Lion population status and ecology in a seasonally-flooded wetland, the Okavango Delta

Christen Robynne Kotze

Thesis submitted for Doctor of Philosophy
Biological Sciences Department
University of Cape Town

Supervisor:
Prof. Justin O' Riain
Institute for Communities and Wildlife in Africa
Department of Biological Sciences
Private Bag Rondebosch 7701
University of Cape Town
Email: justin.oriain@uct.ac.za

Supervisor:
Prof. Andrew J Loveridge
,Wildlife Conservation Research Unit
Recanati-Kaplan Centre
Tubney House
Oxford University
OX13 5QL
Email: andrew.loveridge@zoo.ox.ac.uk

ABSTRACT

The Okavango Delta in north-western Botswana, is a population stronghold for the African lion (*Panthera leo*). As lion populations are declining, there is a pressing need to develop conservation plans that can secure the future for lion populations in natural environments that face increasing anthropogenic pressure. The Okavango Delta is a dynamic wetland that undergoes significant ecological change in response to an annual flood pulse, the extent of which is determined by both short-and long-term climatic variation. The resulting fluctuations in landscape structure and resource availability affect all trophic levels. However, their effects on apex predators are not well understood. In this thesis, I examined which ecological and anthropogenic factors underpin population processes such as population density, home range size and resource selection of lions in the Okavango at various temporal and spatial scales, in order to better inform conservation plans for this population.

As lions can be difficult to count, a situation made more challenging by a seasonally flooded environment, I first looked at camera trapping as a potential survey method for lions. With high resolution images, lions could be individually identified from trap images and spatially-explicit capture-recapture applied to produce reliable population estimates. Furthermore, spatial variation in density could be linked to environmental and anthropogenic covariates. Lion densities were highest along the floodplains, and were correlated strongly with vegetation productivity, but decreased with proximity to human settlements, suggesting an edge effect along the boundaries of the wildlife management areas. This edge effect may result from retaliatory killing in response to livestock predation by lions in adjacent community areas but could also be the effect of prey depletion from bushmeat harvesting along the Okavango's boundaries.

As flooding can induce significant changes in landscape structure, I examined what effect this had on lion home range size at minimum and maximum flood extent. When floods were at their lowest, home range sizes of males were larger than those of females, which is typical of large carnivores. Females appeared to minimize the area used by prioritizing access to prey, and home range was also negatively correlated with habitat heterogeneity and island size and connectivity. Male home range sizes, however, were not affected by prey availability, but instead were negatively correlated with habitat heterogeneity and proportion of woodland, both of which are considered indices of high-quality habitat in this landscape. As higher quality habitat may result in higher female density, males may instead be trying to maximize access to areas which would have a higher density of females. At peak flood, however, males and females had similar range sizes, and home range sizes were positively correlated with dry land fragmentation. During high flood phases, lower availability of dry land, together with the need to increase home range size as land fragments, could exacerbate intraspecific competition for space, and potentially increase conflict with adjacent communities as floods displace lions towards the boundaries of the wildlife management areas. However, in extended phases of low flood, which could result from prolonged drought, rising

temperatures or excessive water abstraction for human use, habitat heterogeneity may decline, with potential negative effects on herbivore and lion populations. Consequently, both scenarios are predicted to ultimately reduce the carrying capacity for resident lions.

Lastly, I examined seasonal resource use at a finer scale, and focused on how changes in flooding could affect the size of population cores in the Okavango and connectivity between these, and connectivity from the Okavango to surrounding areas. Seasonal habitat selection by lions mimicked shifts exhibited by large herbivores in other studies on the Okavango, and habitat selection was therefore likely driven by seasonal prey availability. After translating resource selection into resistance maps, I found that seasonal permeability of the landscape to movement differed significantly based on the flood levels. During maximum flood, the lion population within the Okavango becomes fragmented - the population cores in the central, southern and western Delta decrease in size and become isolated from the rest of the Okavango Delta. During both seasons, lions avoided areas close to people, and as a result, connectivity from the Okavango moving outwards to the south and west was limited. Connectivity towards Chobe National Park to the east, however, remained intact. Therefore, restoring connectivity with neighbouring sub-populations to the south and to the west of the Okavango, and reducing anthropogenic pressure on lions in these regions during high flood phases, will help build resilience for the Okavango's lion population and should be considered a conservation priority.

Ultimately, the consequences of low and high flood scenarios for lions can serve as a proxy for protracted periods of 'dry' and 'wet' environmental conditions that could result from climate change or upstream water extraction. This study shows that both flood extremes, in the long-term, can be detrimental to the Okavango lion population. It also provides a framework for long-term monitoring of lions in this wetland to be able to detect population changes. The future of the Okavango lion population depends largely on compensating for impacts of climate change by minimizing upstream water offtake to maintain natural flood cycles and reducing other anthropogenic pressures. The results of this study may also provide insights into conservation challenges impacting big cat populations in wetlands elsewhere around the world.

DEDICATION

I dedicate this study to God, my Father, who instilled in me a love for lions. To my mom, dad and sister, who encouraged me to chase those lions, and to my husband Kyle, who chased them with me.

DECLARATION

“I hereby:

(a) grant the University free license to reproduce the above thesis in whole or in part, for the purpose of research;

(b) declare that:

(i) this thesis was carried out in accordance with the regulations of the University of Cape Town;

(ii) the data used in this thesis are original except where indicated by special reference in the text;

(iii) this thesis represents my own unaided work, both in conception and execution, apart from the normal guidance of my supervisor;

(iv) neither the substance or any part of this thesis has been submitted for a degree at this University or any other University”

Signed by candidate

Robynne Kotze

ACKNOWLEDGEMENTS

There are many people who deserve thanks for taking this journey with me. I would like to start with the Government of Botswana, and the Department of Wildlife and National Parks, who granted us access to the Delta and enabled us to reside in Botswana to complete this research. The Okavango has become home. Thank you to Christiaan and Hanlie Winterbach, who gave us a start in lion research and in the Okavango of all places, for this I will be forever grateful. Thank you &Beyond: Tony Adams, Jason King, Michelle Goushe and Riaan Venter for allowing us to work in your concessions and for the varied forms of support that came from the company throughout the years. Special mention goes to those who accepted us as friends and made us feel at home whenever we popped by, or gave us a meal or place to stay, or when needed access to a mechanic; Dave and Megan, Patrick, Grant and Dimari, Paolo and Seranne, Anja and Dean, KT, Skipper, Judy, Laetitia and many other camp staff that greeted us with a smile. To the late Cecil Riggs, ever present and ready to share stories. To Grant and Brent Reed, for welcoming us into Kwapa. To our trackers; Karate who was always smiling and ready to teach me Setswana, and to Solomon, who taught me animal, tracks, spent many, many nights in the bush, got stuck in many, many crossings and enjoyed watching lions as much as I do. Thank you to Dr Mark Bing, who spent many nights with us in the Delta and shared much advice and experience, and Dr Rob Jackson who was always ready to make a plan whatever the circumstances.

I would also like to thank our sponsors, Investec Property Division; Robin Magid and the late Sam Hackner for trusting us with your donations, and Glynn Burger for making the introductions. Thank you Glynn for helping us with a research vehicle when we needed it most, and to John Damant from Unispan for your long-term support. Thank you also to Mike Chase and Kelly Landen from Elephants Without Borders for your support with this work and with Kyle’s. Thank you also to CLAWS Conservancy, Andrew Stein and Florian Weise, for sharing your lion data, and to Carolyn Whitesell for sharing yours.

There are many, many friends to mention; those in the research community and Maun community; Kristina Kesch, Dominik Bauer, Steve and Robyn Stockhall, Caroline Rees, Carolyn Whitesell, Matt Rogan, Jess Isden, Leanne van der Weyde, Jane Horgan, Emily Bennitt, Michael Fitt, Simon Dures, Glyn Maude, Kai Collins, Beckie Garbett, Sven Borquin, Caron Botes, Megan Claase – thank you for all the encouragement, work conversations,

conservation conversations and PhD advice. Thank you Map Ives for talking to me about the Delta and the lions and for calling me Doctor before it came true. Thank you Crispin Sanderson for keeping our research vehicle on budget and running.

There are many who provided guidance during the analysis process, with special thanks to Matt Rogan and Genevieve Finerty for much back and forth and encouragement. Thank you Lara L. Sousa for your guidance and optimism and support, especially near to this work’s completion. A big thank you to my supervisors, Justin and Andy. Justin, thank you for making a place for me at ICWild and for helping me to make this work on my own time. Andy, thank you for giving me a chance to be part of WildCRU, and enabling me to do the work that saw this to completion.

To Brigitte, Zoe and Jillian, who have always cheered me on – thank you. Thank you to my family, the Burgers, for your never-ending support in all aspects of life. To mom and dad, I cannot describe how grateful I am for everything, your encouragement, wisdom and never-ending love is a rock to me, to Stacey for always believing in me and for being my best friend. To Kyle, for your friendship, partnership and unconditional love; for roughing it out in the bush with me and always being by my side and tolerating my need to always look for lions.

Table of Contents

Chapter 1

Introduction

Problem Statement

The Okavango Delta is one of the world's largest seasonal wetlands (McCarthy & Ellery, 1998) and forms what is believed to be part of one of the largest contiguous, free-ranging lion populations left on the African continent - spanning from the Okavango Delta westwards through the Linyanti and Chobe regions towards Hwange National Park in north-eastern Zimbabwe (Cushman et al., 2018). The last survey of the Okavango Delta estimated a lion population of approximately 1200 individuals (Winterbach et al., 1998). The Okavango region is thus an important stronghold for the species and may be one of the most important source populations for lions in the southern African region. However, the Okavango Delta is an extremely dynamic environment, the ecological functioning of which is largely affected by both long-term variation in flood extents driven by extrinsic climate cycles as well as significant inter- and intra-annual variation in the extent of the seasonal flood (Murray-Hudson et al., 2014). These flooding patterns affect all trophic levels, from the availability of suitable dry season grazing and herbivore abundance, to the distribution and abundance of large carnivores (Burger, 2020; Kotze et al., 2018, 2021).

Historical data on lion population demographics and prevailing flood patterns from the south-western Okavango Delta suggests that flooding has a significant influence on lion population demographics (Kotze et al., 2018, 2021). During periods of high flood, the decreasing availability of dry land, as well as declining availability of prey, exerts pressure on lion populations, which ultimately results in their local decline. Intraspecific competition for space increases, resulting in lower reproductive rates, lower cub survival and smaller pride sizes (Kotze et al., 2018, 2021). The effects of high flood levels on lion populations have also been observed anecdotally in other wetland systems, such as the Busanga floodplains in Kafue National Park, Zambia (Midlane, 2013). In addition to the cascading demographic responses to flooding patterns, a recent study on the genetic diversity of lion populations within northern Botswana has indicated that lions in the Okavango Delta are to a degree, genetically distinct from surrounding populations (Dures et al., 2019). This too, has been linked to flooding, which appears to act as an ecological barrier to gene flow in the region (Dures et al., 2020), where contrast between wetland and surrounding dryland conditions, and the adaptations to these wetland conditions, may discourage dispersal.

