, etc. could enable a better understanding of the dynamic Delta system and stronger conflict mitigation programs. Technological advancements with collar longevity and data management interfaces could increase the efficacy of this early-warning system and bring the costs down to a more manageable sum.

In addition to novel early-warning systems, it is clear that more secure, consistent livestock husbandry practices minimize losses to wild carnivores (Ogada et al. 2003, Lichtenfeld et al. 2015). Any future human-lion conflict mitigation programs should make sure to include a component that focuses on bolstering local livestock husbandry efforts. In northern Botswana, there remains significant room for growth in regard to

livestock herding. Establishing a livestock herding program where trained herders remain with livestock all day, would ensure that all livestock are successfully kraaled at night when they are most at risk of lion attacks. This would also have the added advantage that herders who were trained in rangeland management could ensure livestock were grazing in a more sustainable fashion, increasing vegetative production and animal nutrition (Schlecht et al. 2020). The establishment of a trained herder program would have a positive impact on local stakeholders as they would likely lose fewer livestock and their herds would be stronger and healthier.

Finally, future human-lion conflict research and mitigation efforts must include components that address and consider human dimensions (Decker et al. 2012). I firmly believe there are no longer any ecological problems that can be solved without human-based solutions. To successfully address human-lion conflicts and impacts, improve coexistence between people and lions, and protect this declining species, management approaches must be tailored so they are system-specific and centered on the input and needs of local stakeholders. These local stakeholders bear the cost of living among lions (Nyhus et al. 2005) and will ultimately decide whether the species will continue on its current population trajectory. The human dimensions of human-lion conflicts and impacts are extremely complex (Dickman 2010), but solving these problems requires shifts in local stakeholder behaviors and belief systems (Reddy et al. 2017). Based on the cognitive hierarchy (Manfredo 2008), behaviors are the manifestation of attitudes (favorable or unfavorable evaluations of a person, object or action), value orientations (i.e., basic belief patterns), and values (i.e., modes of conduct, desirable individual states, or qualities of life). For widespread cultural shifts in behavior to take place (e.g., coexistence with lions,

or no longer killing livestock raiding lions), changes in community values, beliefs, and attitudes must shift as well (Reddy et al. 2017). These human dimensions are often deeply engrained in a community and are often based on factors that researchers gloss over or are completely unaware of.

For decades, indigenous communities across Africa were seen as incompatible with wildlife conservation, conservation practices that stemmed from a management approach designed to protect resources for the elite while excluding common citizens. Fortress conservation grew from the European model of wildlife conservation where resources were protected for hunting and enjoyment by the elite (Igoe 2004). In managing state resources in Africa, it was believed that biodiversity protection was best achieved by creating protected areas where ecosystems could function without human disturbance – disturbance from local people, not colonists and tourists (Plumwood 2003, Igoe 2004). A central assumption was that local people used natural resources in destructive and illogical ways causing biodiversity loss and environmental degradation. Thus, local people dependent on the area's natural resources were forcibly excluded and kept at bay by park rangers and fences (Samson and Gigoux 2017). Tourism, safari hunting, and scientific research were the only appropriate uses for protected areas, while local people were labeled as criminals, poachers, and squatters when utilizing land they had occupied themselves for decades or their ancestors for centuries.

Today, as African governments and countless conservation organizations aim to protect biodiversity in the face of substantial wildlife population declines, local people living around protected areas remain marginalized and frustrated with their inability to manage their own interactions with nature. Many of these interactions are negative as

community members continue to lose livestock to lions and other wildlife that exist in communal lands and range beyond protected areas. These interactions result in a strengthening of negative attitudes towards wildlife and conservation in general, limiting the effectiveness of management measures. Minimizing these negative attitudes and aiming to increase both tolerance of wildlife and human-wildlife coexistence must be at the forefront of all conservation work. However, I argue that future conservation efforts must be established with an understanding of the impacts of colonial and neo-colonial forces. While environmental historians have written about the impacts of colonialism (Adams and Mulligan 2003, Samson and Gigoux 2017, among others), colonialism is often overlooked by conservation biologists, but it remains a confounding factor in conservation management. Even though Botswana and other African nations have cast off the yolk of European colonialism, the European conservation model that protected wildlife for the enjoyment of the elite at the exclusion of local stakeholders may still be influencing the success of conservation programs. This area needs further exploring, more direct connections to applied conflict mitigation and conservation management, as it can help to inform future efforts. I look forward to conducting this research moving forward.

### 6.3. Literature Cited

- Adams, W.M. and M. Mulligan, eds. 2003. *Decolonizing Nature: Strategies for Conservation in a Post-colonial Era*. Earthscan Publications, Ltd. London, United Kingdom.
- Igoe, J. 2004. *Conservation and Globalization: A Study of National Parks and Indigenous Communities from East Africa to South Dakota*
- Decker, D.J., S.J. Riley, and W.F. Siemer, eds. 2012. *Human Dimensions of Wildlife Management*. John Hopkins University Press, Baltimore, Maryland, U.S.A.
- Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict: *Animal Conservation* 13: 458–466.
- Lichtenfeld, L.L., C. Trout, and E.L. Kisimir. 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodiversity Conservation* 24: 483-491.
- Maddox, G., ed. 1993. *Colonialism and Nationalism in Africa: Conquest and Resistance to Colonialism in Africa*. Garland Publishing, Inc. New York, New York, U.S.A.
- Manfredo, M.J. 2008. *Who cares about wildlife?* Springer, New York, New York, U.S.A.
- Nyhus, P.J., S.A. Osofsky, P. Ferraro, F. Madden, and H. Fischer. 2005. Bearing the cost of human-wildlife conflict: the challenges of compensation schemes *In People and Wildlife – Conflict or Coexistence?* pp. 107–121. eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz. Cambridge University Press, Cambridge, UK.
- Ogada, M.O., R. Woodroffe, N.O. Oguge, and L.G. Frank. 2003. Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. *Conservation Biology* 17: 1-10.
- Plumwood, J. 2003. Decolonizing relationships with nature. In *Decolonizing Nature: Strategies for conservation in a Post-colonial Era*. pp. 51-78. eds W.M. Adams and M. Mulligan. Earthscan Publications, Ltd. London, United Kingdom.
- Reddy, S.M.W., J. Montambault, Y.J. Masuda, E. Keenan, W. Butler, J.R.B. Fisher, et al. 2017. Advancing conservation by understanding and influencing human behavior: human behavior and nature. *Conservation Letters* 10: 248–256.
- Samson, C. and C. Gigoux. 2017. *Indigenous Peoples and Colonialism: Global Perspectives*. Polity Press. Cambridge, United Kingdom.
- Schlecht, E., M.D. Turner, C.G. Hülsebusch, and A. Buerkert. 2020. Managing Rangelands Without Herding? Insights From Africa and Beyond. *Frontiers in Sustainable Food Systems* 4: 549954.

Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. Lions at the Gates: Transdisciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution* 6: 242.

**APPENDIX A**  
**CHAPTER 5 SUPPLEMENTAL MATERIAL**

**Human dimensions of human-lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana**

This appendix contains all supplemental tables which support information presented in the publication: a comparison of key demographic and attitudinal metrics between new and repeat follow-up survey respondents (Table S1), the relevant questions asked during both rounds of surveys (Table S2), respondent demographic data (Tables S3 & S4), and total numbers and valuation of livestock lost to wild carnivores (Tables S5 & S6).

Table S1: Comparison of key demographic factors and attitude metrics between new (n=78) and repeat (n=130) follow-up questionnaire respondents. Percent of respondents who answered “yes” or qualified for the given category shown (number of respondents shown in parentheses) or mean/mean tolerance score shown. Tolerance scores were calculated based on responses to questions regarding respondents’ attitudes towards carnivores using a five-point Likert scale; responses ranged from “strongly dislike/approve” to “strongly like/disapprove” and mean tolerance/approval scores were obtained by assigning values ranging from -2 to +2 to this range of responses. Comparisons between new and repeat respondents were made via two-tailed Pearson’s  $\chi^2$  tests and *t*-tests.

Key demographic factor/attitude metric	New	Repeat	Test statistic	<i>p</i> -value	df	95% CI
<b>DEMOGRAPHIC FACTOR</b>						
Sex ratio (# males)	77 (60)	85 (111)	$\chi^2 = 3.600$	0.058	1.00	-0.265, -0.002
Farmer ratio (# farmers)	80 (62)	66 (86)	$\chi^2 = 1.840$	0.175	1.00	-0.037, 0.206
Average age (years)	43.6	44.7	$t = 0.442$	0.659	167.84	-3.624, 5.711
Average number of people/household	6	7	$t = 0.867$	0.387	151.26	-0.558, 1.432
<b>ATTITUDE METRIC</b>						
Believe number of livestock predation events are increasing	78 (61)	72 (93)	$\chi^2 = 0.807$	0.369	1.00	-0.064, 0.197
Believe coexistence with carnivores is possible	23 (18)	32 (41)	$\chi^2 = 1.327$	0.249	1.00	-0.218, 0.049
Believe management interventions increased tolerance of lions	45 (35)	52 (67)	$\chi^2 = 0.621$	0.431	1.00	-0.216, 0.083
Mean tolerance score toward lions	-0.218	-0.077	$t = -0.829$	0.408	151.6	-0.477, 0.195
Mean tolerance score toward lions close to village	-1.603	-1.357	$t = -1.777$	0.077	169.63	-0.519, 0.027
Mean tolerance score toward predators	-0.115	0.023	$t = -0.855$	0.394	142.88	-0.460, 0.182

Table S2: Relevant list of questions asked during initial (2014) and follow-up (2016) surveys. All questions were asked in both years unless otherwise noted.

---

**Question**

---

DEMOGRAPHICS

What is your gender?

Are you the head of your household?

How many people do you support?

How old were you on your last birthday?

What is the highest education level you have completed?

Do you own livestock? If so, how many of each species?

LIVESTOCK MANAGEMENT

Do you kraal your livestock at night? If so, what are the reasons? If not, why?

If you kraal your livestock, do you kraal them every night?

Do you pay a herder?

Do you have a child herd livestock?

If you have a herder, are they with livestock at all times?

Did you lose livestock to predators within the last year? If so, how many and what species?

2014 - Where do most attacks occur, in the kraal or in the veld?

2014 - How many attacks on livestock by predators are you willing to tolerate before killing culprits?

2016 - Did you lose livestock to predators within the last two years? If so, how many and what species?

WILDLIFE & CONSERVATION

Does wildlife benefit you?

Is there more wildlife now than ten years ago?

Do you or your family derive an income from wildlife?

Do you support the hunting ban in the area?

2014 - Do you think national parks are good or bad? Why?

2014 - Do national parks generate money for the government?

2014 - Do national parks take land away from people?

2014 - Do national parks take land away from livestock?

2014 - Do national parks take land away from hunting?

2014 - Do national parks protect wildlife for future generations?

2014 - Can Motswana collect firewood from national parks and game reserves?

2014 - Do national parks keep wildlife away from livestock?

2014 - What are the top three food choices for lions in the area?

#### HUMAN-CARNIVORE COEXISTENCE

How do you feel about lions: strongly like, like, neutral, dislike, or strongly dislike? Why?

How do you feel about lions being close to your village: strongly like, like, neutral, dislike, or strongly dislike? Why?

How do you feel about predators in general: strongly like, like, neutral, dislike, or strongly dislike? Why?

Do you think the number of predation events is increasing, decreasing or staying the same?

Is coexistence between farmers and predators possible?

What are ways to improve coexistence between farmers and predators?

What management techniques do you employ to reduce the chance of predation?

If you kill predators, what method do you use?

How many predators and what species have you killed in the last year?

How many predators and what species do you know of that have been killed by other villagers in the last year?

2014 - Are you willing to make changes to your livestock management if it will help minimize losses to predators?

2014 - If you are willing to make changes, what are you willing to change?

2016 - Do you perceive lions as a problem?

2016 - Do you perceive lions as a security threat?

#### HUMAN-CARNIVORE COEXISTENCE MANAGEMENT PROGRAMMES

2014 - How do you feel about the government's livestock compensation program: strongly like, like, neutral, dislike, or strongly dislike? Why?

2014 - If there was a separate insurance program that would compensate farmers for livestock lost to predators but required you to kraal your livestock every night, hire a herder to stay with livestock at all times, and stop killing predators, would you be interested in participating?

2014 - Would you be willing to pay to participate in this separate livestock insurance program? If yes, how much per year?

2016 - If you lost livestock in the last two years, did you notify the lion conservation program?

2016 - If you lost livestock in the last two years, did you notify DWNP?

2016 - If you lost livestock in the last two years, did you apply for compensation through DWNP? If so have you been compensated?

2016 - Do you know how many lions our program has collared in the area? How many?

2016 - Do you know the given local names of these lions? If so, list the ones you know.

2016 - Have you seen the programme constructed kraals?

2016 - What are your thoughts on the programme constructed kraals? Please share good and bad opinions.

2016 - Have you received any lion alerts? If so, how?

2016 - Do lion alerts benefit you? If yes, how would you like to receive lion alerts in the future?

2016 - If you have received a lion alert, what is your response to these alerts?

2016 - Have the conservation program's activities increased your tolerance of lions in the area?

2016 - Have you made any changes to your livestock management methods since the start of the conservation program?

Table S3: Initial survey (n=201) respondent demographic information by village and location (VC: village center and CP: cattle post).

<b>Village: No. respondents</b>	<b>Avg. age</b>	<b>Gender pct. M / sex ratio M:F</b>	<b>Pct. top schooling level reached None / 1° / 2° / 3°</b>	<b>Avg. no. people in household</b>	<b>Pct. livestock owners</b>
Beetsha: 47					
VC: 23	42	87 / 20:3	30 / 22 / 35 / 9	6	69
CP: 24	40	91 / 22:2	33 / 25 / 25 / 17	9	75
Eretsha: 50					
VC: 25	32	40 / 10:5	32 / 24 / 44 / 0	6	48
CP: 25	48	56 / 14:1	76 / 6 / 16 / 0	6	100
Gudigwa: 49					
VC: 26	43	62 / 16:10	46 / 12 / 38 / 4	8	65
CP: 23	46	91 / 21:2	57 / 13 / 30 / 0	9	70
Gunotsoga: 55					
VC: 26	35	46 / 12:14	15 / 12 / 69 / 4	7	46
CP: 29	41	83 / 24:5	55 / 10 / 34 / 0	7	97
<b>TOTAL: 201</b>	<b>40</b>	<b>69 / 139:62</b>	<b>43 / 15 / 37 / 4</b>	<b>7</b>	<b>71</b>
<b>VC: 100</b>	<b>38</b>	<b>58 / 58:42</b>	<b>31 / 17 / 47 / 4</b>	<b>7</b>	<b>56</b>
<b>CP: 101</b>	<b>43</b>	<b>80 / 81:20</b>	<b>55 / 14 / 27 / 4</b>	<b>8</b>	<b>86</b>

Table S4: Follow-up survey (n=208) respondent demographic information by village and location (VC: village center and CP: cattle post).

<b>Village: No. respondents</b>	<b>Avg. age</b>	<b>Gender pct. M / sex ratio M:F</b>	<b>Pct. top schooling level reached None / 1° / 2° / 3°</b>	<b>Avg. no. people in household</b>	<b>Pct. livestock owners</b>
Beetsha: 48					
VC: 27	46	78 / 21:6	26 / 44 / 30 / 0	7	85
CP: 21	45	86 / 18:3	29 / 24 / 48 / 0	7	90
Eretsha: 51					
VC: 25	37	44 / 11:14	32 / 36 / 32 / 0	6	64
CP: 26	51	65 / 17:9	54 / 23 / 19 / 0	7	89
Gudigwa: 53					
VC: 33	43	85 / 28:5	30 / 30 / 39 / 0	7	67
CP: 20	53	100 / 20:0	50 / 20 / 30 / 0	7	95
Gunotsoga: 56					
VC: 26	34	42 / 11:15	8 / 15 / 69 / 8	6	77
CP: 30	49	73 / 22:8	63 / 13 / 23 / 0	6	97
<b>TOTAL: 208</b>	<b>46</b>	<b>71 / 148:60</b>	<b>37 / 26 / 36 / 1</b>	<b>7</b>	<b>82</b>
<b>VC: 111</b>	<b>40</b>	<b>64 / 71:40</b>	<b>24 / 32 / 42 / 2</b>	<b>7</b>	<b>73</b>
<b>CP: 97</b>	<b>50</b>	<b>79 / 77:20</b>	<b>52 / 20 / 29 / 0</b>	<b>7</b>	<b>93</b>

Table S5: Number of livestock that respondents owned and reported were killed by carnivores in the year before the initial 2014 survey and in the two year span of the project through 2016 follow-up surveys. Follow-up data included which carnivores were reported responsible for lost livestock. The percentage of livestock lost to a given predator is shown with number of livestock lost shown in parentheses. There were 143 livestock owners in 2014 and 171 in 2016.

Livestock	2014			2016							
	Owned	Killed	Pct.	Owned	Killed	Pct.	Lion	Spotted Hyena	African Wild Dog	Leopard	Unknown
Cattle	2,941	346	11.8	2,540	145	5.7	75 (108)	8 (12)	6 (9)	0 (0)	11 (16)
Goat	551	22	4.9	745	29	3.9	76 (22)	3 (1)	7 (2)	14 (4)	0 (0)
Donkey	91	2	2.2	73	2	2.7	50 (1)	50 (1)	0 (0)	0 (0)	0 (0)
Horse	28	1	3.6	25	3	12	100 (3)	0 (0)	0 (0)	0 (0)	0 (0)
<b>TOTAL</b>	<b>3,611</b>	<b>371</b>	<b>10.3</b>	<b>3,383</b>	<b>179</b>	<b>5.3</b>	<b>76 (134)</b>	<b>8 (14)</b>	<b>6 (11)</b>	<b>2 (4)</b>	<b>9 (16)</b>

Table S6: Government valuation in USD (BWP) of livestock respondents reported lost to predators in one year before initial surveys in 2014 and over the course of the two year study as reported in follow-up surveys in 2016 from focal villages (Gunotsoga, Eretsha, Beetsha, and Gudigwa) in the human-lion conflict study area in northern Botswana.

Livestock Lost	Value USD (BWP)	2014		2016	
		No. Lost	Total Value USD (BWP)	No. Lost	Total Value USD (BWP)
<b>Bovids</b>					
Cow	300 (3,000)	268	80,400 (804,000)	102	30,600 (306,000)
Calf	100 (1,000)	39	3900 (39,000)	6	600 (6,000)
Bull	550 (5,500)	N/A	N/A	11	6,050 (60,500)
Ox	300 (3,000)	39	11,700 (117,000)	27	8,100 (81,000)
Goat	45 (450)	22	990 (9,900)	30	1,350 (13,500)
Subtotal		368	96,990 (969,900)	176	46,700 (467,000)
<b>Equids</b>					
Horse	250 (2,500)	1	250 (2,500)	3	750 (7,500)
Donkey	20 (200)	2	40 (400)	2	40 (400)
Subtotal		3	290 (2,900)	5	790 (7,900)
<b>TOTAL</b>		<b>371</b>	<b>97,280 (972,800)</b>	<b>181</b>	<b>47,490 (474,900)</b>

**APPENDIX B**  
**PRIDE IN OUR PRIDES**  
**INITIAL VILLAGER QUESTIONNAIRE**

Name of Interviewer: \_\_\_\_\_

Date of interview: \_\_\_\_\_

Time started: \_\_\_\_\_ Time finished: \_\_\_\_\_

Village: \_\_\_\_\_

Interview Number: \_\_\_\_\_

**INTRODUCTORY STATEMENT:**

Good morning/afternoon. My name is \_\_\_\_\_ and I am from Pride in Our Prides. We are currently conducting a survey of cattle-post farmers in NG11 and NG12. The information will help us understand your thoughts on wildlife. Your answers are confidential and will never be revealed to any other people. All I am requesting from you is that you answer the following questions truthfully, and to the best of your knowledge. If you cannot answer some questions, simply say so. I sincerely thank you for your time.

Do you agree to participate in this survey?  Yes  No

If YES please continue the survey.

**RESPONDENT INFORMATION AND LIVESTOCK HUSBANDRY PRACTICES:**

1 Are you: (Check one)

Male  Female

Head of household?  Yes  No

2 How many people are there in your household?  People

3 How many people are you supporting (include cattle post/village etc.)?

number of people

4 How old were you on your last birthday?

years

5 What is your marital status?

- 5.1  Never married
- 5.2  Living together
- 5.3  Married
- 5.4  Separated
- 5.5  Divorced
- 5.6  Widowed

**6** What is the highest education level you have completed?

- 6.1  No schooling
  - 6.2  Primary (<= 5 years of schooling)
  - 6.3  Secondary / high school (10-12 years of schooling)
  - 6.4  Other, please specify
- 

**7** How many animals do you have?

Animals	Number
Cattle	
Goats	
Sheep	
Donkey	
Horse	
Chickens	

Other, please explain:

---

- 8** Do you own all of the animals in your herd?  Yes  No

If NO please tell us who you share your herd with \_\_\_\_\_

- 9** Do you kraal your livestock at night?  
 Yes  No

If YES please identify the reason

Reason		Tick all those that apply
9.1	To keep them safe from predators	
9.2	To stop them from being stolen	
9.3	Management purposes	

If NO why don't you kraal your livestock?

---

**10** If yes to question 9, do you kraal your livestock every night?

Yes  No

**11** If you have cattle, please describe their movement patterns during the year.

Wet Season:

---



---

Dry Season:

---



---

**12** Do you pay someone as a herder?  Yes  No

**13** Do you have your child herd your livestock?  Yes  No

If YES to question 11 or 12, is the herder with the livestock at all times?

Yes  No

If No, why not? \_\_\_\_\_

**14** Do you practice calving season?  Yes  No

**15** What was the number of livestock that you lost last year? (Write in numbers)

FACTORS	Cattle	Calves (<9 mo)	Oxen	Goats	Donkey	Horse
Disease						
Predators						
Drought						
Poisonous plants						
Vehicle accidents						
Theft						
Unknown/ Disappearance						
Other						

**NATURE & WILDLIFE Perceptions:**

1 Who owns the wildlife?

---

2 Does wildlife benefit you?  Yes  No

If YES please explain in what way wildlife benefit you

---

3 Is there more wildlife now than ten years ago?

Yes  No

If YES why do you think there is more wildlife now?

- 3.1  Better laws to protect them  
3.2  Tourism makes them more valuable so people protect them  
3.3  Better anti-poaching  
3.4 Other, please explain:

---

If NO why do you think there is less wildlife now?

- 3.5  Over hunting  
3.6  Market hunting  
3.7  Habitat loss  
3.8  Lack of protection  
3.9  Better hunting techniques  
3.10  Poaching  
3.11  Don't know  
3.12 Other, please explain:

---

4 Do you, or any of your family, derive an income from wildlife?

Yes  No

If YES please tick the jobs that you and/or members of your family have in wildlife.

- 4.1  Guide  
4.2  Tracker  
4.3  Job at a photographic camp  
4.4  Job with mobile safari company

- 4.5  DWNP employee
  - 4.6  Game fence worker
  - 4.7  Charter company employee
  - 4.8 Other, please explain
- 

5 Do you support the ban of hunting in the area?  Yes  No  
Why or Why not?

---

6 What do you think about National Parks and Game Reserves? (for example: *Moremi Game Reserve*)  
 Good  Bad

Why?

---



---

If you agree with any of the statements about National Parks and Game Reserves below put a tick  in the box, if you disagree put a cross

- 6.1  Generate money for the government
  - 6.2  Take land away from people
  - 6.3  Protect the wildlife for future generations
  - 6.4  Can't collect firewood
  - 6.5  Keep wildlife away from livestock
  - 6.6  Decrease wildlife/livestock conflict
  - 6.7  Protect the Delta from destruction
  - 6.8  Take land away from livestock
  - 6.9  Take land away from hunting
  - 6.10  Other, please explain:
- 

7 What do you think should be done with those animals that live outside protected areas?

---



---

**PREDATOR INFORMATION:**

1 Have you lost any of your livestock to predators in the last 3 years?

Yes  No If Yes, please fill in the table below:

	LIVESTOCK	TYPE OF PREDATOR	KILLED/ INJURED	BODY PART FOUND	AGE	SEX	BREED
1.1							
1.2							
1.3							
1.4							
1.5							
1.6							
1.7							
1.8							
1.9							
1.10							

If YES please answer the following questions, if NO please go to question 3.

1.11 What time do attacks most often happen? \_\_\_\_\_

1.12 What season do you have most conflict with predators?

Wet  Dry

1.13 Do most attacks happen

in kraal  in veld

1.14 Distance from house or homestead?

Within 5km  Greater than 5km

1.15 How did you know which predator killed your livestock?

1.15.1  Saw on kill

1.15.2  Spoor by kill

1.15.3  Told by neighbours

1.15.4  Notice killing bites

1.15.5  Feeding style

1.15.6  Other \_\_\_\_\_

- 2 How often do you see the following predators in your area? 1) Very Rare (once a year or less), (2) Rare (once to twice a year), (3) Common (monthly) (4) Very common (weekly) (5) other (specify).

	Lion		Leopard		Cheetah
	Spotted hyena		Wild Dog		Jackal

- 3 How often does each species attack cattle? 1) Very Rare (once a year or less), (2) Rare (once to twice a year), (3) Common (monthly) (4) Very common (weekly) (5) other (specify).

	Lion		Leopard		Cheetah
	Spotted hyena		Wild Dog		Jackal

- 4 How often does each species attack smaller livestock (ex: goats, sheep)? (1) Very Rare (once a year or less), (2) Rare (once to twice a year), (3) Common (monthly) (4) Very common (weekly) (5) other (specify).

	Lion		Leopard		Cheetah
	Spotted hyena		Wild Dog		Jackal

- 5 How many attacks on livestock by predators are you willing to tolerate before actively removing the “culprits” (predator)?

5.1	Number of cattle	<input type="text"/>	<input type="text"/>	<input type="text"/>
5.2	Number of calves (<9 months)	<input type="text"/>	<input type="text"/>	<input type="text"/>
5.3	Number of oxen	<input type="text"/>	<input type="text"/>	<input type="text"/>
5.4	Number of donkey	<input type="text"/>	<input type="text"/>	<input type="text"/>
5.5	Number of goats	<input type="text"/>	<input type="text"/>	<input type="text"/>
5.6	Number of horses	<input type="text"/>	<input type="text"/>	<input type="text"/>

### LION INFORMATION

- 1 How many lion prides are living around your village?

Prides

- 2 About how many lions are included in each pride?

2.1   Lions in pride 1

2.2   Lions in pride 2

2.3   Lions in pride 3

2.4   Lions in pride 4

2.5   Lions in pride 5

3 What do you think lions eat in the area?

1: \_\_\_\_\_

2: \_\_\_\_\_

3: \_\_\_\_\_

4 Do lion diets change with the seasons?

Yes  No

If Yes, what are the prey species for lion over the different seasons?

Wet Season:

1: \_\_\_\_\_

2: \_\_\_\_\_

3: \_\_\_\_\_

Dry Season:

1: \_\_\_\_\_

2: \_\_\_\_\_

3: \_\_\_\_\_

5 Are there seasonal differences in the movements of lions in the area?

Yes  No

Wet Season:

\_\_\_\_\_

\_\_\_\_\_

Dry Season:

\_\_\_\_\_

\_\_\_\_\_

6 How do you feel about lions?

6.1  I think lions are wonderful

6.2  I think lions are good

6.3  I am indifferent towards lions

6.4  I don't like lions

6.5  I hate lions

Why?

\_\_\_\_\_

\_\_\_\_\_

7 How do you feel about having lions in the area surrounding your village?

7.1  I think they are great to have around

7.2  I think lions are good to have around

- 7.3  I am indifferent to them being here
- 7.4  I don't like them so close to my village
- 7.5  I think they should be removed from the area

Why?

---



---

**PREDATOR MANAGEMENT:**

**1** How do you feel about predators?

- 1.1  I think predators are wonderful
- 1.2  I think predators are good
- 1.3  I am indifferent towards predators
- 1.4  I don't like predators
- 1.5  I hate predators

**2** Do you think that the number of predation conflict cases is...

(Tick one)

- 2.1  Increasing
- 2.2  Decreasing
- 2.3  Staying the same

**3** Is coexistence between farmer and predator possible?

Yes  No

**4** What can be done to improve coexistence?

---



---

**5** What management techniques do you employ to reduce predator conflict? (Select all that apply)

- 5.1  Kraal livestock at night
- 5.2  Actively herd livestock
- 5.3  Hire a herder
- 5.4  Eliminate predators
- 5.5  Maintain fires at night
- 5.6  Utilize guard dogs
- 5.7  Other

---

**6** If you eliminate predators, what methods do you use?

- 6.1  Shot/ Rifle
  - 6.2  Poison
  - 6.3  Snares
  - 6.4  Traps
  - 6.5  Call DWNP
  - Other
- 

**7** Number of predators that you have killed:

Species	Last year	Last 3 years
Lion		
Spotted hyena		
Leopard		
Cheetah		
Wild Dog		
Jackal		
Other		

**8** Number of predators killed by members of your village:

Species	Last year	Last 3 years
Lion		
Spotted hyena		
Leopard		
Cheetah		
Wild Dog		
Jackal		
Other		

**LIVESTOCK COMPENSATION:**

**1** How do you feel about the government compensation for livestock loss?

- 1.1  I am happy with the current program
- 1.2  I am content with the current program
- 1.3  I am indifferent about the current program
- 1.4  I am unhappy with the current program
- 1.5  I hate the current program

Why:

---

---

**2** If there was an insurance program set up that would compensate farmers 85% of all losses to all predators, but required you to kraal your livestock every night, hire a herder to stay with them at all times, and stop killing predators would you be interested in participation?

Yes  No

**3** Would you be willing to pay to participate?

Yes  No

**4** If YES to 3, how much would you be willing to pay per year to participate?

---

**APPENDIX C**

**PRIDE IN OUR PRIDES**

**FOLLOW-UP VILLAGER QUESTIONNAIRE**

Name of Interviewer: \_\_\_\_\_

Date of interview: \_\_\_\_\_

Language used: \_\_\_\_\_

Time started: \_\_\_\_\_ Time finished: \_\_\_\_\_

Village: \_\_\_\_\_ Cattle Post: \_\_\_\_\_

Interview Number: \_\_\_\_\_ Respondent name: \_\_\_\_\_

GPS Coordinates: S \_\_\_\_\_ E \_\_\_\_\_

**INTRODUCTORY STATEMENT:**

Good morning/afternoon. My name is \_\_\_\_\_ and I am from Pride in Our Prides. We are currently conducting a survey of cattle-post farmers in NG11 and NG12. The information will help us understand your thoughts on wildlife. Your answers are confidential and will never be revealed to any other people – only summarised results will be published. All I am requesting from you is that you answer the following questions truthfully, and to the best of your knowledge. If you cannot answer some questions, simply say so. I sincerely thank you for your time.

Do you agree to participate in this survey?  Yes  No If YES, please continue

**RESPONDENT INFORMATION AND LIVESTOCK HUSBANDRY PRACTICES:**

1. Are you: (Check one)  Male  Female
2. Head of household?  Yes  No
3. How many people are there in your household? \_\_\_\_\_ People
4. How many people are you supporting (include cattle post/village etc.)?  
\_\_\_\_\_ People
5. How old were you on your last birthday?  years
6. What is your marital status?
  - a.  Never married

- b.  Living together
- c.  Married
- d.  Separated
- e.  Divorced
- f.  Widowed

7. What is the highest education level you have completed?

- a.  No schooling
- b.  Primary (<= 5 years of schooling)
- c.  Secondary / high school (10-12 years of schooling)
- d.  Other, please specify: \_\_\_\_\_

8. How many animals do you have?

Animals	Number
Cattle	
Goats	
Donkey	
Horse	

Other, please explain: \_\_\_\_\_

9. Do you own all of the animals in your herd?  Yes  No  
 a. If NO please tell us who you share your herd with:

10. Do you kraal your livestock at night?

Yes  No

If YES please identify the reason:

Reason	Tick all those that apply
To keep them safe from predators	
To stop them from being stolen	
Management purposes	
To keep them from roaming freely	

a. If NO, why don't you kraal your livestock?

\_\_\_\_\_

11. If yes to question 9, do you kraal your livestock every night?

Yes  No

12. Do you pay someone as a herder?  Yes  No If YES, wage: \_\_\_\_\_

13. Do you have your child herd your livestock?  Yes  No

14. If YES to question 11 or 12, is the herder with the livestock at all times?  
 Yes  No

If No, why not?