Across their current geographic distribution, lions face several threats resulting from increasing anthropogenic pressure. The top two threats to lion populations are retaliatory killing in response to livestock depredation and the reduction in prey base as a result of bushmeat harvesting. Populations that decline as a result are at increasing risk of extirpation, and loss of habitat caused by conversion of natural habitat to agricultural land further threatens population viability (Bauer et al., 2022; Lindsey et al., 2017a; Riggio et al., 2013). The current global lion population is estimated to be 20 000 individuals (Bauer et al., 2015). As numbers decline, it is vital that we prioritise the conservation of large, free-ranging populations living in ecologically functional natural areas (Bauer et al., 2015; Björkland, 2003; Riggio et al., 2013), particularly if these populations have the potential to be a source for other populations in the region. As a wetland system, the Okavango Delta itself faces additional threats such as increasing water offtake for human use as well as projected climate change (Beilfuss et al., 2010; Erwin, 2009; Keddy et al., 2009), the ecological consequences of which may influence all levels of the trophic chain (Murray-Hudson et al., 2006). Understanding how flooding patterns affect these apex predators is therefore vital for their conservation in the Okavango Delta and can potentially provide insights into big cat conservation in other wetland systems across the world (Cavalcanti & Gese, 2009; Jhala et al., 2019; Khan & Chivers, 2007).

Lion Ecology

Lions occupy a wide range of habitats, from savannah to desert to wetland, and historically covered the entire continent except for true forests and the Sahara Desert (Nowell and Jackson, 1996). The distribution of lions, and their densities, are determined proximately by biomass of preferred prey, and this in turn is influenced by broad climatic factors such as rainfall, soil type and temperature (Celesia et al., 2010; East, 1984; Packer et al., 2005). Lean season prey abundance often limits lion densities through their influence on demographic processes such as cub survival and reproductive rate (Bertram, 1975; Kotze et al., 2021; Schaller, 1972). In areas where prey is plentiful, such as in many of the fenced reserves in South Africa, lion densities can increase dramatically over a short period of time, and management interventions are often required (e.g., contraception and translocation) to prevent resource exhaustion and ensure genetic diversity where natural dispersal is not possible (Miller et al., 2015; Miller & Funston, 2014). However, in many wilderness areas, lion populations are well below their ecological carrying capacity due to anthropogenic pressures rather than ecological limitations (Everatt et al., 2019; Lindsey et al., 2017a; Robson et al., 2021).

Lions are the only social felids, and live in matrilineal, fission-fusion social units known as prides (Schaller, 1972). Pride sizes vary with ecological and social circumstances, ranging in size from 2 to 21 females, their dependent young and a coalition of pride males (Mosser & Packer, 2009). Male coalitions cooperate to defend pride females and territories and can range in size from 1 to 9 adult males (Bertram, 1975; Funston et al., 1998; Schaller, 1972). While in many cases these adult males are related, unrelated males may also choose to cooperate, and larger coalitions often have greater reproductive success (Bygott et al., 1979; Packer & Pusey, 1987). Pride males remain with the pride for an average of 2 – 4 years, after which they are typically replaced by younger or larger coalitions (Bygott et al., 1979) or disperse voluntarily in search of other mating opportunities. While pride members develop strong social bonds and share the same territory, they may split into smaller subgroups and use different areas of the pride’s territory (Schaller, 1972; van Orsdol et al., 1985; Van der Waal et al., 2009).

Adult females are synchronous breeders, and often give birth to cubs within a few months of one another (Bertram, 1975; Schaller, 1972). These adult females then cooperate to rear these cubs, and after an initial separation from the pride of approximately two weeks, will return to the pride and form a creche with cubs from other mothers in the group (Packer et al., 2001; Packer & Pusey, 1983). Communal raising of cubs involves allo-nursing as well as cooperating to hunt and provide food (Mosser & Packer, 2009; Pusey & Packer, 1994). Once cubs reach between 2 and 4 years of age, subadult females are recruited into the pride, but large cohorts may disperse to form their own prides, often settling in territories adjacent to their natal prides (Bertram, 1975; Packer & Pusey, 1987). Subadult males are ousted from the pride, an event mostly coinciding with takeovers by new males (Bertram, 1975). Subadult males then become nomadic and may remain at the fringe of their natal territory or move long distances until they are mature enough to take over a new pride (Elliot, 2013; Spong & Creel, 2001). During male takeovers, incoming males will try to kill any dependent cubs from previous males (Grinnell & McComb, 1996; Packer & Pusey, 1983; Schaller, 1972). This brings females back into estrous within two weeks, allowing the immigrants to mate sooner and so increase the probability that their own cubs will be raised to maturity within their tenure (Bertram, 1975; Packer et al., 1988; Packer & Pusey, 1983).

Prides are territorial, and members of the pride will cooperate to defend the territory against other prides (Packer et al., 2005; Schaller, 1972). The size of territories is dependent largely on ecological factors such as prey abundance, or the distribution of important prey resources such as water (Spong, 2002; Loveridge et al,. 2009; Valeix et al., 2010, 2012). Territory sizes may thus vary ten-fold between various habitats, from 15 km^2 in the Serengeti (Mosser, 2008), to over 4000 km^2 in the Kalahari Desert (Zehnder et al., 2018). While lions may use different areas within their territories seasonally, there is generally high site fidelity in home range use from one year to the next, and territories are inherited from the previous generation (Midlane, 2013; Schaller, 1972). Typically, in savannah environments, territories are exclusive, although neighbouring prides may show some degree of overlap (Mosser & Packer, 2009). In habitats where the distribution of prey is more unpredictable, and territoriality is costly, territories may overlap extensively (Kotze et al., 2018; Spong, 2002; Zehnder et al., 2018).

Lion Conservation Status

Globally, lion populations have declined significantly over the past 50 years and have disappeared from more than 80% of their former range (Ray et al., 2005). After being extirpated from Europe and Asia, except for a small remnant population of lions in the Gir Forest in India (Singh & Gibson, 2011), lions became extinct in north Africa in the last century, and their numbers have more than halved over the last two decades across the rest of the continent (Bauer et al., 2016; Nowell and Jackson, 1996). As a result of these declines, the status of the African lion on the IUCN Redlist has been 'Vulnerable' since 1996 (Bauer et al., 2008). Genetic analyses have indicated that the remaining African lions are split into two genetically distinct subspecies upon which conservation actions should be based (Bertola et al., 2011); central and west African lions (*Panthera leo leo*), and southern and east African lions (*Panthera leo melanochaita*). Central and west African lions have faced precipitous declines, and remaining populations are isolated and scattered across several protected areas (Curry et al. 2021; Henschel et al. 2014). West African lions are under severe threat of extinction, with estimates as low as between 400 and 450 individuals (Bauer et al., 2015; Henschel et al., 2014). Consequently, the conservation status of lions in central and West Africa have been upgraded by the International Union for Conservation of Nature (IUCN) to 'Critically Endangered' (Bauer et al., 2016). While eastern and southern Africa remain the stronghold for the species, all the unfenced populations in these regions are declining (Bauer et al., 2015). Many of the current population estimates and projections are based on best guesses or extrapolations from limited data, and there is a need to establish reliable, accurate and precise methods for counting lions, with appropriate measures of certainty, that can be repeated across vast areas of their range (Braczkowski et al., 2020; Dröge et al., 2020; Riggio et al., 2016).

Although a large proportion of Africa's lions currently reside in what are formally protected areas, the effectiveness of these protected areas is undermined by multiple threats (Lindsey et al., 2017a; Robson et al., 2021). Currently, lion numbers in more than one third of Africa's protected areas are at less than 50% of their potential (Lindsey et al., 2017a). Effectively protecting these areas alone may quadruple the current lion population (Lindsey et al., 2017; Packer et al., 2013), however, this will require considerable economic investment in addition to political stability essential for long term management plans to be effective (Packer et al., 2013; Robson et al., 2021). Some conservationists argue that fencing is largely effective in conserving lions (Packer et al., 2013), and while fenced lion populations in southern Africa are increasing, most unfenced populations in southern and eastern Africa are declining (Bauer et al. 2015; Robson et al., 2021). By acting as a barrier between lions and local communities, well-maintained fences play an important role in reducing negative interactions between humans, their livestock and lions (Ferguson & Hanks, 2010) and fenced reserves generally have lower budgetary requirements for effective conservation than large, unfenced swathes of land (Packer et al., 2013). However, fencing is not viable in many of Africa's vast protected areas, where it is difficult to extrapolate and project population trends with certainty (Riggio et al., 2016), and the negative ecosystem impacts of fencing such reserves (Bartlam-Brooks et al., 2011; Mbaiwa and Mbaiwa, 2006; Williamson and Williamson, 1984) may well outweigh any advantages for lions. Furthermore, most fenced reserves are small, and so conserve far fewer lions in relation to budget spent and require intensive management to keep lions at densities that will not result in local prey depletion or negatively affect competitors (see Creel et al., 2013). For many of these unfenced populations, it is thus more important to understand how conservation efforts are influenced by the local ecological and anthropogenic factors with efforts geared to mitigating the most adverse impacts of people on lions (Dickman et al., 2010; Hazzah et al., 2009).

Threats to lion populations

Agricultural Activities

With the human population in Africa projected to reach 4 billion by the end of the century (Gerland, 2014), maintaining the current status quo, or improving the prospects for lion conservation, will continue to be a challenge. Analyses of lion distribution in relation to human densities indicate that once human densities reach more than 25 people per square kilometre (Riggio et al., 2013; Woodroffe, 2000), the associated land conversion to accommodate activities such as agriculture will result in the loss of lions from these areas. Already, 75% of savannah habitat in sub-Saharan Africa - which would otherwise be classified as suitable for lion - has been converted for human use (Riggio et al., 2013). The concomitant increase in livestock with growing human populations has also resulted in a reduced natural prey base for lions as domestic livestock compete with wildlife for grazing resources both inside and outside protected areas (Ogutu et al., 2009; Tumenta et al., 2010).

Depredation of livestock by lions can have a significant economic impact on rural households, with the retaliatory killing and negative perceptions of lions being widely considered as the single largest threat to lion populations and their survival (Bauer et al.

2022; Woodroffe et al., 2005). Levels of negative interactions are particularly high along the edges of unfenced protected areas, where the likelihood of lions encountering people and domestic animals is highest (Cushman et al. 2018; Dickman, 2009; Patterson et al. 2004). Retaliatory killing of lions is not only a threat to the persistence of lion populations outside protected areas, but also within protected areas due to extensive 'edge' effects (Loveridge et al., 2007, 2010; Woodroffe & Ginsberg, 1998). While the removal of adult males from the population can lead to higher levels of infanticide (Loveridge et al., 2010), the removal of adult females from the population can significantly affect the long-term viability of prides on protected area boundaries (Van Vuuren et al., 2005). More recently, poison has been used to eliminate lions, which may not only contribute to their local decline, but may also result in the death of non-target species (Frank et al. ,2008; Loveridge et al., 2017; Ogada et al., 2014). Many current lion conservation projects are thus focused on cooperative efforts between conservationists, NGOs and local communities to reduce such impacts (Abade et al., 2014; Hazzah et al., 2009, 2014;, Sibanda et al., 2021; Western et al., 2019).