---

15. Have you lost any of your livestock to predators in the last 2 years?

Yes  No

16. If Yes, please fill in the table below:

LIVESTOCK	TYPE OF PREDATOR	KILLED/ INJURED	BODY PART FOUND	AGE	SEX	BREED

**NATURE & WILDLIFE Perceptions:**

1. Does wildlife benefit you?  Yes  No

2. If YES please explain in what way wildlife benefits you:

---

3. Do you, or any of your family, derive an income from wildlife?

Yes  No

4. If YES please tick the jobs that you and/or members of your family have in wildlife.

a.  Guide

b.  Tracker

c.  Job at a photographic camp

- d.  Job with mobile safari company
  - e.  DWNP employee
  - f.  Game fence worker
  - g.  Charter company employee
  - h.  Other, please explain:
- 

5. Do you support the ban of hunting in the area?  Yes  No
- a. Why or Why not?
- 
- 

6. What do you think should be done with those animals that live outside protected areas?

a. Elephants:

---

b. Predators:

---

c. Other wildlife:

---



---

### ATTITUDES TOWARDS PREDATORS

1. How do you feel about lions?

- a.  I think lions are wonderful
- b.  I think lions are good
- c.  I am indifferent towards lions
- d.  I don't like lions
- e.  I hate lions

Why?

- 
2. How do you feel about having lions in the area surrounding your village?

- a.  I think they are great to have around
- b.  I think lions are good to have around
- c.  I am indifferent to them being here
- d.  I don't like them so close to my village
- e.  I think they should be removed from the area

Why?

- 
3. How do you feel about predators in general?

- a.  I think predators are wonderful

- b.  I think predators are good
  - c.  I am indifferent towards predators
  - d.  I don't like predators
  - e.  I hate predators
4. Do you think that the number of predation conflict cases is...(Tick one)
- Increasing                       Decreasing                       Staying the same
5. Is coexistence between farmer and predator possible?     Yes  No
6. What can be done to improve coexistence? (here, record the three main suggestions by priority)
- 
- 

**PiOP ACTIVITIES**

1. If you have lost any livestock to predators in the last 2 years, have you notified PiOP?  
 Yes  No
  2. If you have lost any livestock to predators in the last 2 years, have you notified DWNP?  
 Yes  No
  3. If you have lost livestock to predators in the last 2 years, have you applied for compensation through DWNP?  
 Yes  No
    - a. Have you been compensated?  Yes  No  
       \_\_\_\_\_Pula                      \_\_\_\_\_Species                      \_\_\_\_\_Date
  4. Do you perceive lion as a problem?  Yes  No
  5. Do you perceive lions as a security threat?  Yes  No
  6. Do you know how many lions PiOP has collared?  
 Yes  No                      If Yes, how many? \_\_\_\_\_ number of lions
  7. Do you know the names of any PiOP lions?  
 Yes  No  
 If Yes, list their names:
- 
- 

8. Do you know the pride composition for lions that you named above?  
 Yes  No                      If Yes, describe what you can:
- 
- 

9. Have you seen the PiOP woven kraals?

Yes  No

10. If yes:

a. Do you think PiOP kraals keep livestock safer than traditional kraals?

Yes  No

b. Do you want a PiOP woven kraal for your livestock?

Yes  No

c. Would you be interested in working to build your own kraal in the PiOP style?

Yes  No

d. What are your thoughts about the PiOP kraals? Both good and bad opinions:

Good:

---

---

Bad:

---

---

11. Have you ever received any lion warnings?

Yes  No

12. If Yes, how did you receive those warnings?

a.  Phone call

b.  SMS/Text message

c.  Word of mouth

d.  Other, please identify \_\_\_\_\_

13. Do lion alert messages benefit you?

Yes  No

If Yes, how would you like to receive lion warnings in the future?

a.  Phone call

b.  SMS/Text message

c.  Word of mouth

d.  Other, please identify \_\_\_\_\_

If No, why not?

---

14. If you have received warnings, what is your response to the warnings? Select all that apply

a.  Kraal livestock

b.  Build fires near kraal

c.  Gather noise makers

d.  Gather torches

e.  Gather guard dogs

- f.  Pass along message
  - g.  No response
  - h.  Other, identify \_\_\_\_\_
15. Have PiOP's activities increased your tolerance of lions in the area?  
 Yes  No
16. In general, what management techniques do you employ to reduce predator conflict? (Select all that apply)
- a.  Kraal livestock at night
  - b.  Actively herd livestock
  - c.  Hire a herder
  - d.  Eliminate predators
  - e.  Maintain fires at night
  - f.  Utilize guard dogs
  - g.  Other: \_\_\_\_\_
17. Have you made any changes to your livestock husbandry methods since the start of PiOP?  
 Yes  No
- If Yes, please explain:
- 
- 

18. In general, if you eliminate predators, what methods do you use?
- a.  Shot/ Rifle
  - b.  Poison
  - c.  Snares
  - d.  Traps
  - e.  Call DWNP
  - f.  Other: \_\_\_\_\_

19. Number of predators that you are aware have been killed:

Species	Last year	Last 3 years
Lion		
Spotted hyena		
Leopard		
Cheetah		
Wild Dog		
Jackal		
Other		

## APPENDIX D

### REVIEW OF LION EVOLUTION AND CONSERVATION GENETICS

From prehistoric cave paintings of wild predators to present day domesticated housecats, humans have always been fascinated with felids. While cats have continually been of interest, humans have caused problems for most of the 37 recognized felid species, as many of them are categorized as threatened or endangered by international conservation organizations (O'Brien and Johnson 2005). Increased human development and a rising human population are causing modifications and overall reductions in felid habitat.

The current status of the African lion (*Panthera leo*), one of the most iconic felid species on the planet, is worrisome. While not yet categorized as Endangered, the African lion was listed as Vulnerable by the IUCN and recently listed under the Endangered Species Act by the US Fish & Wildlife Service (Bauer et al. 2016). The lion has undergone massive range constrictions and population declines in the last ~40 years (Myers 1975, Nowell and Jackson 1996, Bauer and Van Der Merwe 2004, Chardonnet 2002). These declines are caused by a number of factors including, but not limited to, conflicts with humans, habitat loss and degradation, and disease. Lions were once the most widely distributed land mammal; during the late Pleistocene, they ranged from southern Africa, through northern Eurasia and to Central America (Barnett et al. 2014). Now they occupy just 17% of their historic range (Riggio et al. 2013), and are found primarily in protected areas (Woodroffe 2001).

Conservation agencies and governments must understand the phylogeographic history of the given focal species to establish the most comprehensive and targeted

conservation strategies for species in decline. This is especially true for lions as the species is in decline and certain isolated populations are classified as endangered (Bauer et al. 2016). Though understanding the various lion lineages has proven difficult as lions have a limited fossil record due to the moist climate during the Pleistocene (Barnett et al. 2014). The widely accepted current landscape of *Panthera leo* subspecies status is that there are two extant subspecies, *P. leo leo* and *P. leo persica*, however recent studies (see below) have made claims that there are regionally distinct populations and these should potentially be classified as unique subspecies and gain conservation priority. To understand the current status and conservation of lions, this literature review focusses on the evolution and divergence of modern felids and lions in particular, the impact of genetics on lion ecology from morphological, behavioral, and disease characteristics.

### **The Late Miocene Radiation of Modern Felids**

According to fossil records, all felids are descendant from a cat called *Pseudaelurus* which was found in Europe between 9 and 20 million years ago (O'Brien and Johnson 2007). Recent molecular studies show that the last common ancestor to all modern felids is one of several *Pseudaelurus* species that was found in Asia approximately 11 million years ago. All modern felids radiated during the Late Miocene (Werdelin et al. 2010), and subsequently dispersed out of Asia and across the globe (O'Brien and Johnson 2007).

Approximately 10.8 million years ago, the first modern felid lineage branch was formed with the establishment of the *Panthera* lineage which includes members of the genera *Panthera* and *Neofelis* (O'Brien and Johnson 2007, Werdelin et al. 2010). Within the *Panthera* lineage, the clouded leopard (*Neofelis*) was placed basally with the two

species *N. nebulosa* and *N. diardi* and their unique morphologies suggesting a distinct evolutionary lineage (Christiansen 2006). The rest of the pantherines radiated within the last 4 Ma (Werdelin et al 2010). The bay cat lineage (genus *Pardofelis*) was the next to diverge approximately 9.4 Ma, and includes three species, the bay cat (*P. badia*), Asian golden cat (*P. temminckii*), and marbled cat (*P. marmorata*). The marbled cat was linked to the *Panthera* lineage by Herrington (1986) but was since shown to be basal to the bay cat lineage, branching closest to the *Panthera* lineage (Johnson et al. 2006, Werdelin et al. 2010).

Members of the *Caracal* lineage, genera *Caracal* and *Leptailurus*, branched off approximately 8.5 Ma (Werdelin et al. 2010). This lineage includes caracal (*C. caracal*), African golden cat (*C. aurata*), and serval (*L. serval*) with the serval placed as basal to the others (Johnson et al. 2006, Werdelin et al. 2010). The ocelot lineage branching occurred approximately 8 Ma and contains the species in the genus *Leopardus*. This genus includes the small South American felids like the ocelot (*L. pardalis*), Andean mountain cat (*L. jacobita*), and the pampas cat (*L. pajeros*), among others. The origin of this lineage is independent from the formation of the land bridge linking the Americas, though radiation of the clade shows a single species origin from a North American ancestor (Werdelin 1989).

Following the ocelot lineage, the *Lynx* lineage which includes members of the genus *Lynx*, branched off approximately 7.2 Ma. Previously, this lineage was believed to be linked to *Panthera* (Collier and O'Brien 1985, Salles 1992) but Johnson et al. (2006) showed a more distant relationship. They went on to show that the bobcat (*Lynx rufus*) is basal to the other species (Johnson et al. 2006).

The next divergence, the *Puma* lineage, occurred at approximately 6.7 Ma and included members of the genera *Puma* and *Acinonyx* (Werdelin et al. 2010). The puma (*Puma concolor*) and the jaguarondi (*Puma yagouaroundi*) are both of North American origin as they split before the formation of the North-South America land bridge leading to the Great American Biotic Interchange (Marshall et al. 1982). The branching of the *Puma* lineage was closely followed by that of the leopard cat lineage at about 6.2 Ma when they split from the eighth and final lineage, the domestic cat lineage (Werdelin et al. 2010). The leopard cat lineage includes members of the genera *Otocolobus* and *Prionailurus* while the domestic cat lineage includes one genus, *Felis*. The domestic cat lineage branched off around 3.4 Ma. The genus *Felis* includes the widest ranging cat species, *F. silvestris*, which is currently found in Africa, Asia, Europe (Werdelin et al. 2010).

There was a relatively short time span between the splits of the 8 lineages as the entire stem of the felid clade radiated during the Late Miocene, across approximately 6.3 Ma (Werdelin et al 2010). This short time frame suggests there was some kind of functional or ecological release but it is not currently known what that release was.

### **The Panthera Lineage: Lion Evolution and Speciation**

While the Panthera lineage has by far the best fossil record, it also has the longest ghost lineage, a lineage which has been cladistically inferred and not fully documented by fossils (Werdelin et al. 2010). Johnson et al. (2006) state that Pantherines split from the Felidae stem lineage approximately 10.8 Ma, though the oldest definitive fossils assigned to the lineage are not older than 3.8 Ma (Barry 1987). These oldest fossils were from Laetoli and included a lion-size and a leopard-size fossil (Werdelin et al. 2010), and

were suggested to belong to the two extant species (Turner 1990). However, Werdelin and Dehghani (2011) showed that they differ from the extant species morphologically. Dates from molecular research suggest the early fossils might belong to the stem lineages for these species, which has not been countered by any details in the fossil record (Werdelin et al. 2010).

The first definite lion fossils were found at Olduvai Bed 1 in northern Tanzania and were dated to <2 Ma (Petter 1973, Werdelin et al. 2010). Lions have been thoroughly shown to have dispersed out of Africa, across Eurasia, and into North America (and potentially even South America) (Vereshchagin 1971, Hemmer 1974, Burger et al. 2004, Yamaguchi et al. 2004a). This large scale expansion of the lion range out of Africa does not occur until the middle Pleistocene (Werdelin et al. 2010). By approximately 500 ka, lions are found across Europe and in parts of Asia, north and east of the Black and Caspian Seas. And by 300 ka they could be found in most of northern and eastern Asia with the exception of the south-east and southern China. This is also when scientists believe they crossed the Bering Strait into North America. After the Illinoian glaciers retreated, lions could expand deeper into North America and, perhaps, northern South America. They eventually became extinct in the Americas and large portions of Asia at the end of the last glaciation. Overall, this extremely wide geographical distribution was the largest of any large terrestrial mammal, with the exception of humans (Yamaguchi et al. 2004a).

While the fossil remains and range expansion of lions have been well studied, intraspecific lion phylogeny continues to be investigated (e.g., Bertola et al. 2011, Bertola et al. 2016, Kitchener et al. 2017; Barnett et al. 2006, Werdelin et al. 2010). Subspecies

recognition in modern lions is not accepted without question, unlike other Pantherine species (Mazak 2010). Some experts place all lion fossils into the modern species, *P. leo*, while many other researchers distinguish those remains into extinct species like the cave lion (*P. spelaea*) or the North American lion (*P. atrox*) (Werdelin et al. 2010). The modern lion is generally classified into two subspecies (*P.l. leo* and *P.l. persica*) but has been classified into 8 subspecies (Hemmer 1974), or even as many as 11 (Wozencraft 2005, Table 1), which have been distinguished by variations in geographic ranges as well as morphological measurements (Hemmer 1974, Barnett et al 2006).

Multiple models have been suggested to explain lion diversification (Barnett et al. 2006). One model, a multiregional origin model that is based on morphological analysis of lion remains from its previous range, names similarities in skull morphometrics between middle Pleistocene European lions (*P.l. fossilis*) and the modern North African-Asian lions as an indication of long-term in situ evolution (Hemmer 1974, Barnett et al. 2006). A more recent bottleneck of the modern lion, which occurred approximately 74-203 ka ago, complicates the interpretation of morphological characteristics and challenges Hemmer's (1974) multiregional origin model (O'Brien et al. 1987; Burger et al. 2004). Yamaguchi et al. (2004a) suggest that after this bottleneck, a single population of lions replaced older populations in Africa and southwestern Eurasia (Barnett et al. 2006). This theory for lion evolution runs parallel to the 'recent African origin' model for human evolution proposed by Stringer (2002) in which modern *Homo sapiens* replaced hominids elsewhere after evolving in Africa (Barnett et al. 2006).

Barnett et al. (2014) investigated mitochondrial DNA (mtDNA) from known origin lion specimens collected from bone and tissue samples found in natural history

collections and extracted DNA sequences for amplification and comparison. The phylogenetic analyses produced trees that suggest five phylogeographical groups of modern lions: North African/Asian, West African, Central African, Eastern African, and Southern African. These various groupings have differentiated over approximately the last 80 ka. They suggest that these five geographical groups of lions should be treated as separate Ecologically Significant Units (ESUs) for the purposes of future conservation and management, or even potentially elevated to subspecific status.

The five phylogeographical groupings suggested by Barnett et al. (2014) were disputed by Kitchener et al. (2017); they state that the Eastern and Southern African groups are partially sympatric in southern Africa making their separation into different subspecies inappropriate while the divergence of the North African/Asian, West African, and Central African groups occurred very recently (within ~50 ka or less). Kitchener et al. (2017) agree that there should be revisions to the current accepted landscape of lion taxonomy, however, citing recent genetic research (Bertola et al. 2011, Bertola et al. 2016), they argue for two new groupings under subspecific distinctions *P. l. leo* and *P. l. melanochaita* which would be separated geographically into North and South groups (Table 2).

The most recent genetic analysis built on the work of Bertola et al. (2011) and compared mtDNA sequences from 194 lions from 22 different countries to describe the phylogeographic patterns present in modern lions (Bertola et al. 2016). This study provided robust support for basal dichotomy between northern and southern lions. Within these two groupings, six phylogenetic groups were determined: West Africa, Central Africa and North Africa/Asia (North group) and North East, East/Southern and South

West (South group; Figure 1). This divergence from the generally accepted lion taxonomy has significant implications for lion conservation (see below). These results, if supported with additional morphological research, have the potential to change the landscape of lion conservation.

### **Lion Morphology**

Lions exhibit a wide range of phenotypic variation, including body size, mane color and form, and skull characteristics, this is probably related to the fact that during the late Pleistocene they had the widest geographical distribution of any large mammal (Mazak 2010). Similarly, other widely distributed Pantherine species (*P. tigris*, *P. pardus*, and *P. onca*), also show substantial variations in morphological characteristics (Pocock 1939, Mazak 1975, Mazak 2004, Patterson 2007, Mazak 2008). These varied phenotypes result from the collective effects of sexual selection, adaptations to different regional environments, and gene flow (Yamaguchi et al. 2004a, Yamaguchi et al. 2004b). Various studies have been published investigating the morphological traits of lions and have resulted in classifications ranging from one monotypic species (Meeter and Setzer 1971, Kingdon 1997) up to eight (Hemmer 1974) or nine (Mazák 1968) subspecies.

To assess and examine patterns of morphological diversity across the lion's geographic range, Mazák (2010) used craniodental morphology metrics from 255 modern, wild lion skulls (male and female) whose origin was known. Skulls from Northern Africa, North-east Africa, Central Africa, East Africa, Southern Africa, West Africa, India, and Iran were included in the analysis. There was a high level of similarity found in skull morphology with little significant subdivision between populations, with the exception being between sub-Saharan Africa and North Africa/Asia populations.

According to this analysis, variation in male skull morphology is greater within populations than between them while female skull morphology shows a more robust differentiation between geographical populations than within. This is probably partially due to the fact that female lions are philopatric, remaining in their natal prides, while males are forced out at puberty to disperse and eventually take over another pride.

While Mazák (2010) showed a significant difference between North Africa/Asia and sub-Saharan lion craniometrics, the degree of variation was less marked than what has been observed in other big cats (e.g., leopards - Miththapala 1992, tigers - Mazák 2008). Furthermore, lions do not show gradual differences in relation to altitude or latitude as has been shown in tigers (Kitchener 1999, Mazák 2008). Mazák (2010) postulates that the less striking geographic variation in lion craniodental morphology is due to the possibility that there were no major geographical or ecological genetic barriers throughout lion populations while lions had their extremely wide range during the late Pleistocene. This would have allowed them to maintain higher levels of genetic contact, resulting in continuous variation throughout the range. Additionally, Mazák (2010) states that because the differentiation of Asian and sub-Saharan lions occurred recently (within the last 74-203 ka), there is a low level of variation in skull morphology. This morphological research supports the theory of two distinct clusters of lion populations, North African/Asian and sub-Saharan, that share a common ancestor.

In similar research, Yamaguchi et al. (2009a) investigated the brain sizes amongst four *Panthera* species: tigers, lions, jaguars and leopards. Tigers were found to have the largest cranial volumes for their brain size, followed by lions, jaguars and leopards. The tiger was shown to have a relatively larger brain than the lion, given the two species'

similar average body sizes. Though it has been suggested that social species have proportionally larger brain sizes (Hemmer 1978), this is refuted given that the social lion has a definitively smaller brain (Yamaguchi et al. 2009a). The brain size to skull size ratios for the lion, jaguar and leopard are similar and probably result from these species being phylogenetically closer to each other than they are to the tiger. The study went on to show that there was significant intraspecific variation in brain sizes between the two generally accepted species of lion (*P. l. leo* and *P. l. persica*). The Asian lion had a smaller brain than the sub-Saharan lion. Results from this study pertaining to lions should be investigated using the newly proposed subspecies above, potentially providing support for the updated two subspecies model called for by Kitchener et al. (2017).

Additional research that investigates the differences in skull characteristics between various populations of lions was conducted by Yamaguchi et al. (2009b). For most of the previous century, biologists have been using the presence of a divided infraorbital foramen (DIF) in lion skulls to distinguish between Asian and African lions. The infraorbital foramen is an opening in the skull where the infraorbital artery, the infraorbital vein and the infraorbital nerve go through and they are found below the orbits on the frontal portion of the zygomatic arch. In Asiatic lions, the infraorbital is regularly divided by a bone bridge, creating a smaller upper portion and larger lower portion (Pocock, 1930). Pocock (1930) stated that DIF never occurred in African lions and until recently, this was a putative distinguishing characteristic. Yamaguchi et al. (2009b) investigated over 500 lion skulls and found that < 1% of lions with origins in Africa had a DIF while about 50% of observed Asian lion skulls exhibited DIF. They conclude that while a minimal number of African lions had DIF, the presence of a DIF remains an

important morphological feature that separates Asian lion skulls from African. This raises the question, however, if it is possible to distinguish northern lions from southern lions in a similar fashion to the proposed classification above. Further study of lion skulls and the presence of divided infraorbital foramen should be conducted, with a special interest in possible differentiations between northern range and southern range lions.

### **Evolutionary Impacts on Lion Ecology**

Lions are the only social felid, as all other species seem to maintain individual territories (Mosser et al. 2015). While other species are sometimes gregarious (typically only during mating), lions are dependent on other pride members for both survival and reproduction (Packer et al. 2001). Lions have a complex social system and are found in prides and male coalitions. Prides consist of several related adult females and their dependent young (Stander 1992). These females will cooperate to hunt (Stander 1992), rear young (Bertram 1975), and defend the territory and young (Packer et al. 1990). Females usually remain resident in their natal pride while males are expelled when they reach sexual maturity (Van Orsdol 1985). Males form coalitions which typically consist of related males (Bertram 1976) that dispersed from their natal pride at the same time but can also consist of unrelated males (Packer and Pusey 1982). These coalitions are nomadic before they gain residence with a pride of females by challenging resident male coalitions (Bygott et al. 1979, Van Orsdol 1985). The length of a coalition's tenure is dependent on its size, though on average for coalitions of 2 males, lengths range from 18 months in Serengeti (Bygott et al. 1979) to 90 months in Queen Elizabeth National Park (Van Orsdol 1981). Coalition sizes range from 1-9 individuals with larger coalitions having greater success rates for pride take-overs and longer tenure durations (Packer

1986, Mosser and Packer 2009) Realistically, resident male coalitions must maintain pride tenure for ~2 years to ensure descendant cubs are reared to independence (Borrego et al. 2018)

One theory as to why lions formed social groups is based on the fact that they are mostly found in savanna habitat where there is high primary productivity (Sinclair 1979) and wide-scale heterogeneity (Pickett et al. 2003, Boulain et al. 2007, Levick and Rogers 2008). Proposed in 1983, the 'resource dispersion hypothesis' discusses the relationship between the distribution of resources and patterns of sociality in wildlife (Macdonald 1983). This hypothesis asserts that the formation of social groups is enabled by the heterogeneity of a given landscape; the economics of defending a heterogeneous, patchy territory are such that the area can support the individual territory owner but also might support added individuals at a low cost to the original territory owner (Macdonald 1983, Mosser et al. 2015).

This theory on its own has been challenged as the driver for the evolution of sociality, but when coupled with the advantages of group living, like cooperative territory defense, could lead to sociality as an adaptive, beneficial behavioral strategy (Johnson and Macdonald 2003, Mosser et al. 2015). It has been repeatedly shown that individuals benefit from the formation of social groups: bigger groups typically win intergroup challenges (Grinnel et al. 1995) and have territories with better habitat quality (Mosser and Packer 2009). Additionally, individuals in a group-territorial structure can share energetic costs of maintaining the territory (Clifton 1990) while also benefitting from natal philopatry and territorial inheritance (Woolfenden and Fitzpatrick 1978, Lindstrom 1986).

Social living in lions yields benefits for both sexes; larger male coalitions are the beneficiaries of increased pride take-over success and longer pride tenure times (Bygott et al. 1979, Packer 1986), larger female prides have a decreased probability of suffering loss of cubs through infanticide (Pusey and Packer 1994). The benefit of cooperative hunting is typically cited as a major reason for female lion grouping (Schaller 1972, Macdonald 1983, Turner), but according to empirical evidence (Packer et al. 1990) groups of two to four lionesses had the lowest food intake rates when compared to individuals and groups of at least five during periods of prey scarcity. Furthermore, when prey resources were abundant, intake rates did not significantly vary with the size of the group (Packer et al. 1990). In general, simulated modelling efforts have shown a substantial long term individual advantage to group living among lions (Mosser and Packer 2009, Mosser et al. 2015). Additionally, they support the above theory that landscape heterogeneity combined with the benefits of social living gave rise to the group territoriality exhibited in African lions (Mosser et al. 2015).

While there are obviously benefits to social living, lions are more susceptible to the transmission of communicable diseases as a result of their gregarious life history. Mortality from disease has contributed to lion declines (Munson et al. 2008, Trinkel et al. 2011), as lions contract canine distemper virus (CDV; Ohishi et al. 2013) and feline immunodeficiency virus (FIV; Roelke et al. 2009). CDV was transferred from domestic dogs (*Canis lupis familiaris*) to wild carnivores and is fatal to both suborders, Caniformia and Feliformia (Nikolin et al. 2017). FIV is typically not fatal on its own in wild felids though it can result in long-term negative health effects with co-infection from other pathogens (Roelke et al. 2009, Troyer et al. 2011). Lions can be chronic carriers of FIV

as over 90% of Serengeti lions were shown to contract it by the age of one (Packer et al. 1999, Troyer et al. 2004), potentially compromising their resistance to other diseases. As free ranging populations of lions continue to decline, their overall genetic fitness will also decline. With smaller populations come increased chances of genetic isolation and inbreeding (Bjorkland 2003), which in turn will make lions more vulnerable to contraction of these, and other, diseases. Bjorkland (2003) estimates that individual lion populations should include at least 50 separate lion prides (100 or more is optimal) to minimize the effects of inbreeding. With only about 10 African lion strongholds left on the continent (Riggio et al. 2013) and most large populations in decline (Bauer et al. 2015), lion conservation is at a critical juncture.

### **Conclusion and Recommendations for Further Study**

Based on the above literature review, I support the reclassification of the *Panthera leo* subspecies from the currently recognized *P. l. leo* and *P. l. persica* to the proposed *P. l. leo* and *P. l. melanochaita* representing northern versus southern and eastern populations. This reclassification will ensure the proper conservation and management actions can occur as wild lion populations continue to decline. Additionally, following this recognition, these two distinct populations can and should be managed as Ecologically Significant Units.

While the genetic information presented above is an important first step in the reclassification of lion subspecies, additional morphological work should build upon previous efforts to test the results of the recent genetic analyses. I propose a study that reassesses the craniometric, brain case, and divided infraorbital foramen research presented above. This study should determine if a similar geographical separation can be

found in the skull characteristics between northern range of lions versus southern and eastern lions. Adjusting the scale that these characteristics are investigated at could more strongly support the genetic findings of two geographically distinct populations.

To further our understanding of lion population connectivity and thus lion conservation genetics, research should be done to determine the ability of lions to disperse into and out of lion population strongholds. A scat analysis would be the simplest way to obtain this information. This research will enable conservation managers to understand what levels of genetic mixing are occurring. Additionally, if the study was carried out over a long period of time, researchers would be able to determine when populations are becoming isolated from others. This work could inform future management actions like the potential to use assisted migration to facilitate genetic mixing.

Along a similar line, the spatial connectivity between areas denoted as lion strongholds and areas where lions are still found should be investigated. The ability of wild lions to move across the landscape is impacted by many ecological factors (e.g., land cover, prey availability, and human activity). A landscape ecology study should be conducted that creates a resistance surface for lions by incorporating the various barriers to dispersal and how they will potentially change over time as a result of human activity and climate change. This would enable governments and conservation agencies to protect integral lion habitat that would maintain habitat connectivity, minimizing the negative effects of isolated populations.

Lastly, I propose a study that builds on the population viability simulations conducted by Bjorkland (2003). Given the current population trends, this study would

investigate which populations are the most at risk and then would go a step further to assess how the potential addition of artificially introduced lions to populations would impact their genetic viability. As wild populations continue to decline, conservationists and managers are going to need to consider the implications of artificially mixing populations to maintain genetic viability if lions are going to persist on the landscape.

With ~30,000 individuals left in the wild in increasingly isolated patches and mostly declining populations, we, as wildlife managers and researchers, need to determine the best way forward for lion conservation. Lions are an integral piece of the savanna ecosystem and governments and managers should ensure they remain extant. The reclassification of the African lion subspecies, the further conservation genetic studies listed above, as well as continued in situ conservation efforts will help inform the management decisions and potentially enable the lion to avoid extinction.

### **Literature Cited**

- Barnett, R., N. Yamaguchi, I. Barnes, and A. Cooper. 2006. The origin, current diversity and future conservation of the modern lion (*Panthera leo*). *Proceedings of the Royal Society B* 273: 2119-2125.
- Barnett R., N. Yamaguchi, B. Shapiro, S. Y. W. Ho, I. Barnes, R. Sabin, L. Werdelin, J. Cuisin, and G. Larson. 2014. Revealing the maternal demographic history of *Panthera leo* using ancient DNA and a spatially explicit genealogical analysis. *BMC Evolutionary Biology* 14: 70.
- Barry, J. C. 1987. Large carnivores (Canidae, Hyaenidae, Felidae) from Laetoli. *In* Laetoli: a Pliocene site in northern Tanzania pp. 235–258. eds Leakey, M.D. and J.M. Harris. Oxford: Clarendon Press.
- Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. Hunter, D. Macdonald, and C. Packer. 2015a. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*: doi: 10.1073/pnas.1500664112.
- Bauer, H., C. Packer, P.F. Funston, P. Henschel, K. Nowell. 2016. *Panthera leo*. (errata version published in 2017) The IUCN Red List of Threatened Species 2016: e.T15951A115130419. <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en>. Downloaded on 15 November 2017.

- Bauer, H. and S. Van der Merwe. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38: 26-31.
- Bertola, L.D., H. Jongbloed, K.J. van der Gaag, P. de Knijff, N. Yamaguchi, H. Hooghiemstra, H. Bauer, P. Henschel, P.A. White, C.A. Driscoll, T. Tende, U. Ottosson, Y. Saidu, K. Vrieling, and H.H. de Iongh. 2016. Phylogeographic Patterns in Africa and High Resolution Delineation of Genetic Clades in the Lion (*Panthera leo*). *Nature Scientific Reports* 6: 30807.
- Bertola, L. D., W.F. van Hooft, K. Vrieling, D.R. Uit de Weerd, D.S. York, H. Bauer, H.H.T. Prins, P.J. Funston, H.A. Udo de Haes, H. Leeirs, W.A. van Haeringen, E. Sogbohossou, P.N. Tumenta, and H.H. de Iongh. 2011. Genetic diversity, evolutionary history and implications for conservation of the lion (*Panthera leo*) in West and Central Africa. *Journal of Biogeography* 38: 1356-1367.
- Bertram, B.C.R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology* 177: 463-482.
- Bertram, B.C.R. 1976. Kin selection in lions and in evolution. *In* growing points in ethology p.281-301. P. Bateson and R.A. Hinde (eds). Cambridge University Press.
- Björkland, M. 2003. The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics* 4: 515-523.
- Borrego, N., A. Ozgul, R. Slotow, and C. Packer. 2018. Lion population dynamics: do nomadic males matter? *Behavioral Ecology* 29: 660-666.
- Boulain, N., G. Simioni, and J. Gignoux. 2007. Changing scale in ecological modelling: a bottom up approach with an individual based vegetation model. *Ecological Modelling*. 203: 257-269.
- Burger, J., W. Rosendahl, O. Loreille, H. Hemmer, T. Eriksson, A. Götherström, J. Hiller, M.J. Collins, T. Wess, and K.W. Alt. 2004 Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Molecular Phylogenetics and Evolution* 30: 841-849.
- Bygott, J. D., B.C. Bertram, and J.P. Hanby. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282: 839-841.
- Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA, Paris, France.
- Christiansen, P. 2006. Sabertooth characteristics in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). *Journal of Morphology* 267: 1186-1198.
- Clifton, K.E. 1990. The costs and benefits of territory sharing for the Caribbean coral reef fish, *Scarus iserti*. *Behavioral Ecology and Sociobiology*. 26:139-147.
- Collier, G.E. and S.J. O'Brien. 1985. A molecular phylogeny of the Felidae: immunological distance. *Evolution* 39: 473-487.