Loss of prey

For many rural households, particularly for those which border national parks, bushmeat is the main source of protein; it is easily accessible, harvesting has relatively low risk and the process is low-cost (Lindsey et al. 2013a; Loveridge et al., 2020; Rogan et al. 2017). Due to increasing demand and lack of alternative livelihoods, the bushmeat trade is also becoming more financially appealing through commercial sale (Rogan et al., 2017). Illegal bushmeat harvesting affects lions indirectly by significantly reducing the availability of natural prey, and, as many aspects of lion population demographics are often directly linked to resource abundance, this contributes significantly to the low number of lions even within Africa's protected areas (Lindsey et al., 2017a; Robson et al., 2021, Vinks et al., 2020). In addition, wire snares set by poachers to target prey species often kill lions as by-catch, further contributing to their decline (Becker et al., 2013; Everatt et al., 2015; Loveridge et al., 2020).

Poaching for parts and trophy hunting

Recently, and often in conjunction with illegal bushmeat harvesting and retaliatory killing, the poaching of lions for their body parts has emerged as a new threat to wild lion populations (Everatt et al., 2019b; Williams et al., 2017). Lion bones, claws and teeth are increasingly in demand in south-east Asia, where they are being used for traditional medicine, either independently or as a substitute for tiger products (Coals et al., 2020; Williams et al., 2015). While many of these products are sourced legally from the captive-bred lion industry in South Africa (Williams et al., 2015), there is increasing evidence that demand is creating opportunity for poaching in wild lion populations (see Everatt et al., 2019b; Williams et al., 2017). Indiscriminate poaching can easily accelerate the loss of lions in protected areas (Everatt et al., 2019b).

Lastly, while well-regulated trophy hunting has been advocated as a useful conservation tool, unregulated trophy hunting and excessive offtake have undermined the viability of hunting as a means of effectively conserving lion populations (Lindsey et al., 2013b; Packer et al. 2009). Unregulated hunting across Africa has had deleterious effects on populations in designated hunting areas, and in cases where these areas border national parks and reserves, significant edge effects on protected populations (Davidson et al., 2011; Kiffner et al., 2009; Loveridge et al., 2007). Hunting of young animals and excessive offtake of males causes considerable disruption to local prides, resulting in increased levels of infanticide and low recruitment and ultimately resulting in local population decline (Kiffner et al., 2009; Loveridge et al., 2007). These effects are particularly detrimental in populations which are already decreasing (Creel et al., 2016). Unless strict regulations on ages of trophies are upheld, and quotas are set and maintained at sustainable levels of offtake, trophy hunting is likely to continue to contribute to the decline of lions in both fenced and unfenced populations (Becker et al., 2013; Loveridge et al., 2016; Rosenblatt et al., 2014).

Habitat Fragmentation

Of more recent concern is the fragmentation of lion habitat, and the increasing isolation of protected populations (Bauer et al., 2022; Curry et al., 2021). Small, isolated populations are vulnerable to inbreeding and other stochastic events such as drought or disease (Gilbert et al. 1998; Taylor et al., 1993). For lions, a population size of 500 individuals is considered viable provided there are no limits to dispersal (Björkland, 2003). As most populations within existing parks are well below this threshold, natural or assisted immigration and emigration between populations is necessary to bolster genetic diversity and buffer populations against extinction. In this way, if local extinctions do occur, natural or assisted re-colonization is possible (LaRue and Nielsen, 2008). Consequently, there is a need to develop corridors for movement of surplus and dispersing individuals between sub-populations (Cushman et al., 2013, 2016; Fahrig, 2003) to maintain genetically robust sub-populations (Curry et al., 2021; Dures. et al., 2019).

The need to connect fragmented patches of suitable habitat for wildlife has been recognized in the establishment of several Transfrontier Conservation Areas (TFCAs). These areas extend beyond protected area boundaries to incorporate multiple land-use areas such as communal land, forest reserve, communal conservancies, wildlife management areas used for consumptive or non-consumptive purposes and private land, with the aim of restoring meta-population processes for large mammals and encouraging transboundary tourism (Hanks, 2003). One of the largest trans-frontier initiatives is the Kavango-Zambezi TFCA, which spans five southern-African countries including Botswana, Zambia, Angola, Namibia and Zimbabwe. This area hosts a considerable proportion of Africa's large carnivores, including almost 25% of the remaining population of the endangered wild dog (*Lycaon pictus;* Woodroffe ,2013), as well as an estimated 15% of Africa's lions (*Panthera leo;* KAZA, 2018). This area is of thus of great significance to the conservation of lions in southern Africa.

Lions of the Okavango Delta: Status, Threats and Ecology

The country of Botswana has designated almost 38% of its land area to wildlife, including national parks, reserves, sanctuaries and wildlife management areas (Winterbach et al., 2015). In a recent analysis of the conservation performance of countries worldwide, Botswana was recognized as the top performing country for the conservation of large herbivores and carnivores (Lindsey et al., 2017b). Wildlife tourism is the second largest contributor to the county's Gross Domestic Product (GDP) and in 2017, contributed 11.6% to the country's GDP, bringing in just over 2 billion US dollars, and accounting for 2.6% of employment in the country (World Travel and Tourism Council, 2017). This positive return on the conservation of vast tracts of land means that northern Botswana has one of the largest lion conservation units in Africa, stretching from the Okavango Delta through the Chobe and Linyanti systems and across to Hwange National Park in north-eastern Zimbabwe

(Cushman et al., 2016, 2018). This lion conservation unit is believed to contain up to 2000 lions, with half of these lions occurring in the Okavango Delta (Riggio et al. 2013; Bauer et al., 2015). However, population projections based on current information suggests that the Okavango Delta population is likely to decline by one third in the next 50 years (Bauer et al., 2015).

The Okavango Delta forms one of the world's largest inland freshwater deltas (Gumbricht et al., 2004; McCarthy & Ellery, 1998). The annual flood pulse produced in the Okavango Delta originates from seasonal rainfall in Angola, which falls between October and April, and then moves down through the Okavango River into Botswana (McCarthy et al., 2000; Ramberg et al., 2006). The front of the pulse arrives at the panhandle of the Okavango Delta around April each year and may take several months to reach the distal end of the system (Gumbricht et al., 2004; Murray-Hudson et al., 2014). Flooding in the Okavango Delta varies inter-annually, and flood levels are determined not only by rainfall patterns in the catchment area in Angola, but by levels of local rainfall and the extent of the previous flood (Murray-Hudson et al., 2014, 2015). This seasonal flood pulse is the main driver of ecological change, from altering the vegetation composition in seasonal floodplains on which herbivores depend, to determining the amount of dry land available to support populations of large carnivores (Burger, 2020; Kotze et al. 2021; Murray-Hudson et al., 2014). In addition to these inter-annual changes, flooding patterns also follow a multi-decadal pattern, alternating between phases of low and high floods over a 30 to 40-year period (Mazvimavi & Wolski, 2006; McCarthy et al., 2000; Murray-Hudson et al., 2014).

Aerial surveys of the Okavango Delta in 2011, revealed significant declines in herbivore numbers, particularly in populations of grazing herbivores such as wildebeest (*Connochaetes taurinus*) and tsessebe (*Damaliscus lunatus;* Chase & Landen, 2011), which fall within the lion's preferred prey range (Hayward et al., 2007). More recent studies on the ecology of grazing herbivores within the Okavango suggest that these declines may be related to the decadal cyclical phases of high flood (Bennitt et al., 2014, 2019; Burger, 2020). Increased flooding regimes over the past decade have resulted in the conversion of seasonal floodplain grasslands to sedge communities, which are less favorable for grazing species (Burger, 2020). Furthermore, there is growing concern that the local bushmeat trade, particularly on the western edge of the Okavango Delta, has significantly added to the decline of these herbivores, and that current rates of offtake may be unsustainable in the long-term (Rogan et al., 2017).

Historical data on lion population demographics from the south-western Okavango, revealed that changes in lion population are driven by long-term flood patterns; dry periods in the Okavango Delta are conducive to population growth, while extended wet periods lead to population decline (Kotze et al., 2018, 2021). During the last decadal dry cycle, prey densities were relatively high, resulting in high reproductive rates, and consequently, high densities of lions (Kotze et al., 2021). During wetter periods, however, large areas of previously accessible floodplains become inundated for longer periods, and as the amount of available dry land decreases, lions come into increasing competition for space, both within and between prides (Kotze et al., 2018, 2021). This leads to lower reproductive rates, and as prey availability decreases, this also leads to lower cub survival and ultimately, population declines (Kotze et al., 2021). As seasonal floods cause significant constraints in terms of access and research, and due to its large spatial extent, the current lion population status for large areas of the Okavango Delta, is unknown.

As changes in vegetation and habitat are closely linked to hydrology in wetland systems, it is important that we understand the consequences of these changes for resident fauna and flora, particularly in the face of impending climate change (Milzow et al., 2010). Across southern Africa, climate change models predict a 10% decrease in average annual rainfall, which in semi-arid areas such as Botswana, may reduce the availability of surface water by between 30 and 50% (Batisani & Yarnal, 2010; De Wit & Stankiwiecz, 2006). Hydrological modelling showing changes in the Okavango Delta under projected drying scenarios predict a decrease in seasonal floodplains and concomitant increase in dryland areas (Murray-Hudson et al., 2006; Milzow et al. 2010). This would significantly decrease the carrying capacity for grazing herbivores, and similarly negatively affect the capacity to support large carnivores such as lions (Murray-Hudson et al., 2006). Furthermore, climate change may increase pressure for water extraction from the Okavango Delta both locally for dryland agriculture (Batisani & Yarnal 2010) and upstream for damming, agriculture or hydropower schemes (Andersson et al., 2006), with similar negative consequences for biodiversity (Andersson et al. 2006, Batisani & Yarnal 2010). Understanding how lion populations respond to changes in hydrology is thus important for their long-term conservation in this system.

Recent analyses of lion genetic diversity in northern Botswana, have indicated that there is a degree of genetic isolation between lion populations in the Okavango are and the Chobe-Linyanti system to the north-east (Dures et al., 2020), as well as to other core populations such as the Central Kalahari Game Reserve (CKGR) to the south. Surprisingly, the Okavango population is more closely linked, genetically, to those in Etosha, Namibia, which historically, was also a seasonal wetland (Moore et al., 2015). Both Moore et al. (2015) and Dures et al. (2020) studies suggest habitat specialization as the main reason for this isolation, and that the seasonal flooding may act as an ecological barrier to gene flow from dryland populations. Understanding the differences in adaptation to these seasonal wetlands may thus be integral to ensuring that the genetic isolation does not lead to inbreeding and low genetic diversity within the Okavango Delta itself and may also help explain the genetic patterns observed throughout the landscape. This information is not only important in the context of the Okavango Delta, but in providing information for the creation of corridors for dispersal in the KAZA region (Cushman et al., 2018).