- Grinnell, J., C. Packer, and A.E. Pusey. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour*. 49:95-105.
- Hemmer, H. 1974. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae) III. Zur Artgeschichte des Löwen *Panthera leo* (Linnaeus 1758). *Veröff. Zool. Staatssamml. München* 17, 167–280.
- Hemmer, H. 1978. Socialization by intelligence. *Carnivore* 1: 102–105.
- Herrington, S.J. 1986. Phylogenetic relationships of the wild cats of the world. PhD dissertation, University of Kansas, Lawrence, KS.
- Johnson, D.D.P. and D.W. Macdonald. 2003. Sentenced without trial: reviling and revamping the resource dispersion hypothesis. *Oikos*. 101: 433-440.
- Johnson, W.E., E. Eizirik, J. Pecon-Slattery, W.J. Murphy, A. Antunes, E. Teeling, and S.J. O'Brien. 2006. The Late Miocene Radiation of Modern Felidae: A Genetic Assessment. *Science* 311: 73-77. [doi: 10.1126/science.1122277]
- Kingdon, J. 1997. *The Kingdon field guide to African mammals*. London / New York: Academic Press/ Natural World.
- Kitchener, A.C. 1999. Tiger distribution, phenotypic variation and conservation issues. In *Riding the tiger, tiger conservation in human-dominated landscapes*: 19-39. J. Seidensticker, S. Christie, and P. Jackson (eds). Cambridge, Cambridge University Press.
- Kitchener, A.C., Ch. Breitenmoser-Würsten, E. Eizirik, A. Gentry, L. Werdelin, A. Wilting, N. Yamaguchi, A.V. Abramov, P. Christiansen, C. Driscoll, J.W. Duckworth, W. Johnson, S.J. Luo, E. Meijaard, P. O'Donoghue, J. Sanderson, K. Seymour, M. Bruford, C. Groves, M. Hoffmann, K. Nowell, Z. Timmons, and S. Tobe. 2017. A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. *Cat News Special Issue* 11.
- Levick S.R. and K.H. Rogers. 2008. Structural biodiversity monitoring in savanna ecosystems: integrating LiDAR and high resolution imagery through object-based image analysis. In: *Object-based image analysis: spatial concepts for knowledge-driven remote sensing applications*. T. Blaschke, S. Lang, G.J. Hay, eds. Berlin, Germany. Springer.
- Lindstrom, E. 1986. Territory inheritance and the evolution of group-living in carnivores. *Animal Behavior*. 34: 1825–1835.
- Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature*. 301: 379-384.
- Marshall, L.G., S.D. Webb, J.J. Sepkoski, and D.M. Raup. 1982. Mammalian evolution and the great American interchange. *Science* 215: 1351-1357.
- Mazák, J.H. 2004. On the sexual dimorphism in the skull of the tiger (*Panthera tigris*). *Mammalian Biology* 69: 392-400.

- Mazák, J.H. 2008. Craniometric variation in the tiger (*Panthera tigris*): implications for patterns of diversity, taxonomy and conservation. *Mammalian Biology*. (Online Doi:10.1016/j.mambio.2008.06.003).
- Mazák, J.H. 2010. Geographical variation and phylogenetics of modern lions based on craniometric data. *Journal of Zoology* 281: 194–209.
- Mazák, V. 1968. Die Löwe. *Das Pelzgewerbe*, Berlin-Frankfurt/M.-Leipzig-Wien, 19.Jhrg. (N.F.), Nr. 3, pp. 3–27, 7 figs.
- Mazák, V. 1975. Notes on the black-maned lion of the Cape, *Panthera leo melanochaita* (Ch.H. Smith, 1842) and a revised list of preserved specimens. *Verh. Koninkl. Nederlandse Akad. Wetenschappen* 64: 1-44.
- Meester, J. and H. Setzer. 1971. *Mammals of Africa: an identification manual*. Smithsonian Institution Press, Washington.
- Miththapala, S. 1992. Genetic and morphological variation in the leopard (*Panthera pardus*): a geographically widespread species. Ph.D. thesis, Univ. Florida, Gainesville.
- Mosser, A. A., M. Kosmala, and C. Packer. 2015. Landscape heterogeneity and behavioral traits drive the evolution of lion group territoriality. *Behavioral Ecology* 26: 1051-1059.
- Mosser A. and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behavior*. 78:359-370.
- Munson L., K.A. Terio, R. Kock, T. Mlengeya, M. E. Roelke, E. Dubovi, B. Summers, A. R. E. Sinclair, and C. Packer. 2008. Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. *PLoS ONE*, 3, e2545.
- Myers, N. 1975. The silent savannahs. *International Wildlife* 5: 5–10.
- Nikolin, V.M., X.A. Olarte-Castillo, N. Osterriender, H. Hofer, E. Dubovi, C.J. Mazzoni, E. Brunner, K.V. Goller, R.D. Fyumagwa, P.D. Moehlman, D. Thierer, and M.L. East. 2017. Canine distemper virus in the Serengeti ecosystem; molecular adaptation to different carnivore species. *Molecular Ecology* 26: 2111-2130.
- Nowell, K. and P. Jackson. 1996. *Wild Cats: Status Survey and Conservation Action Plan*. World Conservation Union, Gland, Switzerland 5577.
- O'Brien, S.J. and W.E. Johnson. 2005. Big Cat Genomics. *Annual Review of Genomics and Human Genetics* 6: 407-429.
- O'Brien, S.J. and W.E. Johnson. 2007. The Evolution of Cats. *Scientific American* p. 68-75.
- O'Brien, S. J., J.S. Martenson, C. Packer, L. Herbst, V. De Vos, P. Joslin, J. Ott-Joslin, D. E. Wildt, and M. Bush. 1987. Biochemical genetic variation in geographic isolates of African and Asiatic lions. *National Geographic Research* 3: 114-124.

- Ohishi, K., R. Suzuki, T. Maeda, M. Tsuda, E. Abe, T. Yoshida, Y. Endo, M. Okamura, T. Nagamine, H. Yamamoto, M. Ueda, and T. Maruyama. 2013. Recent Host Range Expansion of Canine Distemper Virus and Variation in its Receptor, the Signaling Lymphocyte Activation Molecule, in Carnivores. *Journal of Wildlife Diseases* 50: 596-606.
- Packer, C. 1986. The ecology of sociality in felids. In: *Ecological Aspects of Social Evolution* D.I. Rubenstein and R.W. Wrangham (eds). p. 429-451. Princeton, New Jersey: Princeton University Press.
- Packer, C., S. Altizer, M. Appel, E. Brown, J. Martenson, S.J. O'Brien, M. Roelke-Parker, R. Hofmann-Lehmann, and H. Lutz. 1999. Viruses of the Serengeti: Patterns of infection and mortality in African lions. *Journal of Animal Ecology* 68: 1161-1178.
- Packer, C. and A.E. Pusey. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 286:740-742.
- Packer C., A.E. Pusey, and L.E. Eberly. 2001. Egalitarianism in female African lions. *Science*. 293:690-693.
- Packer, C., D. Scheel, and A.E. Pusey. 1990. Why lions form groups: food is not enough. *American Naturalist*, 136: 1-19.
- Patterson, B.D. 2007. On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology* 34: 55-60.
- Petter, G. 1973. Carnivores Pleistocènes du Ravin d'Olduvai (Tanzanie). In L.S.B. Leakey, R.J.G. Savage, and S.C. Coryndon (eds), *Fossil vertebrates of Africa* 3: 43-100. London: Academic Press.
- Pickett, S.T.A., M.L. Cadenasso, and T.L. Benning. 2003. Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. In: J.T. du Toit, K.H. Rogers, and H.C. Biggs (eds). *The Kruger experience: ecology and management of Savanna heterogeneity*. Washington (DC): Island Press. p. 22-40.
- Pocock, R.I. 1930. The lions of Asia. *Journal of the Bombay Natural History Society* 34: 638-665.
- Pocock, R.I. 1939. *The Fauna of British India, including Ceylon and Burma. Mammalia, volume 1, Primates and Carnivora (in part), Families Felidae and Viverridae*. London: Taylor and Francis.
- Pusey, A. E. and C. Packer. 1994. Non-offspring nursing in social carnivores: minimizing the costs. *Behavioral Ecology* 5: 362-374.
- Riggio, J., A. Jacobson, L. Dollar, H. Bauer, A. Dickman, P. Funston, P. Henschel, H. de Iongh, L. Lichtenfeld, C. Packer, and S. Pimm. 2013. The size of savannah Africa: a lion's view. *Biodiversity and Conservation* 22: 17-35.

- Roelke M.E., M.A. Brown, J.L. Troyera, H. Winterbach, C. Winterbach, G. Hemson, D. Smith, R.C. Johnson, J. Pecon-Slattery, A.L. Roca, K.A. Alexander, L. Klein, P. Martelli, K. Krishnasamy, and S.J. O'Brien. 2009. Pathological manifestations of feline immunodeficiency virus (FIV) infection in wild African lions. *Virology* 390: 1-12.
- Salles, L.O. 1992. Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea). *American Museum Novitates* 3047: 1-67.
- Schaller, G. B. 1972. *The Serengeti Lion*. Chicago: University of Chicago Press.
- Sinclair, A.R.E. 1979. The Serengeti environment. In: A.R.E. Sinclair and M. Norton-Griffiths (eds). *Serengeti*. Chicago (IL): University of Chicago Press. p. 31-45.
- Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology* 29: 445-454.
- Stringer, C. 2002. Modern human origins: progress and prospects. *Philosophical Transactions of the Royal Society B* 357: 563-579. (doi:10.1098/rstb.2001.1057).
- Trinkel, M., D. Cooper, C. Packer, and R. Slotow. 2011. Inbreeding Depression Increases Susceptibility to Bovine Tuberculosis in Lions: An Experimental Test Using an Inbred-Outbred Contrast Through Translocation. *Journal of Wildlife Diseases* 47:494-500.
- Troyer, J.L., J. Pecon-Slattery, M.E. Roelke, L. Black, C. Packer, and S.J. O'Brien. 2004. Patterns of feline immunodeficiency virus multiple infection and genome divergence in a free-ranging population of African lions. *Journal of Virology*. 78: 3777-3791.
- Troyer, J. L., M.E. Roelke, J.M. Jespersen, N. Baggett, V. Buckley-Beason, D. MacNulty, M. Craft, C. Packer, J. Pecon-Slattery, S.J. O'Brien. 2011. FIV diversity: FIV -Ple subtype composition may influence disease outcome in African lions. *Veterinary Immunology and Immunopathology* 143: 338-346.
- Turner, A. 1997. *The Big Cats and their Fossil Relatives*. New York: Columbia University Press.
- Turner, A. 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-pleistocene in Africa. *Geobios* 23: 349-68.
- Van Orsdol, K.G. 1981. *Lion Predation in Rwenzori National Park, Uganda*. PhD Thesis, University of Cambridge.
- Van Orsdol, K.G., J.P. Hanby, and J.D. Bygott. 1985. Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*. 206: 97-112.
- Vereshchagin, N.K. 1971. Cave lions of Holarctics. *Trudy Zoologicheskogo Instituta* 49:123-199.

- Werdelin, L. 1989. The radiation of felids in South America: when and where did it occur? In 5<sup>th</sup> International Theriological Congress, Rome, Abstracts of Papers and Posters, p. 290-291. Rome, Italy.
- Werdelin, L. and R. Dehghani. 2011. Carnivora. In T. Harrison (ed), *Paleontology and Ecology of Laetoli, Tanzania: Human Evolution in Context*. Springer, New York.
- Werdelin, L., N. Yamaguchi, W.E. Johnson, and S.J. O'Brien. 2010. Phylogeny and evolution of cats (*Felidae*). P. 59-82. In D.W. Macdonald and A.J. Loveridge (eds), *Biology and Conservation of Wild Felids*. Oxford University Press, New York.
- Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. In *Carnivore conservation* p. 61-92. J.L. Gittleman, S. Funk, D.W. Macdonald, and R.K. Wayne (eds). Cambridge: Cambridge University Press.
- Woolfenden, G.E. and J.W. Fitzpatrick. 1978. The inheritance of territory in group-breeding birds. *BioScience*. 28:104-108.
- Wozencraft W.C. 2005. Order Carnivora. In *Mammal species of the world. A taxonomic and geographic reference* (3rd ed.). D.E. Wilson and D.M. Reeder (eds). Johns Hopkins University Press, Baltimore, p. 532-628.
- Yamaguchi, N., A. Cooper, L. Werdelin, and D.W. Macdonald. 2004a. Evolution of the mane and group-living in the lion (*Panthera leo*): a review. *Journal of Zoology* (London) 263: 329-342.
- Yamaguchi, N., C.A. Driscoll, A.C. Kitchener, J.M. Ward, and D.W. Macdonald. 2004b. Craniological differentiation between European wildcats (*Felis silvestris silvestris*), African wildcats (*F.s.lybica*) and Asian wildcats (*F.s.ornata*): implications for their evolution and conservation. *Biological Journal of the Linnean Society* 83: 47-63.
- Yamaguchi, N., A.C. Kitchener, C.A. Driscoll, and D.W. Macdonald. 2009b. Divided infraorbital foramen in the lion (*Panthera leo*): its implications for colonization history, population bottlenecks, and conservation of the Asian lion (*P. l. persica*). *Contributions to Zoology* 78: 77-83.
- Yamaguchi, N., A.C. Kitchener, E. Gilissen, and D.W. Macdonald. 2009a. Brain size of the lion (*Panthera leo*) and the tiger (*P. tigris*): implications for intrageneric phylogeny, intraspecific differences and the effects of captivity. *Biological Journal of the Linnean Society* 98: 85–93.

## Tables and Figures

Table 1: Subspecies of *Panthera leo* recognized by Wozencraft (2005).

Subspecies		Identifier (year)	Distribution
<i>P. l. leo</i>	North African Lion	Linnaeus (1758)	Northern Africa
<i>P. l. azandica</i>	Central African Lion	Allen (1924)	Northeastern Democratic Republic of Congo and Western Uganda
<i>P. l. persica</i>	Asiatic Lion	Meyer (1826)	Southwest Asia
<i>P. l. senegalensis</i>	West African Lion	Meyer (1826)	West Africa
<i>P. l. hollisteri</i>	Sri Lankan Lion	Allen (1924)	Kenya
<i>P. l. kamptzi</i>	Cameroon Lion	Matschie (1900)	Cameroon
<i>P. l. krugeri</i>	Transvaal Lion	Roberts (1929)	South Africa
<i>P. l. massaica</i>	Massai Lion	Neumann (1900)	Tanzania
<i>P. l. melanochaita</i>	Cape Lion	Hamilton Smith (1842)	Cape of Good Hope, South Africa
<i>P. l. nyanzae</i>	Uganda Lion	Heller (1913)	Uganda
<i>P. l. bleyenberghi</i>	Southwest African Lion	Lönnerberg (1914)	Namibia, Angola, Democratic Republic of Congo, Western Zambia, Western Zimbabwe, and Northern Botswana

Table 2. Simplified subspecific classification according to Kitchener et al. (2017).

<b>Subspecies</b>	<b>Previous Subspecies</b>	<b>Identifier (year)</b>	<b>Distribution</b>	
<i>P. l. leo</i>	<i>P. l. leo</i>	North African Lion	Linnaeus (1758)	Northern Africa
<i>P. l. leo</i>	<i>P. l. azandica</i>	Central African Lion	Allen (1924)	Northeastern Democratic Republic of Congo and Western Uganda
<i>P. l. leo</i>	<i>P. l. persica</i>	Asiatic Lion	Meyer (1826)	Southwest Asia
<i>P. l. leo</i>	<i>P. l. senegalensis</i>	West African Lion	Meyer (1826)	West Africa
<i>P. l. leo</i>	<i>P. l. hollisteri</i>	Sri Lankan Lion	Allen (1924)	Kenya
<i>P. l. leo</i>	<i>P. l. kamptzi</i>	Cameroon Lion	Matschie (1900)	Cameroon
<i>P. l. melanochaita</i>	<i>P. l. krugeri</i>	Transvaal Lion	Roberts (1929)	South Africa
<i>P. l. melanochaita</i>	<i>P. l. massaica</i>	Massai Lion	Neumann (1900)	Tanzania
<i>P. l. melanochaita</i>	<i>P. l. melanochaita</i>	Cape Lion	Hamilton Smith (1842)	Cape of Good Hope, South Africa
<i>P. l. melanochaita</i>	<i>P. l. nyanzae</i>	Uganda Lion	Heller (1913)	Uganda
<i>P. l. melanochaita</i>	<i>P. l. bleyenberghi</i>	Southwest African Lion	Lönnerberg (1914)	Namibia, Angola, Democratic Republic of Congo, Western Zambia, Western Zimbabwe, and Northern Botswana

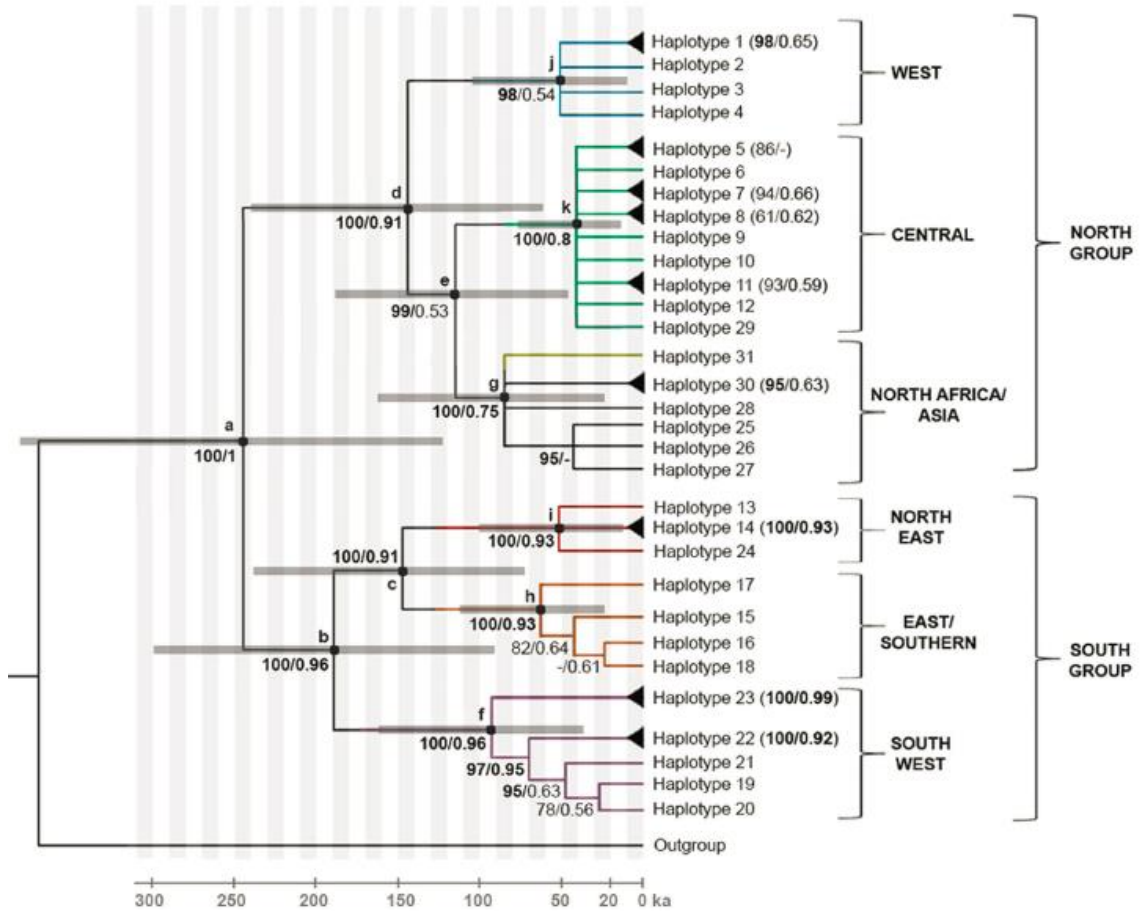


Figure 1: Phylogeographic divergence of modern lions (from Bertola et al. 2016). This figure shows the North vs. South haplotype groupings and supports the authors claim that there should be a reclassification of modern lions to include two subspecies, *P. l. leo* and *P. l. melanochaita*.

## BIBLIOGRAPHY

- Adams, W.M. and M. Mulligan, eds. 2003. *Decolonizing Nature: Strategies for Conservation in a Post-colonial Era*. Earthscan Publications, Ltd. London, United Kingdom.
- Aryal, A., D. Brunton, W. Ji, R.K. Barraclough, and D. Raubenheimer. 2014. Human–carnivore conflict: Ecological and economical sustainability of predation on livestock by snow leopard and other carnivores in the Himalaya. *Sustainability Science* 9:321–329.
- Bangs, E.E., S.H. Fritts, J.A. Fontaine, D.W. Smith, K.M. Murphy, C.M. Mack, and C.C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho and Wyoming. *Wildlife Society Bulletin* 26:785–793.
- Barnett R., N. Yamaguchi, B. Shapiro, S. Y. W. Ho, I. Barnes, R. Sabin, L. Werdelin, J. Cuisin, and G. Larson. 2014. Revealing the maternal demographic history of *Panthera leo* using ancient DNA and a spatially explicit genealogical analysis. *BMC Evolutionary Biology* 14: 70.
- Barnett, R., N. Yamaguchi, I. Barnes, and A. Cooper. 2006. The origin, current diversity and future conservation of the modern lion (*Panthera leo*). *Proceedings of the Royal Society B* 273: 2119-2125.
- Barry, J. C. 1987. Large carnivores (Canidae, Hyaenidae, Felidae) from Laetoli. In *Laetoli: a Pliocene site in northern Tanzania* pp. 235–258. eds Leakey, M.D. and J.M. Harris. Oxford: Clarendon Press.
- Bauer, H. and H.H. De Iongh. 2005. Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology* 43: 208-214.
- Bauer, H. and S. Van der Merwe. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38: 26-31.
- Bauer, H., C. Packer, P. Funston, P. Henschel, and K. Nowell. 2016. *Panthera leo* in the IUCN Red List of Threatened Species. Available at <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en> Accessed October 8, 2016.
- Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. Hunter, D. 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.
- Bauman, P.J. 1998. *The Wind Cave National Park Elk Herd: Home Ranges, Seasonal Movements, and Alternative Control Methods*. South Dakota State University, Brookings, SD, USA.

- Begg, C. and H. Kushnir. 2010. eds Human-lion conflict toolkit. Ratel Trust, Cape Town, South Africa. [http://www.rateltrust.org/library\\_files/Human-Lion%20Conflict%20Toolkit.pdf](http://www.rateltrust.org/library_files/Human-Lion%20Conflict%20Toolkit.pdf). Accessed June 28 2014.
- Benhamou, S., M. Valeix, S. Chameillé-Jammes, D.W. Macdonald, and A.J. Loveridge. 2014. Movement-based analysis of interactions in African lions. *Animal Behavior* 90:171-180.
- Bertola, L. D., W.F. van Hooft, K. Vrieling, D.R. Uit de Weerd, D.S. York, H. Bauer, H.H.T. Prins, P.J. Funston, H.A. Udo de Haes, H. Leeirs, W.A. van Haeringen, E. Sogbohossou, P.N. Tumenta, and H.H. de Iongh. 2011. Genetic diversity, evolutionary history and implications for conservation of the lion (*Panthera leo*) in West and Central Africa. *Journal of Biogeography* 38: 1356-1367.
- Bertola, L.D., H. Jongbloed, K.J. van der Gaag, P. de Knijff, N. Yamaguchi, H. Hooghiemstra, H. Bauer, P. Henschel, P.A. White, C.A. Driscoll, T. Tende, U. Ottosson, Y. Saidu, K. Vrieling, and H.H. de Iongh. 2016. Phylogeographic Patterns in Africa and High Resolution Delineation of Genetic Clades in the Lion (*Panthera leo*). *Nature Scientific Reports* 6: 30807.
- Bertram, B.C.R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology* 177: 463-482.
- Bertram, B.C.R. 1976. Kin selection in lions and in evolution. In *growing points in ethology* pp281-301. P. Bateson and R.A. Hinde. Eds. Cambridge University Press.
- Björkland, M. 2003. The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics* 4: 515-523.
- Botswana Population and Housing Census. 2011. Available at [www.catalog.ihsn.org/index.php/catalog/4243/download/55990](http://www.catalog.ihsn.org/index.php/catalog/4243/download/55990). Accessed on October 15, 2015.
- Boulain, N., G. Simioni, and J. Gignoux. 2007. Changing scale in ecological modelling: a bottom up approach with an individual based vegetation model. *Ecological Modelling*. 203: 257-269.
- Bouley, P., P. Michael, R. Branco, and N.H. Carter. 2018. Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biological Conservation* 227: 233-242.
- Breitenmoser U., C. Angst, J-M. Landry, C. Breitenmoser-Würsten, J.D.C. Linnell, and J-M. Weber. 2005. Non-lethal techniques for reducing depredation. In *People and Wildlife – Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz pp. 49–71. Cambridge University Press, Cambridge, UK.
- Bruskotter, J.T., and R.S. Wilson. 2014. Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. *Conservation Letters* 7: 158-165.

- Burger, J., W. Rosendahl, O. Loreille, H. Hemmer, T. Eriksson, A. Götherström, J. Hiller, M.J. Collins, T. Wess, and K.W. Alt. 2004 Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Molecular Phylogenetics and Evolution* 30: 841-849.
- Bygott, J. D., B.C. Bertram, and J.P. Hanby. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282: 839-841.
- C. Márquez, C., J.M. Vargas, R. Villafuerte, and J.E. Fa. 2013. Understanding the propensity of wild predators to illegal poison baiting. *Animal Conservation* 16: 118–129.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516-519.
- Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA, Paris, France.
- Christiansen, P. 2006. Sabertooth characteristics in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). *Journal of Morphology* 267: 1186-1198.
- Clifton, K.E. 1990. The costs and benefits of territory sharing for the Caribbean coral reef fish, *Scarus iserti*. *Behavioral Ecology and Sociobiology*. 26:139-147.
- Cole, L.C. .1949. The measurement of interspecific association. *Ecology* 30: 411–424.
- Collier, G.E. and S.J. O’Brien. 1985. A molecular phylogeny of the Felidae: immunological distance. *Evolution* 39: 473-487.
- Conover, M. 2002. Resolving Human–Wildlife Conflicts: The Science of Wildlife Damage Management. Lewis, Florida.
- Cozzi, G., F. Broekhuis, J.W. McNutt and B. Schmid. 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation* 22: 2937–2956.
- Creel, S., M.G.L. Mills, and J.W. McNutt. 2004. Demography and Population Dynamics of African Wild Dogs in Three Critical Ecosystems. In: D.W.Macdonald & C. Sillero-Zubiri (eds) *The Biology & Conservation of Wild Canids*. pp. 337–350. Oxford University Press.
- Davidson, Z., M. Valeix, A.J. Loveridge, H. Madzikanda, and D.W. Macdonald. 2011. Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation* 144: 114-121.
- Decker, D.J., S.J. Riley, and W.F. Siemer, eds. 2012. *Human Dimensions of Wildlife Management*. John Hopkins University Press, Baltimore, Maryland, U.S.A.
- Department of Wildlife and National Parks, 1998. *Guidelines for Compensation*. Department of Wildlife and National Parks, Gaborone.

- Department of Wildlife and National Parks, 2013. Compensation Guidelines for Damages Caused by Elephants and Lion. Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism. Government of Botswana, Gaborone, Botswana.
- Dickman A.J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation* 13: 458-66.
- Dickman A.J., E.E. Macdonald, 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.
- Dickman, A. 2005. An assessment of pastoralist attitudes and wildlife conflict in the Rungwa-Ruaha region, Tanzania, with particular reference to large carnivores. M.Sc. Thesis, University of Oxford, Oxford, United Kingdom.
- Dickman, A.J. 2009. Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania. Ph.D. Thesis, University College London, London, United Kingdom.
- Dickman, A.J. and L. Hazzah. 2016. Money, myths and man-eaters: Complexities of human-wildlife conflict. In *Problematic wildlife: A cross-disciplinary approach*, ed F.M. Angelici, pp. 339-56. Switzerland: Springer International Publishing.
- Dickman, A.J., E.A. Macdonald, and D.W. Macdonald DW. 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.
- Dickman, A.J., L. Hazzah, C. Carbone, and S.M. Durant. 2014. Carnivores, culture and ‘contagious conflict’: Multiple factors influence perceived problems with carnivores in Tanzania’s Ruaha landscape. *Biological Conservation* 178: 19-27.
- Doncaster, C.P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* 143: 431-443.
- Dures, S.G., C. Carbone, V. Savolainen, G. Maude, and D. Gottelli. Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation* 23: 502-515.
- Dyar, J.A. and J. Wagner. 2003. Uncertainty and species recovery program design. *Journal of Environmental Economics and Management* 45:505–522.
- Eklund, A., J.V. López-Bao, M. Tourani, G. Chapron, and J. Frank. 2017. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific Reports* 7:2097.
- Elliot, N., M. Valeix, D.W. Macdonald, and A.J. Loveridge. 2014. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos* 123: 1049-1056.

- Estes, R.D. 1991. *The behavior guide to African Mammals: including hoofed mammals, carnivores, primates*. University of California Press. Berkeley and Los Angeles, California.
- Fieberg, J. and C.O. Kochanny. 2005. Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management* 69:1346-1359.
- Frank, L., G. Hemson, H. Kushnir, and C. Packer. 2006. *Lions, conflict and conservation*. Background paper for the east and southern African lion conservation workshop Johannesburg, South Africa, 8-13 January 2006.
- Frank, L.G. 1998. *Living with lions: carnivore conservation and livestock in Laikipia District, Kenya*. Development Alternatives, Bethesda, Maryland.
- Frank, L.G., R. Woodroffe, and M.O. Ogada. 2005. People and predators in Laikipia District, Kenya. In *People and Wildlife: Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 286-304. Cambridge, UK: Cambridge University Press.
- Funston, P. 2001. *Kalahari Transfrontier Lion Project: Final Report*. Endangered Wildlife Trust, South Africa.
- Funston, P. 2014. The Kavango-Zambezi Transfrontier Conservation Area – critical for African lions. *Cat News* 60: 4-7.
- Fynn, R.W.S., M. Murray-Hudson, M. Dhliwayo, and P. Scholte. 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management* 23: 559-581.
- Gebresenbet, F., H. Bauer, J.M. Vadjunec, and M. Papeş. 2018. Beyond the numbers: Human attitudes and conflict with lions (*Panthera leo*) in and around Gambella National Park, Ethiopia. *PLoS ONE* 13: e0204320.
- Gittleman, J.L. and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Social Biology* 10: 57-63.
- Graham, K., A.P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159-171.
- Grinnell, J., C. Packer, and A.E. Pusey. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour*. 49:95-105.
- Gusset, M., M.J. Swarner, L. Mponwane, K. Keletile, and J.W. McNutt. 2009. Human-wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. *Oryx* 43: 67-72.
- Hayward, M.W. and G.I.H. Kerley. 2005. Prey preferences of the lion (*Panthera leo*). *The Journal of Zoology* 267:309–322.

- Hazzah, L., M. Borgehoff Mulder, and L. Frank. 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., S. Dolrenry, L. Naughton, C.T.T. Edwards, O. Mwebi, F. Kearney, and L. Frank. 2014. Efficacy of Two Lion Conservation Programs in Maasailand, Kenya. *Conservation Biology* 28: 851-860.
- Hemmer, H. 1974. Untersuchungen zur stammesgeschichte der Pantherkatzen (Pantherinae) III. Zur artgeschichte des Löwen *Panthera leo* (Linnaeus 1758). Veröff. Zool. Staatssamml. München 17, 167–280.
- Hemmer, H. 1978. Socialization by intelligence. *Carnivore* 1: 102–105.
- Hemson, G. 2003. The ecology and conservation of lions: human-wildlife conflict in semi-arid Botswana. University of Oxford, UK (Dissertation Thesis).
- Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. Macdonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74: 455-463.
- Hemson, G., S. MacLennan, G. Mills, P. Johnson, and D. Macdonald. 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.
- Herrington, S.J. 1986. Phylogenetic relationships of the wild cats of the world. PhD dissertation, University of Kansas, Lawrence, KS.
- Hussain, S. 2000. Protecting the snow leopard and en-hancing farmers' livelihoods. *Mountain Research and Development* 20: 226-31.
- Igoe, J. 2004. Conservation and Globalization: A Study of National Parks and Indigenous Communities from East Africa to South Dakota
- Ikanda, D., C. Packer. 2008. Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania. *Endangered Species Research* 6:67–74.
- Inskip, C. and A. Zimmermann. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43:18–34.
- Inskip, C., N. Carter, S. Riley, T. Roberts, and D. MacMillan. 2016. Toward Human-Carnivore Coexistence: Understanding Tolerance for Tigers in Bangladesh. *PLoS ONE* 11: e0145913.
- Johnson, D.D.P. and D.W. Macdonald. 2003. Sentenced without trial: reviling and revamping the resource dispersion hypothesis. *Oikos*. 101: 433-440.