Thesis Outline

Effective conservation measures for species in a particular ecosystem require understanding the complex temporal and spatial landscape patterns that underpin population processes like distribution, abundance and habitat preferences (Cushman, 2006). Understanding species-environment relationships at different spatial scales is often done as a hierarchical process, for example, by investigating species distributions (first-order), the selection of home ranges within a landscape (second-order) and selection of resources within the home range (third-order; Johnson, 1980). However, these ecological relationships can also vary over time – both seasonally, and, particularly in the case of climate change, on longer time scales – a factor which is often overlooked in ecological studies (Osipova et al., 2019; Kazsta et al., 2020; Uroy et al., 2021). Drawing conclusions from short term or limited spatial scales, which represent only a fraction of broader ecological and population processes, can lead to erroneous inferences in species-habitat relationships, which can in turn compromise effective conservation action (Farris et al., 2017; Osipova et al., 2019). Accounting for spatial and temporal changes in species-covariate relationships is therefore important for fully understanding a species' relationship with its environment. As a seasonally inundated wetland, the flood pulse is the primary driver of change in the Okavango Delta and causes significant temporal and spatial shifts in resource availability. The main aims of this study were to i) investigate a novel method for surveying lions in a large, open and highly heterogenous environment and ii) further our understanding of the ecological and anthropogenic drivers of lion density, home range size and resource selection in the Okavango Delta in order to better inform conservation of lions in the landscape. This study also uses the Okavango Delta and changes induced by seasonal flooding as a case study to highlight the importance of accounting for spatial and temporal fluctuations in resources in conservation planning.

Due to the challenge of providing precise estimates for determining lion population sizes in large, open systems (Braczkowski et al., 2020; Dröge et al., 2020; Riggio et al., 2016), in **Chapter 2** I test the efficacy of camera trapping as a means of estimating lion density in the south-western Okavango Delta. The goal was to obtain repeated captures of known individual lions, thus allowing for an estimate of lion density using spatially explicit capture-recapture methods. I also link the distribution of lions across the landscape to various environmental and anthropogenic covariates to determine which factors are most important in driving the spatial distribution of lions across a part of the Okavango characterised by significant inter-annual variation in flooding.

As densities are intrinsically linked to home range sizes, in **Chapter 3,** I examine the influence of maximum and minimum flood conditions on lion home range size and examine how temporal changes in landscape structure and configuration, habitat configuration and prey availability influence resource acquisition strategies of males and females. I then discuss the conservation implications of these correlations for lions in context of long-term flood patterns or predicted climate change.

In **Chapter 4**, I examine resource selection within the home range, and determine how this varies with temporal changes in flooding. I develop resource selection functions for lions at minimum and maximum flood and use these to develop resistance surfaces for lions within the Okavango and its immediate surrounds. I then identify core areas and key movement corridors within and around the Okavango and examine how these differ between maximum and minimum flood conditions. I use the results to discuss potential conservation interventions to ensure the resilience of the lion population in the future.

In **Chapter 5**, I discuss the study in the context of our current knowledge on large carnivore ecology in wetlands, summarize observations, outline the study's limitations, make conservation recommendations for lions in the Okavango Delta in the face of threats like climate change and anthropogenic water offtake and identify future areas of study.

References

Abade, L., Macdonald, D. W., & Dickman, A. J. (2014). Assessing the relative importance of landscape and husbandry factors in determining large carnivore depredation risk in Tanzania's Ruaha landscape. *Biological Conservation*, *180*, 241-248.

Andersson, L., Wilk, J., Todd, M. C., Hughes, D. A., Earle, A., Kniveton, D., & Savenije, H. H. (2006). Impact of climate change and development scenarios on flow patterns in the Okavango River. *Journal of Hydrology*, 331, 43-57.

Bartlam-Brooks, H. L. A., Bonyongo, M. C., & Harris, S. (2011). Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra *Equus burchelli* migration in Botswana. *Oryx*, 45, 210-216.

Batisani, N. & Yarnal, B. (2010) Rainfall variability and trends in semi-arid Botswana: Implications for climate change adaptation policy. *Applied Geography,* 30, 483-489.

Bauer, H., et al. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112, 14894-14899.

Bauer, H., Nowell, K., & Packer, C., (2008) *Panthera leo*. *IUCN Red List of Threatened Species, Version 2010.4,* 2011, from www.iucnredlist.org

Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S. K., Sillero-Zubiri, C., Hunter, L., Linsdsey, P., & Macdonald, D. W. (2022). Threat analysis for more effective lion conservation. *Oryx*, 56, 108-115.

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. (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 29 September 2019.

Becker, M., McRobb, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J., & Kakumbi, C. (2013). Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation*, 158, 26-36.

Becker, M. S., Watson, F. G., Droge, E., Leigh, K., Carlson, R. S., & Carlson, A. A. (2013). Estimating past and future male loss in three Zambian lion populations. *The Journal of Wildlife Management*, 77, 128-142.

Beilfuss, R. D., Bento, C. M., Haldane, M., & Ribaue, M. (2010). Status and distribution of large herbivores in the Marromeu Complex of the Zambezi Delta, Mozambique. *Unpublished report. WWF, Maputo, Mozambique.*

Bennitt, E., Bonyongo, M. C., & Harris, S. (2014). Habitat selection by African buffalo (*Syncerus caffer*) in response to landscape-level fluctuations in water availability on two temporal scales. *PloS ONE*, 9, 1–14.

Bennitt, E., Hubel, T. Y., Bartlam-Brooks, H. L., & Wilson, A. M. (2019). Possible causes of divergent population trends in sympatric African herbivores. *PloS ONE,* 14, e0213720.

Bertola, L. D. et al. (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.B. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology*, London, 177, 463–482.

Björkland, M. (2003). The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics,* 4, 515-523.

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., Biggs, D & Allan, J. R. (2020). Restoring Africa's Lions: Start with good counts. *Frontiers in Ecology and Evolution*, 8, 138.

Burger, K. (2020). *The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta.* PhD Thesis. University of the Witwatersrand.

Bygott, J. D., Bertram, B. C., & Hanby, J. P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature*, 282, 839.

Cavalcanti, S. M. C., & Gese, E. M. (2009). Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 90, 935–945.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K., & Gnoske, T.P. (2009). Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology,* 48, 58-71.

Coe, M. J., Cumming, D. H., & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22, 341-354.

Coals, P., Moorhouse, T. P., D'Cruze, N. C., Macdonald, D. W., & Loveridge, A. J. (2020). Preferences for lion and tiger bone wines amongst the urban public in China and Vietnam. *Journal for Nature Conservation,* 57, 125874.

Chase, M. & Landen, K. (2011). A view from the top. *Africa Geographic,* 19, 38-47.

Creel, S., Becker, M. S., Durant, S. M., M'soka, J., Matandiko, W., Dickman, A. J., ... & Zimmermann, A. (2013). Conserving large populations of lions–the argument for fences has holes*. Ecology Letters*, 16, 1413-e3.

Creel, S., M'soka, J., Dröge, E., Rosenblatt, E., Becker, M. S., Matandiko, W., & Simpamba, T. (2016). Assessing the sustainability of African lion trophy hunting, with recommendations for policy. *Ecological Applications*, 26, 2347-2357.

Curry, C. J., Davis, B. W., Bertola, L. D., White, P. A., Murphy, W. J., & Derr, J. N. (2021). Spatiotemporal genetic diversity of lions reveals the influence of habitat fragmentation across Africa. *Molecular Biology and Evolution*, 38, 48–57.

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., & Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS ONE*, 13, e0196213.

Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological conservation*, 2, 231-240.

Cushman, S. A., Elliot, N. B., Macdonald, D. W & Loveridge, A. J. (2016). A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecology,* 31, 1337-1353.

Cushman, S.A., McRae, B., Adriaensen, F., Beier, P., Shirley, M. & Zeller, K. (2013) Biological corridors and connectivity. In: *Key Topics in Conservation Biology 2. 1st Ed*. (Ed by D.W. MacDonald and K.J. Willis). John Wiley & Sons. United Kingdom.

Davidson, Z., Valeix, M., Loveridge, A. J., Madzikanda, H., & Macdonald, D. W. (2011). Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation*, 144, 114-121.

De Wit, M. & Stankiewicz, J. (2006). Changes in surface water supply across Africa with predicted climate change. *Science,* 311, 1917-1921.

Dickman, A. J. (2009). *Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania.* PhD Thesis. University of London.

Dickman, A. J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal conservation*, 13, 458-466.

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, 10, 3276-3292.

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion-conservation stronghold. *Diversity and Distributions*, 25, 870–879.

Dures, S. G., Carbone, C., Savolainen, V., Maude, G., & Gottelli, D. (2020). Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation,* 23, 502-515.

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, 22, 245–270.

Elliot, N. B. (2013). *The ecology of dispersal in lions*. PhD Thesis, University of Oxford.

Erwin, K. L. (2009). Wetlands and global climate change: The role of wetland restoration in a changing world. *Wetlands Ecology and Management*, 17, 71–84.

Everatt, K. T., Andresen, L. & Somers, M. J. (2015). The influence of prey, pastoralism and poaching on the hierarchical use of habitat by an apex predator. *African Journal of Wildlife Research,* 45, 187-196.

Everatt, K. T., Moore, J. F., & Kerley, G. I. H. (2019). Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. *Global Ecology and Conservation*, 20, e00758.

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

Farris, Z. J., Gerber, B. D., Valenta, K., Rafaliarison, R., Razafimahaimodison, J. C., Larney, E., Rajonarivelo, T., Randriana, Z., Write, P. C., & Chapman, C. A. (2017). Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. *Biological Conservation*, 210, 116-124.

Ferguson, K., & Hanks, J. (2010). Fencing impacts: A review of the environmental, social and economic impacts of game and veterinary fencing in Africa with particular reference to the Great Limpopo and Kavango-Zambezi Transfrontier Conservation Areas. Mammal Research Institute, Pretoria. *Available at: www. wcs-ahead. org/gltfca_grants/grants. html*.

Frank, L., Hemson, G., Kushnir, H., Packer, C., & Maclennan, S. (2008). Lions, conflict and conservation. *Management and conservation of large carnivores in West and Central Africa*, 81.

Funston, P. J., Mills, M. G. L., Biggs, H. C., & Richardson, P. R. K. (1998). Hunting by male lions: Ecological influences and socioecological implications. *Animal Behaviour*, 56, 1333–1345.

Gerland, P., et al. (2014). World population stabilization unlikely this century. *Science*, 346, 234-237.

Gilbert, G., Gonzalez, A. & Evans-Freke, I. (1998). Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London, Series B,* 265, 577-582.

Grinnell, J., & McComb, K. (1996). Maternal grouping as a defense against infanticide by males: Evidence from field playback experiments on African lions. *Behavioral Ecology*, 7, 55–59.

Gumbricht, T.P., Wolski, P.F., & McCarthy, T.S. (2004). Forecasting the spatial extent of the annual flood in the Okavango Delta, Botswana. *Journal of Hydrology,* 290, 178-191.

Hanks, J. (2003) Transfrontier Conservation Areas (TFCAs) in southern Africa: their role in conserving biodiversity, socioeconomic development and promoting a culture of peace. *Journal of Sustainable Forestry,* 17, 127-148.

Hayward, M. W., O'Brien, J. & Kerley, G. I. H. (2007). Carrying capacity of large African predators: predictions and tests. *Biological Conservation*, 139, 219-229.