- Johnson, W.E., E. Eizirik, J. Pecon-Slattery, W.J. Murphy, A. Antunes, E. Teeling, and S.J. O'Brien. 2006. The Late Miocene Radiation of Modern Felidae: A Genetic Assessment. *Science* 311: 73-77.
- Kansky, R., M. Kidd, and A.T. Knight. 2014. Meta-analysis of attitudes toward damage-causing mammalian wildlife. *Conservation Biology* 28: 924-938.
- Karani, I.W. 1994. An Assessment of Depredation by Lions and other Predators in the Group Ranches Adjacent to Masai Mara National Reserve. M.Sc. Thesis, Moi University, Eldoret, Kenya.
- Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements. *Radio Tracking and Animal Populations* (eds J. Millspaugh and J.M. Marzluff), pp. 125-166. Academic Press, New York.
- Kgathi, D.L., D. Kniveton, S. Ringrose, A.R. Turton, C.H.M. Vanderpost, J. Lundqvist, and M. Seely. 2006. The Okavango; a river supporting its people, environment and economic development. *Journal of Hydrology* 331: 3-17.
- Kingdon, J. 1997. *The Kingdon field guide to African mammals*. London / New York: Academic Press/ Natural World.
- Kitchener, A.C. 1999. Tiger distribution, phenotypic variation and conservation issues. In *Riding the tiger, tiger conservation in human-dominated landscapes*: 19-39. J. Seidensticker, S. Christie, and P. Jackson (eds). Cambridge, Cambridge University Press.
- Kitchener, A.C., Ch. Breitenmoser-Würsten, E. Eizirik, A. Gentry, L. Werdelin, A. Wilting, N. Yamaguchi, A.V. Abramov, P. Christiansen, C. Driscoll, J.W. Duckworth, W. Johnson, S.J. Luo, E. Meijaard, P. O'Donoghue, J. Sanderson, K. Seymour, M. Bruford, C. Groves, M. Hoffmann, K. Nowell, Z. Timmons, and S. Tobe. 2017. A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. *Cat News Special Issue* 11.
- Kolowski, J.M. and K.E. Holekamp. 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* 128:529–541.
- Kotze, R., M. Keith, C. Winterbach, H. Winterbach, and J.P. Marshal. 2018. The influence of social and environmental factors on organization of African lion (*Panthera leo*) prides in the Okavango Delta. *Journal of Mammalogy* 99: 845-858.
- Krafte Holland, K., L.R. Larson, and R.B. Powell. 2018. Characterizing conflict between humans and big cats *Panthera* spp: A systematic review of research trends and management opportunities. *PLoS ONE* 13: e0203877.
- Kruuk, H. 1981. *The Effects of Large Carnivores on Livestock and Animal Husbandry in Marsabit District, Kenya*. IPAL Technical Report E-4, UNEP-MAB integrated project in arid lands.

- Lagendijk, D.D.G. and M. Gusset. 2008. Human–Carnivore Coexistence on Communal Land Bordering the Greater Kruger Area, South Africa. *Environmental Management* 42: 971-6.
- Lamarque, F., J. Anderson, R. Fergusson, M. Lagrange, Y. Osei-Owusu, and L. Bakker. 2009. Human-Wildlife Conflict in Africa. Causes, Consequences and Management Strategies. Food and Agriculture Organization of the United Nations Forestry, Rome, Italy.
- LeFlore E.G., T.K. Fuller, M. Tomeletso, T.C. Dimbindo, and A.B Stein 2020 Human dimensions of human–lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana. *Environmental Conservation* 47: 182-189.
- LeFlore, E.G., T.K. Fuller, M. Tomeletso, and A.B Stein. 2019. Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation* 18: e00592.
- Levick S.R. and K.H. Rogers. 2008. Structural biodiversity monitoring in savanna ecosystems: integrating LiDAR and high resolution imagery through object-based image analysis. In: *Object-based image analysis: spatial concepts for knowledge-driven remote sensing applications*. T. Blaschke, S. Lang, GJ.. Hay, eds. Berlin, Germany. Springer.
- Li, C., Z. Jiang, C. Li, S. Tang, F. Li, Z. Luo, X. Ping, et al. 2015. Livestock depredations and attitudes of local pastoralists toward carnivores in the Qinghai Lake Region, China. *Wildlife Biology* 21: 204-212.
- Liberg, O., C. Chapron, P. Wabakken, H.C. Pedersen, N.T. Hobbs, and H. Sand. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society, Series B*, 279: 910-915.
- Lichtenfeld, L.L., C. Trout, and E.L. Kisimir. 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodiversity Conservation* 24: 483-491.
- Lindsey, P.A., J.T. duToit, and M.G.L. Mills. 2005. Attitudes of ranchers towards African wild dogs *Lycaon pictus*: conservation implications on private land. *Biological Conservation*. 125: 113-121.
- Lindstrom, E. 1986. Territory inheritance and the evolution of group-living in carnivores. *Animal Behavior*. 34: 1825–1835.
- Linnell, J., J. Odden, M. Smith, R. Aanes, and J. Swenson. 1999. Large carnivores that kill livestock: do “problem individuals” really exist? *Wildlife Society Bulletin* 27, 698–705.
- Long, J.A., T.A. Nelson, S.L. Webb, and K.L. Gee. 2014. A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology* 83: 1216-1233.

- Loveridge, A.J. 2005. Conflict synthesis. In *Lion Conservation Research: From Conflict to Socioecology*. Workshop 3 & 4, eds A.J. Loveridge, T. Lynam, and D.W. Macdonald, Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.
- Loveridge, A.J., G. Hemson, Z. Davidson, and D.W. Macdonald. 2010. African lions on the edge: reserve boundaries as 'attractive sinks'. *Biology and Conservation of Wild Felids* (eds D.W. Macdonald and A.J. Loveridge), pp. 283-304. Oxford University Press, Oxford, UK.
- Loveridge, A.J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz, and D.W. Macdonald. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32: 953-962.
- Mabille, G., A. Stein, T. Tveraa, A. Mysterud, H. Brøseth, and J. D. C. Linnell. 2015. Sheep farming and large carnivores: What are the factors influencing claimed losses? *Ecosphere* 6:82.
- Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature*. 301: 379-384.
- Macdonald, D.W., A.J. Loveridge, and A. Rabinowitz. 2010. Felid futures: crossing disciplines, borders and generations. In: D.W. Macdonald, A.J. Loveridge (eds) *Biology and Conservation of Wild Felids*. Oxford University Press, Oxford. pp. 599–649.
- Macdonald, D.W., F.G. Ball, and N.G. Hough. 1980. The evaluation of home range size and configuration using radio tracking data. *A Handbook on Biotelemetry and Radio Tracking: Proceedings of an International Conference on Telemetry and Radio Tracking in Biology and Medicine* (eds C.J. Amlaner and D.W. Macdonald), pp. 405-424. Pergamon Press, Oxford, UK.
- Madden, F. and B. McQuinn. 2014. Conservation's blind spot: the case for conflict transformation in wildlife conservation. *Biological Conservation* 178: 97–106.
- Maddox, G., ed. 1993. *Colonialism and Nationalism in Africa: Conquest and Resistance to Colonialism in Africa*. Garland Publishing, Inc. New York, New York, U.S.A.
- Manfredo, M.J. 2008. *Who cares about wildlife?* Springer, New York, New York, U.S.A.
- Marker, L.L., M.G.L. Mills, D.W. Macdonald. 2003. Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology* 17: 1290-1298.
- Marshall, L.G., S.D. Webb, J.J. Sepkoski, and D.M. Raup. 1982. Mammalian evolution and the great American interchange. *Science* 215: 1351-1357.
- Mazák, J.H. 2004. On the sexual dimorphism in the skull of the tiger (*Panthera tigris*). *Mammalian Biology* 69: 392-400.
- Mazák, J.H. 2008. Craniometric variation in the tiger (*Panthera tigris*): implications for patterns of diversity, taxonomy and conservation. *Mammalian Biology* 75: 45–68.

- Mazák, J.H. 2010. Geographical variation and phylogenetics of modern lions based on craniometric data. *Journal of Zoology* 281: 194–209.
- Mazák, V. 1968. Die Löwe. *Das Pelzgewerbe*, Berlin-Frankfurt/M.-Leipzig-Wien, 19.Jhrg. (N.F.), Nr. 3, pp. 3–27, 7 figs.
- Mazák, V. 1975. Notes on the black-maned lion of the Cape, *Panthera leo melanochaita* (Ch.H. Smith, 1842) and a revised list of preserved specimens. *Verh. Koninkl. Nederlandse Akad. Wetenschappen* 64: 1-44.
- Mbaiwa, J.E. 2018. Effects of the safari hunting tourism ban on rural livelihoods and wildlife conservation in Northern Botswana. *South African Geographical Journal* 100: 41-61.
- Mbaiwa, J.E., B.N. Ngwenya, and D.L. Kgathi. 2008. Contending with unequal and privileged access to natural resources and land in the Okavango Delta, Botswana. *Singapore Journal of Tropical Geography* 29: 155-172.
- Mbizah, M.M., M. Valeix, D.W. Macdonald, and A.J. Loveridge. 2019. Applying the resource dispersion hypothesis to a fission-fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution* 9: 9111-9119.
- McCarthy, J.M., T. Gumbrecht, T. McCarthy, P. Frost, K. Wessels, and F. Seidel. 2003. Flooding Patterns of the Okavango Wetland in Botswana between 1972 and 2000. *Journal of the Human Environment* 32: 453-457.
- McCarthy, T.S., G.R.J. Cooper, P.D. Tyson, and W.N. Ellery. 2000. Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *South African Journal of Science* 96: 25-33.
- McComb, K., A. Pusey, C. Packer, and J. Grinnell. 1993. Female lions can identify potentially infanticidal males from their roars. *Proceedings of the Royal Society B: Biological Sciences*, 252: 59-64.
- McComb, K., C. Packer, and A. Pusey. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour* 47: 379-387.
- Meester, J. and H. Setzer. 1971. *Mammals of Africa: an identification manual*. Smithsonian Institution Press, Washington.
- Messmer, T.A. 2000. Emergence of human-wildlife conflict management: turning challenges into opportunities. *International Biodeterioration and Biodegradation* 45: 97-102.
- Mishra, C. 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24: 338-343.
- Mishra, C., P. Allen, T. McCarthy, M.D. Madhusudan, A. Bayarjargal, and H.H.T. Prins. 2003. The role of incentive programs in conserving the snow leopard. *Conservation Biology* 17: 1512-1520.

- Miththapala, S. 1992. Genetic and morphological variation in the leopard (*Panthera pardus*): a geographically widespread species. Ph.D. thesis, Univ. Florida, Gainesville.
- Mossaz, A., R.C. Buckley, and J.G. Castley. 2015. Ecotourism contributions to conservation of African big cats. *Journal for Nature Conservation* 28:112–118.
- Mosser A. and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behavior*. 78:359-370.
- Mosser, A. A., M. Kosmala, and C. Packer. 2015. Landscape heterogeneity and behavioral traits drive the evolution of lion group territoriality. *Behavioral Ecology* 26: 1051-1059.
- Mponzi, B.P., C.A. Lepczyk, and B.M. Kissui. 2014. Characteristics and distribution of livestock losses caused by wild carnivores in Maasai Steppe of northern Tanzania. *Human-Wildlife Interactions* 8:218–227.
- Munson L., K.A. Terio, R. Kock, T. Mlengeya, M. E. Roelke, E. Dubovi, B. Summers, A. R. E. Sinclair, and C. Packer. 2008. Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. *PLoS ONE*, 3, e2545.
- Murray-Hudson, M. 2009. Floodplain Vegetation Responses to Flood Regime in the Seasonal Okavango Delta, Botswana. University of Florida.
- Mweze, M. 2014. Botswana Department of Wildlife and National Parks. Personal Communication. October 2014, Seronga, Ngamiland, Botswana.
- Myers, N. 1975. The silent savannahs. *International Wildlife* 5: 5–10.
- Naughton-Treves, L. 1997. Farming the forest edge: vulnerable places and people around Kibale National Park, Uganda. *The Geographical Review* 87: 27-47.
- Naughton-Treves, L. and A. Treves. 2005. Socio-ecological factors shaping local support for wildlife: crop raiding by elephants and other wildlife in Africa. In *People and Wildlife: Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 252-277. Cambridge, UK: Cambridge University Press.
- Naughton-Treves, L., R. Grossberg, and A. Treves 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology* 17:1500–1511.
- Newsome, T.M., A.C. Greenville, D. Ćirović, C.R. Dickman, C.N. Johnson, M. Krofel, M. Letnic, W.J. Ripple, E.G. Ritchie, S. Stoyanov, and A.J. Wirsing. 2017. Top predators constrain mesopredator distributions. *Nature Communications* 8:15469.
- Ngwenya, M.M., N.M. Mkandhla, and J.V. Muzvondiwa. 2013. A Comparison of Lion Home Range Sizes in Two Management Blocks in a Semi-Arid Savannah National Park of Zimbabwe. *International Journal of Science and Research* 2: 388-396.

- Nikolin, V.M., X.A. Olarte-Castillo, N. Osterriender, H. Hofer, E. Dubovi, C.J. Mazzoni, E. Brunner, K.V. Goller, R.D. Fyumagwa, P.D. Moehlman, D. Thierer, and M.L. East. 2017. Canine distemper virus in the Serengeti ecosystem; molecular adaptation to different carnivore species. *Molecular Ecology* 26: 2111-2130.
- Nowell, K. and P. Jackson. 1996. *Wild Cats: Status Survey and Conservation Action Plan*. World Conservation Union, Gland, Switzerland 5577.
- Nyhus, P., H. Fischer, F. Madden, and S. Osofsky. 2003. Tak-ing the bite out of wildlife damage: the challenges of wildlife compensation schemes. *Conservation in Practice* 4: 37-43.
- Nyhus, P.J., S.A. Osofsky, P. Ferraro, F. Madden, and H. Fischer. 2005. Bearing the cost of human-wildlife conflict: the challenges of compensation schemes In *People and Wildlife – Conflict or Coexistence?* pp. 107–121. eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz. Cambridge University Press, Cambridge, UK.
- O'Brien, S. J., J.S. Martenson, C. Packer, L. Herbst, V. De Vos, P. Joslin, J. Ott-Joslin, D. E. Wildt, and M. Bush. 1987. Biochemical genetic variation in geographic isolates of African and Asiatic lions. *National Geographic Research* 3: 114-124.
- O'Brien, S.J. and W.E. Johnson. 2005. Big Cat Genomics. *Annual Review of Genomics and Human Genetics* 6: 407-429.
- O'Brien, S.J. and W.E. Johnson. 2007. The Evolution of Cats. *Scientific American* p. 68-75.
- Ogada, M.O., R. Woodroffe, N.O. Oguge, and L.G. Frank. 2003. Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. *Conservation Biology* 17: 1-10.
- Ohishi, K., R. Suzuki, T. Maeda, M. Tsuda, E. Abe, T. Yoshida, Y. Endo, M. Okamura, T. Nagamine, H. Yamamoto, M. Ueda, and T. Maruyama. 2013. Recent Host Range Expansion of Canine Distemper Virus and Variation in its Receptor, the Signaling Lymphocyte Activation Molecule, in Carnivores. *Journal of Wildlife Diseases* 50: 596-606.
- Ohrens, O., A. Treves, and C. Bonacic. 2015. Relationship between rural depopulation and puma-human conflict in the high Andes of Chile. *Environmental Conservation* 43:24 - 33.
- Packer C., A.E. Pusey, and L.E. Eberly. 2001. Egalitarianism in female African lions. *Science*. 293:690-693.
- Packer, C. 1986. The ecology of sociality in felids. In: *Ecological Aspects of Social Evolution* D.I. Rubenstein and R.W. Wrangham (eds). p. 429-451. Princeton, New Jersey: Princeton University Press.
- Packer, C. and A.E. Pusey. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 286: 740-742.

- Packer, C., D. Scheel, and A.E. Pusey. 1990. Why lions form groups: food is not enough. *American Naturalist* 136: 1-19.
- Packer, C., H. Brink, B.M. Kissui, H. Maliti, H. Kushnir, and T. Caro. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology* 25: 142-153.
- Packer, C., S. Altizer, M. Appel, E. Brown, J. Martenson, S.J. O'Brien, M. Roelke-Parker, R. Hofmann-Lehmann, and H. Lutz. 1999. Viruses of the Serengeti: Patterns of infection and mortality in African lions. *Journal of Animal Ecology* 68: 1161-1178.
- Palmeira, F.B.L., P.G. Crawshaw Jr., C.M. Haddad, K.M.P.M.B. Ferraz and L. M. Verdade. 2008. Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biological Conservation* 141:118–125.
- Patterson, B.D. 2007. On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology* 34: 55-60.
- Patterson, B.D., S.M. Kasiki, E. Selempo, and R.W. Kays. 2004 Livestock depredation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119: 507-516.
- Petter, G. 1973. Carnivores Pleistocènes du Ravin d'Olduvai (Tanzanie). In L.S.B. Leakey, R.J.G. Savage, and S.C. Coryndon (eds), *Fossil vertebrates of Africa* 3: 43-100. London: Academic Press.
- Pettigrew, M., Y. Xie, A. Kang, M. Rao, J. Goodrich, T. Liu, and J. Berger. 2012. Human-carnivore conflict in China: a review of current approaches with recommendations for improved management. *Integrative Zoology* 7:21-226.
- Pickett, S.T.A., M.L. Cadenasso, and T.L. Benning. 2003. Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. In: J.T. du Toit, K.H. Rogers, and H.C. Biggs (eds). *The Kruger experience: ecology and management of Savanna heterogeneity*. Washington (DC): Island Press. p. 22-40.
- Plumwood, J. 2003. Decolonizing relationships with nature. In *Decolonizing Nature: Strategies for conservation in a Post-colonial Era*. pp. 51-78. eds W.M. Adams and M. Mulligan. Earthscan Publications, Ltd. London, United Kingdom.
- Pocock, R.I. 1930. The lions of Asia. *Journal of the Bombay Natural History Society* 34: 638-665.
- Pocock, R.I. 1939. *The Fauna of British India, including Ceylon and Burma. Mammalia, volume 1, Primates and Carnivora (in part), Families Felidae and Viverridae*. London: Taylor and Francis.
- Powell, R.A. 2000. Animal home ranges and territories and home range estimators. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani and T.K. Fuller), pp. 65-110. Columbia University, New York.

- Pozo, R.A., E.G. LeFlore, A.B. Duthie, N. Bunnefeld, I.L. Jones, J. Minderman, O.S. Rakotonarivo, and J.J. Cusack. 2020. A multispecies assessment of wildlife impacts on local community livelihoods. *Conservation Biology* 35: 297-306.
- Pusey, A. E. and C. Packer. 1994. Non-offspring nursing in social carnivores: minimizing the costs. *Behavioral Ecology* 5: 362-374.
- R Core Team. 2018 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <<http://www.r-project.org>>.
- Ramberg, L., P. Hancock, M. Lindholm, T. Meyer, S. Ringrose, J. Sliva, J. Van As, and C. VanderPost. 2006. Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences* 8: 310-337.
- Ravenelle, J., Nyhus, P.J., 2017. Global patterns and trends in human-wildlife conflict compensation. *Conservation Biology* 31: 1247–1256. <https://doi.org/10.1111/cobi.12948>
- Reddy, S.M.W., J. Montambault, Y.J. Masuda, E. Keenan, W. Butler, J.R.B. Fisher, et al. 2017. Advancing conservation by understanding and influencing human behavior: human behavior and nature. *Conservation Letters* 10: 248–256.
- Rientjes, S. 2001. Nature conservation: much more than an exercise in applied ecology. *European Nature* 6: 5-7.
- Riggio, J., A. Jacobson, L. Dollar, H. Bauer, A. Dickman, P. Funston, P. Henschel, H. de Iongh, L. Lichtenfeld, C. Packer, and S. Pimm. 2013. The size of savannah Africa: a lion's 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.
- Roelke M.E., M.A. Brown, J.L. Troyera, H. Winterbach, C. Winterbach, G. Hemson, D. Smith, R.C. Johnson, J. Pecon-Slattery, A.L. Roca, K.A. Alexander, L. Klein, P. Martelli, K. Krishnasamy, and S.J. O'Brien. 2009. Pathological manifestations of feline immunodeficiency virus (FIV) infection in wild African lions. *Virology* 390: 1-12.
- Roskaft, E., B. Handel, T. Bjerke, and B.P. Kaltenborn. 2007. Human attitudes towards large carnivores in Norway. *Wildlife Biology* 13: 172-85.
- Salles, L.O. 1992. Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea). *American Museum Novitates* 3047: 1-67.

- Samson, C. and C. Gigoux. 2017. *Indigenous Peoples and Colonialism: Global Perspectives*. Polity Press. Cambridge, United Kingdom.
- Schaller, G. B. 1972. *The Serengeti Lion*. Chicago: University of Chicago Press.
- Scheel, D. and C. Packer 1991. Group hunting behavior of lions: a search for cooperation. *Animal Behaviour* 41: 697-709.
- Schlecht, E., M.D. Turner, C.G. Hülsebusch, and A. Buerkert. 2020. Managing Rangelands Without Herding? Insights From Africa and Beyond. *Frontiers in Sustainable Food Systems* 4: 549954.
- Sinclair, A.R.E. 1979. The Serengeti environment. In: A.R.E. Sinclair and M. Norton-Griffiths (eds). *Serengeti*. Chicago (IL): University of Chicago Press. p. 31-45.
- Singh, R., P. Nigam, Q. Qureshi, K. Sankar, P.R. Krausman, S. P. Goyal, and K.L. Nicholoso. 2015. Characterizing human-tiger conflict in and around Ranthambhore Tiger Reserve, western India. *European Journal of Wildlife Research* 61:255–261.
- Spong, G. 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: Social and ecological factors. *Behavioral Ecology and Sociobiology* 52: 303-307.
- Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology* 29: 445-454.
- Stedman, R.C. 2012. Sociological Considerations in Wildlife Management. In *Human Dimensions of Wildlife Management* 2nd ed. D.J. Decker, S.J. Riley, and W.F. Siemer eds pp. 58-67. John Hopkins University Press, Baltimore, Maryland, U.S.A..
- Stringer, C. 2002. Modern human origins: progress and prospects. *Philosophical Transactions of the Royal Society B* 357: 563-579. (doi:10.1098/rstb.2001.1057).
- Swenson, J.E. and H. Andren. 2005. A tale of two countries: large carnivore deprecations and compensation schemes in Sweden and Norway. In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 323–339. Cambridge University Press, Cambridge, UK.
- Thirgood, S., R. Woodroffe, and A. Rabinowitz. 2005. The impact of human-wildlife conflict on human lives and livelihoods. In: R. Woodroffe, S. Thirgood, and A.R. Rabinowitz (eds) *People and Wildlife – Conflict or Coexistence?* pp. 13–26. Cambridge University Press, Cambridge, UK.
- Thomas, B., J.D. Holland, and E.O Minot. 2011. Wildlife tracking technology options and cost considerations. *Wildlife Research* 38: 653–663.
- Thorn, M., M. Green, D. Scott, K. Marnewick. 2013. Characteristics and determinants of human-carnivore conflict in South African farmland. *Biodiversity Conservation* 22:1715–1730.

- Thorn, M., M. Green, F. Dalerum, P.W. Bateman, and D.M. Scott. 2012. What drives human-carnivore conflict in the North West Province of South Africa? *Biological Conservation* 150:23–32.
- Treves A., M. Krofel, and J. McManus. 2016. Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment* 14: 380-388
- Treves, A. and J. Bruskotter. 2014. Tolerance for predatory wildlife. *Science* 344: 476-477.
- Treves, A. and K.U. Karanth. 2003 Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491-1499.
- Treves, A., R.L. Jurewicz, L. Naughton-Treves, and D.S. Wilcove. 2009. The price of tolerance: wolf damage payments after recovery. *Biodiversity and Conservation* 18:4003–4021.
- Trinkel, M., and F.M. Angelici. 2016. The decline in the lion population in africa and possible mitigation measures. In *Problematic Wildlife*, pp. 45–68. ed F. M. Angelici. Springer International Publishing, Switzerland.
- Trinkel, M., D. Cooper, C. Packer, and R. Slotow. 2011. Inbreeding Depression Increases Susceptibility to Bovine Tuberculosis in Lions: An Experimental Test Using an Inbred-Outbred Contrast Through Translocation. *Journal of Wildlife Diseases* 47:494-500.
- Trinkel, M., and F.M. Angelici. 2016. The decline in the lion population in africa and possible mitigation measures. In *Problematic Wildlife*, ed F. M. Angelici. Springer International Publishing, Switzerland. pg 45–68.
- Troyer, J. L., M.E. Roelke, J.M. Jaspersen, N. Baggett, V. Buckley-Beason, D. MacNulty, M. Craft, C. Packer, J. Pecon-Slattery, S.J. O’Brien. 2011. FIV diversity: FIV -Ple subtype composition may influence disease outcome in African lions. *Veterinary Immunology and Immunopathology* 143: 338-346.
- Troyer, J.L., J. Pecon-Slattery, M.E. Roelke, L. Black, C. Packer, and S.J. O’Brien. 2004. Patterns of feline immunodeficiency virus multiple infection and genome divergence in a free-ranging population of African lions. *Journal of Virology*. 78: 3777-3791.
- Tumenta, P.N., H.H. de Iongh, P.J. Funston, and H.A. Udo de Haes. 2013. Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx* 47: 237-242.
- Tumenta, P.N., M. van't Zelfde, B.M. Croes, R. Buij, P.J. Funston, H.A. Udo De Haes, and H.H. De Iongh. 2013. Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology* 78: 461-469.
- Tuqa, J.H., P. Funston, C. Musyoki, G.O. Ojwang, N.N. Gichuki, H. Bauer, W. Tamis, S. Dolrenry, M. Van't Zelfde, G.R. de Snoo, and H.H. de Iongh. 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation* 2: 1-10.

- Turner, A. 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-pleistocene in Africa. *Geobios* 23: 349-68.
- Turner, A. 1997. *The Big Cats and their Fossil Relatives*. New York: Columbia University Press.
- Valeix, M., A.J. Loveridge, and D.W. Macdonald. 2012. Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. *Ecology* 93: 2490-2496.
- Valeix, M., S. Chamaillé-Jammes, A.J. Loveridge, Z. Davidson, J.E. Hunt, H. Madzikanda, and D.W. Macdonald. 2011. Understanding Patch Departure Rules for Large Carnivores: Lion Movements Support a Patch-Disturbance Hypothesis. *The American Naturalist* 178: 269-275.
- van Eeden, L. M., A. Eklund, J.R.B. Miller, J.V. López-Bao, G. Chapron, M.R. Cejtin, et al. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16:e2005577.
- van Eeden, L.M., A. Eklund, J.R.B. Miller, J.V. López, G. Chapron, M.R. Cejtin, M.S. Crowther, C.R. Dickman, J. Frank, M. Krofel, D.W. Macdonald, J. McManus, T.K. Meyer, A.D. Middleton, T.M. Newsome, W.J. Ripple, E.G. Ritchie, O.J. Schmitz, K.J. Stoner, M. Tourani, and A. Treves. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16(9): e2005577.
- van Eeden, L.M., A. Eklund, J.R.B. Miller, J.V. López, G. Chapron, M.R. Cejtin, M.S. Crowther, C.R. Dickman, J. Frank, M. Krofel, D.W. Macdonald, J. McManus, T.K. Meyer, A.D. Middleton, T.M. Newsome, W.J. Ripple, E.G. Ritchie, O.J. Schmitz, K.J. Stoner, M. Tourani, and A. Treves. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* 16(9): e2005577. <https://doi.org/10.1371/journal.pbio.2005577>
- Van Orsdol, K.G. 1981. *Lion Predation in Rwenzori National Park, Uganda*. PhD Thesis, University of Cambridge.
- Van Orsdol, K.G., J.P. Hanby, and J.D. Bygott. 1985. Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*. 206: 97-112.
- Vaske, J.J. and M.J. Manfredo. 2012. Social Psychological Considerations in Wildlife Management. In *Human Dimensions of Wildlife Management* 2nd ed. D.J. Decker, S.J. Riley, and W.F. Siemer eds pp. 43-57. John Hopkins University Press, Baltimore, Maryland, U.S.A. *Human Dimensions of Wildlife Management*.
- Vereshchagin, N.K. 1971. Cave lions of Holarctics. *Trudy Zoologicheskogo Instituta* 49:123-199.
- Wall, J., G. Wittemyer, B. Klinkenberg, and I. Douglas-Hamilton. 2014. Novel opportunities for wildlife conservation and research with real-time monitoring. *Ecological Applications* 24: 593–601.
- Wang, S. and D. Macdonald. 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation* 129: 558-565.

- Weise, F.J., M.W. Hayward, R. Casillas Aguirre, M. Tomeletso, P Gadimang, M.J. Somers, et al. 2018. Size, shape and maintenance matter: a critical appraisal of a global carnivore conflict mitigation strategy – livestock protection kraals in northern Botswana. *Biological Conservation* 225: 88–97.
- Weise, F.J., H. Hauptmeier, K.J. Stratford, M.W. Hayward, K. Aal, M. Heuer, M. Tomeletso, V. Wulf, M.J. Somers, and A.B. Stein. 2019. Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence. *Frontiers in Ecology and Evolution* 6:242.
- Werdelin, L. 1989. The radiation of felids in South America: when and where did it occur? In 5th International Theriological Congress, Rome, Abstracts of Papers and Posters, p. 290-291. Rome, Italy.
- Werdelin, L. and R. Dehghani. 2011. Carnivora. In T. Harrison (ed), *Paleontology and Ecology of Laetoli, Tanzania: Human Evolution in Context*. Springer, New York.
- Werdelin, L., N. Yamaguchi, W.E. Johnson, and S.J. O’Brien. 2010. Phylogeny and evolution of cats (Felidae). P. 59-82. In D.W. Macdonald and A.J. Loveridge (eds), *Biology and Conservation of Wild Felids*. Oxford University Press, New York.
- Western, G., D.W. Macdonald, A.J. Loveridge, and A.J. Dickman. 2019. Creating Landscapes of Coexistence: Do Conservation Interventions Promote Tolerance of Lions in Human-dominated Landscapes? *Conservation and Society* 17: 204-217.
- Winterbach, C. 2008. Draft national predator strategy, Botswana. Department of Wildlife and National Parks, Gaborone.
- Winterbach, H.E.K., C.W. Winterbach, and M.J. Somers. 2014. Landscape Suitability in Botswana for the Conservation of Its Six Large African Carnivores. *PLOS One* 9: e100202.
- Winterbach, H.E.K., C.W. Winterbach, M.J. Somers, and M.W. Hayward. 2013. Key factors and related principles in the conservation of large African carnivores. *Mammal Review* 43: 89-110.
- Wittemyer, G., P. Elsen, W.T. Bean, A.C.O. Burton, and J.S. Brashares. 2008. Accelerated human population growth at protected area edges. *Science* 321: 123-126.
- Wolski, P. and H.H.G. Savenije. 2006. Dynamics of floodplain-island groundwater flow in the Okavango Delta, Botswana. *Journal of Hydrology* 320: 283-301.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165–173.
- Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. In *Carnivore Conservation*, eds J.L. Gittleman, R.K. Wayne, D.W. Macdonald, and S.M. Funk, pp. 61-92. Cambridge, UK: Cambridge University Press.

- Woodroffe, R. and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128.
- Woodroffe, R. and L.G. Frank. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* 8: 91-98.
- Woodroffe, R., L.G. Frank, P.A. Lindsey, S.M.K. ole Ranah, S. Romañach. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity Conservation* 16:1245–1260.
- Woodroffe, R., S. Thirgood, and A. Rabinowitz. 2005. The impact of human-wildlife conflict on natural systems. In *People and Wildlife: Conflict or Coexistence?* eds R. Woodroffe, S. Thirgood, and A.R. Rabinowitz, pp. 1-12. Cambridge, UK: Cambridge University Press.
- Woolfenden, G.E. and J.W. Fitzpatrick. 1978. The inheritance of territory in group-breeding birds. *BioScience*. 28:104-108.
- World Bank. 2016. Botswana Population Rate. World Development Indicators, The World Bank. URL <http://data.worldbank.org/indicator/SP.POP.GROW?locations=BW> Accessed November 25, 2016.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164-168.
- Wozencraft W.C. 2005. Order Carnivora. In *Mammal species of the world. A taxonomic and geographic reference* (3rd ed.). D.E. Wilson and D.M. Reeder (eds). Johns Hopkins University Press, Baltimore, p. 532-628.
- Yamaguchi, N., A. Cooper, L. Werdelin, and D.W. Macdonald. 2004a. Evolution of the mane and group-living in the lion (*Panthera leo*): a review. *Journal of Zoology* (London) 263: 329-342.
- Yamaguchi, N., A.C. Kitchener, C.A. Driscoll, and D.W. Macdonald. 2009b. Divided infraorbital foramen in the lion (*Panthera leo*): its implications for colonization history, population bottlenecks, and conservation of the Asian lion (*P. l. persica*). *Contributions to Zoology* 78: 77-83.
- Yamaguchi, N., A.C. Kitchener, E. Gilissen, and D.W. Macdonald. 2009a. Brain size of the lion (*Panthera leo*) and the tiger (*P. tigris*): implications for intrageneric phylogeny, intraspecific differences and the effects of captivity. *Biological Journal of the Linnean Society* 98: 85–93.
- Yamaguchi, N., C.A. Driscoll, A.C. Kitchener, J.M. Ward, and D.W. Macdonald. 2004b. Craniological differentiation between European wildcats (*Felis silvestris silvestris*), African wildcats (*F.s.lybica*) and Asian wildcats (*F.s.ornata*): implications for their evolution and conservation. *Biological Journal of the Linnean Society* 83: 47-63.
- Zehnder, A., S. Henley, and R. Weibel. 2018. Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability. *Zoology* 128: 46-54.

Zimmermann, A., M.J. Walpole, and N. Leader-Williams. 2005. Cattle ranchers' attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. *Oryx* 39: 406-412.