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

Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C. T., Mwebi, O., Kearney, F., & Frank, L. (2014). Efficacy of two lion conservation programs in Maasailand, Kenya. *Conservation Biology*, 28, 851-860.

Henschel, P. et al. (2014). The lion in West Africa is critically endangered. *PloS ONE*, 9, e83500.

Jhala, Y., Qureshi, Q., & Nayak AK. (2019). Status of tigers, co-predators and prey in India in 2018. *National Tiger Conservation Authority, Government of India, New Dehli and Wildlife Institute of India, Dehradun.*

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.

Kaszta, Ż., Cushman, S. A., & Macdonald, D. W. (2020). Prioritizing habitat core areas and corridors for a large carnivore across its range. *Animal Conservation*, 23, 607–616.

KAZA (2018). The Kavango Zambezi Transfrontier Conservation Area Carnivore Conservation Strategy*. KAZA TFCA Secretariat, Hwange, Zimbabwe.*

Keddy, P. A., Fraser, L. H., Solomeshch, A. I., Junk, W. J., Campbell, D. R., Arroyo, M. T. K., & Alho, C. J. R. (2009). Wet and Wonderful: The World's Largest Wetlands Are Conservation Priorities. *BioScience*, 59, 39–51.

Khan, M. M. H., & Chivers, D. J. (2007). Habitat preferences of tigers *Panthera tigris* in the Sundarbans East Wildlife Sanctuary, Bangladesh, and management recommendations. *Oryx*, 41, 463–468.

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? *Oryx* 43, 52-59.

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E. K., & Marshal, J. P. (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.

Kotze, R., Marshal, J. P., Winterbach, C. W., Winterbach, H. E. K., & Keith, M. (2021). Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment. *African Journal of Ecology*, 59, 63–73.

LaRue, M.A. & Nielsen, C.K. (2008). Modelling potential dispersal corridors for cougars in Midwestern North America using least-cost path methods. *Ecological Modelling,* 212, 372-381.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A. E., Kasiki, S., Loveridge, A., Macdonald, D. W., Mandisodza, R., Mgoola, W., Miller, S. M., Nazerali, S., Siege, L., Uiseb, K., & Hunter, L. T. B. (2017a). The performance of African protected areas for lions and their prey. *Biological Conservation,* 209, 137-149.

Lindsey, P. A., Chapron, G., Petracca, L. S., Burnham, D., Hayward, M. W., Henschel, P., Hinks, A. E., Garnett, S. T., Macdonald, D. W., Macdonald, E. A., Ripple, W. J., Zander, K., & Dickman, A. (2017). Relative efforts of countries to conserve world's megafauna. *Global Ecology and Conservation*, 10, 243-252.

Lindsey, et al. (2013a). The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation*, 160, 80-96.

Lindsey, P. A., Balme, G. A., Funston, P., Henschel, P., Hunter, L., Madzikanda, H., Midlane, N., & Nyirenda, V. (2013b). The trophy hunting of African lions: scale, current management practices and factors undermining sustainability. *PloS ONE*, 9, e73808.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (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.

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). African lions on the edge: reserve boundaries as “attractive sinks”: In D. W. Macdonald & A. J. Loveridge (Eds.), *Biology and Conservation of Wild Felids* (p. 183). Oxford University Press.

Loveridge, A. J., Searle, A. W., Murindagomo, F., & Macdonald, D. W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134, 548-558.

Loveridge, A. J., Sousa, L. L., Seymour-Smith, J., Hunt, J., Coals, P., O'Donnell, H., Lindsey, P. A., Mandisodza-Chikerema, R., & Macdonald, D. W. (2020). Evaluating the spatial intensity and demographic impacts of wire-snare bushmeat poaching on large carnivores. *Biological Conservation*, 244, 108504.

Loveridge, A. J., Valeix, M., Chapron, G., Davidson, Z., Mtare, G., & Macdonald, D. W. (2016). Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. *Biological Conservation*, 204, 247-254.

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, 54, 815-825.

Mazvimavi, D., & Wolski, P. (2006). Long-term variations of annual flows of the Okavango and Zambezi Rivers. *Physics and Chemistry of the Earth, Parts A/B/C,* 31, 944-951.

Mbaiwa, J. E., & Mbaiwa, O. I. (2006). The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. http://hdl.handle.net/10311/28

McCarthy, T.S. & Ellery, W.N. (1998). The Okavango Delta. *Transactions of the Royal Society of South Africa,* 53, 157-182.

McCarthy, T. S., Cooper, G. R., Tyson, P. D., & Ellery, W. N. (2000). Seasonal flooding in the Okavango Delta, Botswana-recent history and future prospects. *South African Journal of Science*, 96, 25-33.

Midlane, N. (2013). *The conservation status and dynamics of a protected African lion Panthera leo population in Kafue National Park, Zambia*. PhD Thesis. University of Cape Town.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: a management dilemma. *South African Journal of Wildlife Research*, 44, 43-55.

Miller, S. M., Tambling, C. J., & Funston, P. J. (2015). GrowLS: Lion (*Panthera leo*) population growth simulation for small reserve management planning. *African Journal of Wildlife Research*, 45, 169.

Milzow, C., Burg, V., & Kinzelbach, W. (2010). Estimating future ecoregion distributions within the Okavango Delta Wetlands based on hydrological simulations and future climate and development scenarios. *Journal of Hydrology*, 381, 89-100.

Moore, A. E., Cotterill, F. P. D., Winterbach, C. W. W., Winterbach, H. E. K., Antunes, A., & O'Brien, S. J. (2015). Genetic evidence for contrasting wetland and savannah habitat specializations in different populations of lions. *Journal of Heredity,* 107, 101-103.

Mosser, A. (2008). *Group territoriality of the African lion: behavioural adaptation in a heterogeneous landscape*. PhD Thesis, University of Minnesota.

Mosser, A. & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour,* 78, 359-370.

Murray-Hudson, M., Wolski, P., Murray-Hudson, F., Brown, M. T. & Kashe, K. (2014). Disaggregating hydroperiod: components of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands,* 34, 927-942.

Murray-Hudson, M., Wolski, P., Cassidy, L., Brown, M. T., Thito, K., Kashe, K., & Mosimanyana, E. (2015). Remote Sensing-derived hydroperiod as a predictor of floodplain vegetation composition. *Wetlands Ecology and Management*, 23, 603–616.

Murray-Hudson, M., Wolski, P. & Ringrose, S. (2006). Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. *Journal of Hydrology,* 331, 73-84.

Nowell, K., & Jackson, P. (Eds.). (1996). *Wild cats: status survey and conservation action plan* (Vol. 382). Gland, IUCN.

Ogada, D. L. (2014). The power of poison: pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences*, 1322, 1-20.

Ogutu, J. O., Piepho, H.-P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara-Serengeti ungulates in relation to land use changes. *Journal of Zoology*, 278, 1–14.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. *Animal Conservation*, 22, 35–48.

Packer, C., & Pusey, A. E. (1983). Adaptations of female lions to infanticide by incoming males. *The American Naturalist*, 121, 716-728.

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science*, 293, 690–693.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J., & Mulder, M. B. (1988). Reproductive success of lions. In *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed.) T. H. Clutton-Brock (pp. 363–383). University of Chicago Press.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., Zander, K. K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C. M., Begg, K. S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A. C., … Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters*, 16, 635–641.

Packer C., & Pusey, A. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, 101, 275-310.

Packer, C., Kosmala, M., Cooley, H. S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L., & Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *PloS ONE*, 4, e5941.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, W., Mduma, S., & Sinclair, A. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science,* 436, 927-928.

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

Pennycuick, C.J. & Rudnai, J. (1970). A method of identifying individual lions *Panther leo* with an analysis of the reliability of identification. *Journal of Zoology, London,* 160, 497-508.

Pusey, A.E. & Packer, C. (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behavioural Ecology,* 5, 362-374.

Ray, J. C., Hunter, L., & Zigouris, J. (2005). *Setting conservation and research priorities for larger African carnivores* (Vol. 24, pp. 1-203). New York: Wildlife Conservation Society.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Silva, J., Van As, J. & Vanderpost, C. (2006). Species diversity in the Okavango Delta, Botswana. *Aquatic* Sciences, 68, 310-337.

Riggio, J., Caro, T., Dollar, L., Durant, S. M., Jacobson, A. P., Kiffner, C., Pimm, S. L. & van Aarde, R. J. (2016). Lion populations may be declining in Africa but not as Bauer et al. suggest. *Proceedings of the National Academy of Sciences*, 113, E107-E108.

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

Robson, A., Trimble, M., Bauer, D., Loveridge, A., Thomson, P., Western, G., & Lindsey, P. (2021). Over 80% of Africa's savannah conservation land is failing or deteriorating according to lions as an indicator species. *Conservation Letters*, e12844.

Rogan, M. S., Lindsey, P. A., Tambling, C. J., Golabek, K. A., Chase, M. J., Collins, K., & McNutt, J. W. (2017). Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, 210, 233-242.

Rosenblatt, E., Becker, M. S., Creel, S., Droge, E., Mweetwa, T., Schuette, P. A., Watson, F., Merkle, J., & Mwape, H. (2014). Detecting declines of apex carnivores and evaluating their causes: an example with Zambian lions. *Biological conservation*, 180, 176-186.

Schaller, G. B. (1972). *The Serengeti lion: a study of predator prey relations*. Chicago University Press. Chicago, USA.

Singh, H. S., & Gibson, L. (2011). A conservation success story in the otherwise dire megafauna extinction crisis: the Asiatic lion (*Panthera leo persica*) of Gir forest. *Biological Conservation*, 144, 1753-1757.

Sibanda, L., Johnson, P. J., van der Meer, E., Hughes, C., Dlodlo, B., Mathe, L. J., Hunt, J.E., Parry, R. H., Macdonald, D. W., & Loveridge, A. J. (2021). Effectiveness of community-based livestock protection strategies: a case study of human–lion conflict mitigation. *Oryx*, 1-9

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.

Spong, G., & Creel, S. (2001). Deriving dispersal distances from genetic data. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 2571-2574.

Taylor, P.D., Fahrig, L., Henein, K. & Gray, M. (1993). Connectivity is a vital element of landscape structure. *Oikos,* 68, 571-573.

Tumenta, P. N., Kok, J. S., Van Rijssel, J. C., Buij, R., Croes, B. M., Funston, P. J., De Iongh, H. H., & Udo de Haes, H. A. (2010). Threat of rapid extermination of the lion (*Panthera leo leo*) in Waza National Park, Northern Cameroon. *African Journal of Ecology*, 4, 888-894.

Uroy, L., Alignier, A., Mony, C., Foltête, J. C., & Ernoult, A. (2021). How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review. *Landscape Ecology*, 36, 2487–2504.

Voeten, M. M., & Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, 120, 287–294.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337-351.

Valeix, M., Loveridge, A. J., & Macdonald, D. W. (2012). Influence of prey dispersion on territory and group size of African lions: A test of the resource dispersion hypothesis. *Ecology*, 93, 2490–2496.

Van der Waal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, 77, 949-954.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985). Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology, London,* 206, 97–112.

Van Vuuren, J., Hermann, E., & Funston, P. J. (2005) Lions in the Kgalagadi Transfrontier Park: modelling the effect for human-caused mortality. *International Transactions in Operational Research* 12, 145-171.

Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., Chifunte, C., Midlane, N. & Simukonda, C.

(2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications*, 31, e02298.

Western, G., Macdonald, D. W., Loveridge, A. J., & Dickman, A. J. (2019). Creating landscapes of coexistence. *Conservation & Society*, 17, 204-217.

Williams, V. L., Loveridge, A. J., Newton, D. J., & Macdonald, D. W. (2017). Questionnaire survey of the pan-African trade in lion body parts. *PloS ONE*, 12, e0187060.

Williams, V. L., Newton, D. J., Loveridge, A. J., & Macdonald, D. W. (2015). Bones of contention: an assessment of the South African trade in African lion *Panthera leo* bones and other body parts. *TRAFFIC, Cambridge, UK & WildCRU, Oxford, UK*.

Williamson, D., & Williamson, J. (1984). Botswana's fences and the depletion of Kalahari wildlife. *Oryx*, 18, 218-222.

Winterbach, C. W., Winterbach, H., Rutina, L., & Kat, P. W. (1998) Results of the coordinated dry season lion survey for the Okavango Delta, 1998. *Tau Constultants, Unpublished report. Maun, Botswana.*

Winterbach, H. E., Winterbach, C. W., Boast, L. K., Klein, R., & Somers, M. J. (2015). Relative availability of natural prey versus livestock predicts landscape suitability for cheetahs *Acinonyx jubatus* in Botswana. *PeerJ*, 3, e1033.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. In: *Animal Conservation forum* (Vol.3 pp. 165-173). Cambridge University Press.

Woodroffe, R. (2013) Biology and Conservation of African Wild Dogs. In*: Conservation of the African Wild Dog (Lycaon pictus) across the KAZA TFCA Landscape. Proceedings of a Symposium on the African Wild Dog.* (Ed.) R. Taylor (pp. 7-16). WWF in Namibia. Windhoek, Namibia.

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280, 2126-2128.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds.) (2005). *People and wildlife: conflict or coexistence?* Cambridge University Press. Cambridge.

World Travel and Tourism Council (2017). Travel & Tourism Economic Impact 2017 - March 2017. All rights reserved.

Zehnder, A., Henley, S., & Weibel, R. (2018). Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability. *Zoology*, 128, 46–54,

Chapter 2

The efficacy of camera trapping for estimating lion density in heterogeneous environments: a case study in a seasonally flooded wetland, the Okavango Delta

Abstract

Accurately counting carnivores has historically been challenging; carnivores occupy large ranges, are secretive and occupy a range of habitats, some of which are difficult to access for direct counts. Camera trap surveys, however, together with advances in spatially-explicit capture-recapture analyses, have solved many of these issues, and have recently produced reliable estimates for various large carnivores around the world. We used camera trap surveys in the south-western Okavango Delta, an area which can be difficult to access due to seasonal flooding, to survey African lions (*Panthea leo*). High quality pictures from modern camera traps allowed for individual identification of lions necessary to conduct capture recapture analyses, and the spatial variation in density could be linked to anthropogenic and ecological drivers across the landscape. Surveys produced an estimate of 4.7 lions per 100km^2, which is comparable to other areas in the Okavango Delta, and resulting in a final estimate of 119 lions for the study site (95% Confidence Interval 88 – 170). Densities were positively influenced by the naturalized difference vegetation index (NDVI) which can serve as a proxy for prey distribution or habitat quality in the dry season, and negatively influenced by proximity to human settlements along the buffalo fence and within the concession, as expected. Lions along the buffalo fence are vulnerable to retaliatory killing for livestock depredation and competition with humans for prey through bushmeat harvesting, and conservation efforts should focus on mitigating both of these factors for the benefit of both people and lions.

Introduction

Despite their importance in maintaining robust ecosystems (Dalerum et al., 2008; Ripple et al., 2014; Wallach et al., 2015) and their cultural and religious significance throughout the world (Li et al., 2014; Saunders, 1994; Schaller, 1972), many of the world's large carnivores have faced significant declines, primarily because of habitat loss and conflict with humans (Treves & Karanth, 2003). An essential part of managing and monitoring the remaining large carnivore populations is being able to reliably estimate population size, detect population declines and understand which factors drive or limit population processes both spatially and temporally (Balme et al., 2019). However, large carnivores are notoriously difficult to count; they are rare, elusive, have extensive home range areas, and in some cases, live in difficult terrain or habitats with thick vegetation (Carbone et al., 2001; Karanth et al., 2011; Soisalo & Cavalcanti, 2006). Robust, wide-scale surveys of large carnivores using direct counts have historically been costly, both economically and logistically (Funston et al., 2010; Stander, 1998), and indirect methods for counting large carnivores have been criticized for being imprecise and inaccurate (Dröge et al., 2020; Karanth, 2011; Norton, 1990).

Recent advances in camera trapping technology, however, have overcome many of these issues; cameras are i) non-invasive, ii) can cover large areas systematically, iii) can be used in remote areas, or densely vegetated habitats that would be difficult to survey using direct counts (Silveira et al., 2003; Sollmann et al., 2013a) and iv) have become increasingly cost-effective (Sollmann, 2018). To date, camera trapping has been used, with much success, to study several large carnivore species including tigers (*Panthera tigris;* Karanth et al. 2004; O'Brien et al. 2003), jaguars (*Panthera onca;* Boron et al., 2016; Sollmann et al., 2011), snow leopards (*Panthera uncia;* Alexander et al., 2015) and leopards (*Panthera pardus;* Balme et al. 2019; Chapman and Balme, 2010). In addition to advances in technology, there have also been developments in statistical analyses which increase the reliability of density estimates produced by capture-recapture methodology (Efford, 2004; Royle et al., 2009; Royle & Young, 2008).

Spatially-explicit capture (SECR) has largely replaced conventional capture-recapture models in animal surveys by incorporating spatial information from 'detectors', relating the probability of detecting an individual animal at a detector in relation to the distance between the detector and the individual's activity centre (Efford, 2004). The incorporation of a movement parameter which allows for more accurate estimation of the effective trapping area in SECR models, solves the issue of estimating this area arbitrarily, making associated estimates of density and their translation into estimates of abundance more reliable than in conventional capture recapture models (Efford, 2004). This information can then also be used to model variation in density across the study area, allowing the linkage of habitat and resource covariates to observed patterns (Alexander et al., 2015; Broekhuis & Gopalaswamy, 2016; Efford & Boulanger, 2019; Royle et al., 2013). Providing a functional link between density and the underlying environmental or anthropogenic covariates allows informed management decisions to be made, particularly in the face of future change (Das et al., 2014; Gavin, 1991; Hobbs & Hanley, 1990).

The African lion (*Panthera leo*), despite being one of the most charismatic and well-known species on the planet, has faced significant decline over the last century (Bauer et al., 2015; Dures et al., 2019; Riggio et al., 2013). While the current worldwide lion population is estimated to be around 20 000 individuals (Bauer et al., 2015), many of the estimates from unfenced populations are unreliable. The majority of these estimates are based on best guesses by experts (Chardonnet 2002; Bauer & van der Merwe 2004; Riggio 2011), or based on index-calibration methods which have poor precision and are not reliable across a range of different densities or across different environmental conditions (Braczkowski et al., 2020; Dröge et al., 2020). Therefore, despite their conspicuous nature due to their social structure, lions, like other large carnivores, can be difficult to count based on their extensive home range sizes, shy nature in high-conflict areas or areas not frequented by tourists and residence in areas with limited road access. As accurate abundance estimates are important for conservation planning, monitoring population viability and measuring effectiveness of conservation interventions, it is vital to develop reliable, and repeatable, survey methods for unfenced lion populations (Braczkowksi et al., 2020, Funston et al., 2010; Smallwood & Fitzhugh, 1993; Stander, 1998). Linking these estimates to environmental or anthropogenic drivers can further inform conservation action.

As apex predators, lion densities are often driven by 'bottom-up' processes, more specifically by the biomass of available prey (Hayward et al., 2007; van Orsdol et al., 1985; Vinks et al., 2020). In turn, prey biomass is driven by environmental covariates which determine primary productivity, and lion population densities therefore fluctuate over time according to prevailing ecological conditions (Celesia et al., 2010; Packer et al., 2005; Vinks et al., 2020). However, lion densities may also be driven by human density or activity, a 'top-down' effect that is increasingly impacting large carnivores, even within protected areas (Lindsey et al. 2017; Everatt et al. 2019b). Not only do lions and people compete for space as savannah habitat is increasingly converted to agricultural land (Riggio et al., 2013; Woodroffe, 2000), but they also compete for food, with bushmeat poaching activities within and around protected areas severely depleting natural prey species of lion (Bauer et al. 2022; Rogan et al., 2017). Bushmeat poaching using snares also directly increases lion mortalities as they are frequently caught as by-catch in snares (Becker et al., 2018; Bouley et al., 2018; Loveridge et al., 2017). In addition, livestock may compete with wild herbivores for grazing resources, which further reduces the carrying capacity for wild herbivores and lions, and in some cases may exacerbate human-lion conflict (Ogutu et al., 2009; Tumenta et al. 2010; Voeten & Prins, 1999). Retaliatory killing in response to livestock depredation is one of the most significant threats to lions across their range (Bauer et al. 2022; Frank et al. 2006; Hazzah et al. 2009; Lichtenfeld et al. 2015). Lastly, and perhaps most worryingly, lions are increasingly being targeted for body parts for the illegal wildlife trade or for local medicinal use (Everatt et al. 2019a; Williams et al., 2015).

The Okavango Delta in north-western Botswana is one of only six remaining populations in Africa believed to have over 1000 individuals (Riggio, 2011). As such it is an important lion conservation unit and has the potential to act as a source population for other areas in the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA; IUCN SCSG 2006). Due to complex flooding patterns, the Okavango Delta is a difficult area to survey, and the main aim of this paper was to determine whether camera trapping could be used to: i) reliably estimate lion population size, and ii) determine the ecological and anthropogenic factors that influence the density of lions in this highly heterogeneous landscape. I therefore used a large camera trap array to survey three wildlife management areas in the south-western Okavango Delta for lions and used spatially-explicit capture recapture to analyse the results. I hypothesized that density, as in other areas, would be positively influenced by prey abundance and indices of habitat quality, and negatively influenced by human activity along the concession borders that are adjacent to human settlements, as well as around villages within the study area (Everatt et al., 2014).

Methods

Study area

The Okavango Delta is a seasonally flooded wetland situated in north-western Botswana (Gumbricht et al., 2000). Local mean annual rainfall is 460 mm, but the single annual flood pulse originates from seasonal rains that fall between November and March in the catchment area within the Angolan highlands (Ramberg et al., 2006). This rainwater then travels down the Okavango River, arriving in the panhandle of the Okavango Delta between March and April, and reaches the distal ends of the delta towards July or August, terminating in an alluvial fan which varies between 4000 km^2 and 18 000 km^2 in extent across the Kalahari Basin in Botswana (Gumbricht et al., 2000). Long-term flooding patterns follow a multi-decadal cycle of low and high floods, which can span 30 to 40 years (Murray-Hudson et al., 2014).

In this dynamic wetland, broad-scale ecological changes are closely tied to seasonal flooding (Murray-Hudson et al., 2014). Changes in primary productivity, particularly in the dry season, depend on flooding parameters such as frequency, duration and depth (Murray-Hudson et al., 2015) and the flood water therefore has significant effects on both the distribution and abundance of prey biomass, as well as the amount of available dry land (Bennitt et al., 2014; Burger, 2020; Fynn et al., 2015). Together these variables have been shown to influence lion pride sizes and population demographics such as such as reproduction and cub survival rates (Kotze et al., 2021).

The study area included three wildlife management areas, NG30, NG29 and NG27A, in the south-western Okavango Delta. The study area was bounded by the Kiri and Boro tributaries to the east, and the Matsibi and Xudum systems to the west. The area is highly heterogeneous and has habitats ranging from extensive seasonal floodplains to the north, to a dry sandveld tongue which extends to the centre of the study area from the south. The southern border of NG29 and NG30 is bounded by the southern buffalo fence, erected in

1982/83 to prevent transmission of foot-and-mouth disease between African buffalo (*Syncerus caffer*) and domestic cattle (*Bos taurus;* Cassidy et al., 2013) kept in adjacent concessions.

Data collection

Camera trap surveys were conducted between September and December 2017. A total of 83 camera trap stations were set up in a grid design, approximately 4km apart to maximize the likelihood of detecting lions (see Figure 2. 1.). This spacing ensured multiple captures of individuals within each pride home range (Borchers & Efford, 2008), based on median home range sizes of 225.45 km^2 for females during high flood and 366.03 km^2 for males during low flood (see Chapter 3). The original camera trap grid was predetermined using Google Earth satellite imagery, and in the field, camera stations were placed within 400m of the original identified station point. Most of the cameras were placed on roads owing to the good road network, but if a point was too far from a road, cameras were placed on the best available game trail to maximise the chances of detection (Forman & Alexander, 1998; Karanth, 1995). Each station consisted of two Cuddeback C1 Color Xchange Trail Cameras (Wisconsin, www.cuddeback.com) with white flash, placed on opposite sides of the road or game trail, approximately 7 – 8 metres apart. Cameras were mounted on steel poles, with the sensors at a height of approximately 60cm above the ground. To avoid false triggers caused by flash interference (Sollmann et al., 2011), the two cameras at each station were slightly offset from one another. Cameras were active for 24 hours a day for and the white flash ensured high quality colour images at night which were necessary for individual identification of lions. The two cameras allowed images to be captured of both sides of individual lions moving through the station which aided in accurate identification of individuals and the recording of recaptures. To meet the assumption of population closure, the camera trap survey was conducted within a three-month period (Nichols & Karanth, 2002).

Data Analysis

Data preparation

Camera trap data were analysed within a spatially-explicit mark-recapture (SECR) framework. Density estimates were calculated using the package *secr* (Efford, 2018) in R (R

Core Team, 2019), which calculates densities based on maximum-likelihood estimation (Borchers & Efford, 2008). This capture recapture method requires individual identification, which can be difficult for species which lack distinguishing stripes or spots (Kelly et al., 1998). However, due to high quality imagery, lions were identified individually primarily from whisker spot patterns (Pennycuick & Rudnai, 1970). For photos in which these were not clearly captured, other marks such as scars and ear notches, or in the case of males, mane size, shape and colour, were used to aid individual identification (see Strampelli et al., 2022). Lions photographed by field staff throughout the course of the survey, as well as photographs I had collected of known lions from the study area, were used as reference pictures to assist with the identification process. Pictures of lions which could not be identified were discarded from the analysis. Binary capture histories, with '0' representing not captured and '1' representing captured, were then constructed for each individual, for each capture occasion (Otis et al., 1978). Capture occasions were defined as 24 hours, ranging from 12:00 pm (noon) to 12:00 pm (noon) each day to account for the lion's predominantly nocturnal activity patterns (Hayward & Slotow, 2009; Sogbohossou et al., 2018). I constructed a camera trap functionality matrix to account for occasions when camera traps were not functioning over the survey period due to fire, interference by elephants, loss of battery power or camera malfunction.

To create the state-space, I constructed a habitat mask with a 500 x 500m grid over the study area, with the centre of each pixel representing a possible activity centre. I differentiated between habitat and non-habitat based on models of the relationship between vegetation communities and flooding frequency over the preceding three years (Murray-Hudson et al., 2015). I considered all areas flooded on average for more than 5 months as non-habitat. The flood takes approximately 5 months to move through the system (Ramberg et al., 2006), and therefore areas flooded for 5 months or less were considered to be representative of dry land available in non-flood season. An area that is consistently flooded for 5 months or more over a three-year period is also the threshold at which vegetation shifts from seasonal floodplain grassland to sedge and aquatic communities, and so areas not flooded for that long we considered to represent consistently 'dry' habitat in the short-term (Burger 2020; Murray-Hudson et al., 2015). We therefore used flood data frequency from monthly flood maps for 2015, 2016 and 2017 and considered pixels inundated for less than 5 months on average over that period to represent available ‘dry’ habitat for which lion densities could be estimated (Inman & Lyons, 2020). To derive flood maps, 30m resolution Landsat 7 maps were downloaded using Google Earth Engine, and composites created on a monthly basis for each year. Then, using band 7 data, which is the short-wave infrared (SWIR) band, median SWIR values were calculated for areas known to be wet (SWIRwet) and dry (SWIRdry). Based on these median SWIR values, a SWIR threshold was calculated for each composite according to the following equation (Inman & Lyons, 2020):

$$\text{SWIRthreshold} = \text{SWIRwet} - 0.3*(\text{SWIRdry}-\text{SWIRwet}).$$

All pixels below the threshold were then classified as wet, and those above classified as dry, with a 91.5 – 98% accuracy compared to ground-truthed and satellite-image truthed data (Inman & Lyons, 2020). To calculate the average flood frequency for each pixel over the three years, we summed monthly flood maps into annual maps, summed the annual maps and then divided by three to get an average flood duration for each pixel over the study period. This raster was then reclassified to represent average ‘dry’ habitat and ‘wet’ habitat based on the 5 month threshold, with areas flooded for more than 5 months considered ‘wet’. Lastly, to select an appropriate buffer size to which the sampling applies for estimating lion densities, as is characteristic of SECR modelling (Efford, 2004), I ran a series of density estimates with varying buffer sizes and selected a buffer width after which density estimates reached a plateau (Strampelli et al., 2018) to represent the full extent of the study area.

Modelling detection and movement

In addition to density, two other real parameters are estimated which jointly represent the probability of detection as a function of location: g(0), which describes the probability of capture in relation to the activity centre, and sigma (σ), which is a spatial parameter related to movement behaviour, and which may be indicative of home range size (Efford, 2004). Probability of capture for each individual i at trap x is therefore determined by $Pix = g0$ exp ($-dix/2\sigma^2$), where d is the distance between trap x and the activity centre of individual i. To describe the relationship between probability of detection and distance to activity centre for individuals captured at specific traps, SECR requires the specification of a detection function (Ramesh et al., 2017). For this study, I used the half-normal detection function, which is commonly used in other studies of large carnivores (Boron et al., 2016; Strampelli et al., 2018) to describe the decay in detection probability as individuals move away from the activity centre.

The first step in the modelling process was to derive a suitable sub-model to describe recapture probability g(0) and the movement parameter sigma (σ). Both parameters may be influenced by heterogeneity related to movement behaviour exhibited by different groups within the study populations. For example, in large carnivores, males and females often differ in their movement behaviour and home range sizes related to fulfilling sex-specific needs (Boron et al., 2016; Loveridge et al., 2009, Chapter 3). Alternatively, other factors, such as whether an individual is resident or transient, or whether an individual is still a dependent (Elliot et al., 2014), can influence movement behaviour and thus probability of recapture. Capturing this heterogeneity is important in reducing bias in density estimates (Pledger, 2000). Given that lions are group-living, and the population was likely to be composed of individuals of different age, sex and dominance status, I decided to use latent mixture models as an appropriate sub-model for detection probability g(0) and movement parameter sigma (σ) to account for heterogeneity. I therefore examined four different model combinations to include potential latent heterogeneity: 1) heterogeneity exists in capture probability g0, (2) heterogeneity exists in both capture probability g0 and movement parameter sigma, c) heterogeneity exists only in the movement parameter sigma, and d) a null model without heterogeneity in either parameter. I then used the corrected Akaike's Information Criterion (AICc) to select the best model (Burnham & Anderson, 2004) and this model structure was used in subsequent modelling. This model was also used to predict the density of lions in the study area. To examine the precision of the final estimate, the half relative confidence interval width was calculated as follows as suggested by Dröge et al., (2020):

$$\text{HRCIW} = \frac{(UCL-LCL)\ x\ 0.5}{N}\ x\ 100$$

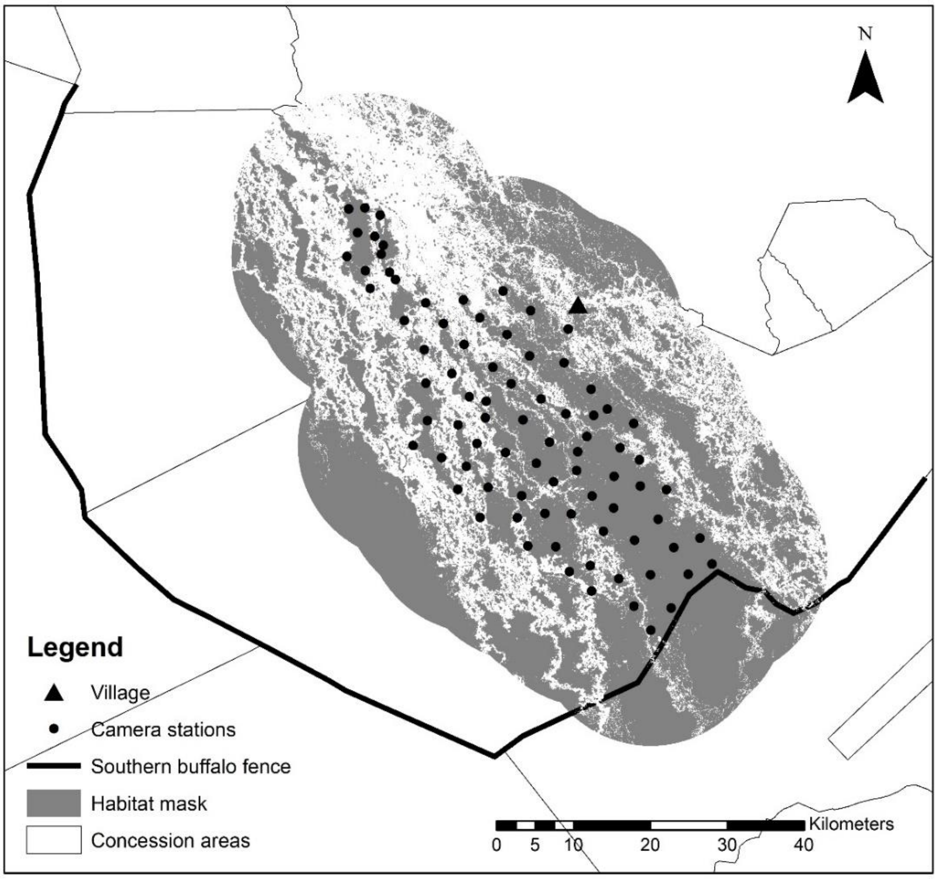

Figure 2. 1. Camera trap array used to survey lions (*Panthera leo*) across three wildlife management areas (WMAs) in the south-western Okavango Delta, Botswana. The habitat mask, represented by the grey shaded area, includes the 15km buffer zone, and excludes areas flooded for longer than 5 months of the year as functional habitat. The southern buffalo fence surrounds the management concessions, and the triangle represents a local village situated within the study area. Concessions surrounding the buffalo fence are community concessions which can be residential, pastoral or crops.

Modelling variation in density

As density can vary across the state space, and this spatial variation can be explained by covariates, I used an inhomogeneous Poisson point process to model density as a function of ecological and anthropogenic covariates across the state space (Borchers & Efford, 2008). I selected ecological covariates based on resource availability for lions and their prey. This included vegetation productivity, vegetation cover, distance to water and a relative prey encounter rate as detailed below (Celesia et al., 2010; Henschel et al., 2016; Rich et al., 2017).

I used the Normalized Difference Vegetation Index (NDVI) as a representative of primary productivity which may influence prey distribution and abundance, and by extension, lion distribution, during the dry season (Everatt et al., 2014; Henschel et al., 2016; Loveridge & Canney, 2009). NDVI data were derived from the red and near-infrared bands of a composite image created from Landsat 8 Level 2 imagery (https://earthexplorer.usgs.gov/). These data had a spatial resolution of 30m for the study area for the month of October, which corresponded to the middle of the survey period. For vegetation cover, which is known to influence lion hunting success, and is important in lion resource selection (Hopcraft et al., 2005; Midlane et al., 2014), I investigated the importance of both tree cover and non-tree cover (bush cover) across the landscape. This information was derived from the MODIS Vegetation Continuous Fields (VCF) dataset (MOD44B.051; https://lpdaac.usgs.gov/) for 2017, which has a 250m resolution.

As an index of prey activity in an area, I calculated a 'prey encounter rate' (PER) for each camera station. As the repeated detections of prey at a camera station are a function of both abundance and frequency of site use, photographic rates cannot strictly be interpreted as abundance (Sollmann et al., 2013b). Prey encounter rates were thus used as a proxy for the frequency with which lions would encounter prey, rather than an indication of prey abundance (Cusack et al., 2017). Prey encounter rate was thus determined by counting the number of independent encounters, divided by the number of days the camera was active, and multiplied by 100 (Carbone et al., 2001; Cusack et al., 2017). Pictures of the same species were considered independent if non-consecutive, or if consecutive, when pictures were separated by more than 1 hour (Cusack et al., 2017).

In the Okavango Delta, lions are known to utilize a variety of prey sources throughout the year (Kotze et al., 2018). Due to the diversity of habitats from floodplain to dry mopane woodland, there was a diverse prey base that consisted of both wetland and dryland species (see Bonyogo & Harris, 2007). Relative to surrounding agricultural zones and to other arid protected areas in Botswana, the Okavango Delta hosts a high density of prey, particularly of larger-bodied ungulates (Winterbach et al., 2014). Potential ungulate prey recorded during the survey included buffalo (*Syncerus caffer*), warthog (*Phacochoerus africanus*), zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), tsessebe (*Damaliscus lunatus*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*), roan antelope (*Hippotragus equinus*), red lechwe (*Kobus leche*), reedbuck (*Redunca arundinum*), sitatunga (*Trapgelaphus spekii*), bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicarpa grimmia*) and steenbok (*Raphicerus campestris*).

However, lion densities are often linked to the biomass of prey in the lion's preferred weight range (Hayward & Kerley, 2005). I therefore tested two different categories of prey for prey encounter rates (Ramesh et al., 2017). Firstly, I used all prey species recorded which had an average adult female weight of 30kg or more to represent potential prey, and secondly, I used all ungulate prey species with an average adult female weight above 100kg to represent medium to large prey – prey that falls within the lion's preferred prey weight range (Hayward & Kerley, 2005). Using the prey encounter rate for each camera trap, I then conducted ordinary kriging to create a continuous field of prey distribution across the state space. Prey encounter rates were determined using camtrapR, and kriging surfaces were created using the packages automap (Hiemstra et al., 2009) and gstat (Graler et al., 2016) in R (R Core Team 2019). For NDVI, vegetation cover and prey encounter rate, I expected the influence of each covariate to decline with increasing distance from the sampling point (Chandler & Hepinstall-Cymerman, 2016). For each of these covariates, I therefore extracted values for each mask point using a distance-weighted mean (Chandler & Hepinstall-Cymerman, 2016).

Lastly, distance to water can be an important influence on habitat quality, and therefore lion density, as prey species congregate around water sources during the dry season (Mosser et al., 2009; Valeix et al., 2010). In the Okavango Delta in the dry season, herbivores congregate in floodplain areas not only to access water when ephemeral water sources have dried up, but also to access the 'green flush' of grazing produced by receding flood water (Bennitt et al., 2014). Floodplains are thus considered higher quality habitat, and these may host higher densities of lions than other habitats (Cozzi et al., 2013). To identify flooded areas, I used Landsat 8 Level 2 imagery (https://earthexplorer.usgs.gov/) with 30m spatial resolution and distinguished between wet and dry pixels using a thresholding method involving the SWIR band (Band 7; Inman & Lyons, 2020). This thresholding method was adapted from Wolski et al. (2017) and uses image specific SWIR values from known dry and wet pixels to determine a composite-specific threshold. Values above this threshold are then considered flooded, and those below the threshold are classified as dry (Inman & Lyons, 2020). For this study, I created a composite image for October 2017 using Landsat 8 imagery, masking pixels classified as cloud or cloud shadow, and then applied the composite specific SWIR thresholding technique to delineate flooded areas. All calculations were done using code provided by Inman and Lyons (2020) in Google Earth Engine.

As a first step in the modelling process, and to reduce the number of model parameters, I used univariate analyses to determine which ecological factors were most important in determining lion density across the WMA, before combining ecological and anthropogenic variables in multivariate models. I first determined which prey encounter rate, medium-sized prey or all prey, best explained the variation in lion density, and this prey index was carried forward in subsequent models. Prior to univariate model testing for ecological covariates, I tested for collinearity between all variables using variance inflation factors (VIF), and where pairs of variables showed high collinearity, (VIF>3, Zuur et al., 2010) I retained that which made the most sense biologically for further analysis. Furthermore, all covariates were scaled to ensure comparability. Model comparisons were conducted using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2004). For ecological covariates, only covariate models with Δ AICc < 2 were retained for further multivariate analyses. I considered models with AICc < 2 to represent the best models explaining the variation in density across the landscape (Efford, 2018). All statistical analyses were performed using the package secr (R Core Team, 2019) in R.

Results

The survey ran for a total of 83 days. The mean number of trap nights per camera was 53.6, leading to a total of 4456 trap nights. On average, traps were spaced 3.19 km apart across the sampling grid. Lions were captured on 113 occasions during the survey, and 40 individuals were identified (excluding cubs < 1 year old), 20 of which were female and 20 of which were male. For the females, 18 were adults and two sub-adults (between one and four years old), and for the males, 14 were adults and six were sub-adults. Four cubs were identified on two occasions, three were from one cohort and estimated to be between seven and eight months old, and one from a separate cohort was estimated to be about 10 weeks old. All individuals could be sexed due to clear sexual dimorphism between adult male and female lions. Density estimates stabilized at a buffer size of 15km, and after excluding areas flooded for an average of 5 months or longer, the total mask area covered 2537 km^2.

Results for the detection sub-models indicated that finite mixture models with two latent classes showed heterogeneity in detection probability, but no heterogeneity in the spatial scale parameter (Table 2. 1.). This model outperformed all other models and had a model weight of 1 (Table 2. 1.). This detection sub model was therefore retained in all further analyses and to estimate density for the study area. Detection varied between the two latent groups: the first group, which comprised 90% of the population, had a detection probability of 0.004, and the second group, which comprised 10% of the population, had a detection probability of 0.45. The size of the spatial scale parameter was estimated at 4.01km ± 295m. The estimated density for the area was 0.047 (SE 0.009) lions per square kilometre, and the estimated number of lions for the study area was 119 (95% CI 88 – 170). The precision of the estimate, measured using the half-relative confidence interval width, was 34.5%.

For univariate analyses on prey indices, encounter rates of all prey (AIC = 0, AIC weight = 0.67) was selected over encounter rates of medium-large prey (AIC = 1.37, AIC weight = 0.33). When testing for collinearity between all variables for density models using variance inflation factors, I found that tree cover and NDVI were collinear. As there were two indices of potential cover (bush and tree) I dropped tree cover as a covariate and retained NDVI as a more general indicator of habitat productivity for further analysis.

Univariate analyses revealed that NDVI was the top ecological covariate explaining the distribution of lion density across the WMA. Only NDVI had $\Delta AICc < 2$ (Table 2. 2.) and was thus the only ecological variable included in the multivariate modelling. When combining NDVI with anthropogenic pressure, the top models included NDVI alone, distance to human disturbance alone and a combination of the two covariates (AICc <2, Table 2. 3.). Summed

Akaike weights revealed that NDVI was most influential in determining lion density, followed by distance to human disturbance (0.74 and 0.47 respectively, Table 2. 4.).

Table 2. 1. Selection of detection probability sub-model for spatially-explicit capture recapture analysis on lions (*Panthera leo*) in the south-western Okavango Delta, Botswana, using finite mixture models to account for latent heterogeneity in capture and spatial scale parameters.

Model	Notation	Detecfn	k	AICc	dAICc	w
Heterogeneity in g0	g0~h2, sigma ~ 1	HN	5	564.78	0.00	1
Heterogeneity in g0 and σ	g0~h2, sigma ~ h2	HN	6	584.05	19.27	0
Heterogeneity in σ	g0~1, sigma~h2	HN	5	588.52	23.74	0
No heterogeneity in g0 or σ	g0~1, sigma~1	HN	3	617.03	52.25	0

g0 = capture probability
σ = movement parameter related to activity centres
Detectfn = detection function
HN = half normal detection function describing the decline in capture probability as an animal moves away from the activity centre
k = number of parameters
AICc = Aikaike's Information Criterion adjusted for small sample size
ΔAICc = difference in AICc score from best-ranking model (AICc =0)
w = model weight

Table 2. 2. Univariate models relating ecological covariates to lion (*Panthera leo*) density across the south-western Okavango Delta, Botswana. NDVI (Normalized Difference Vegetation Index) represents vegetation productivity, D_water represents distance to water, bush represents bush cover and prey (all) represents relative prey encounter rates.

Density	Detection	Detecfn	k	AICc	ΔAICc	W
NDVI	g0~h2 sigma~1	HN	6	556.85	0.00	0.85
D_water	g0~h2 sigma~1	HN	6	561.48	4.64	0.08
Bush	g0~h2 sigma~1	HN	6	563.05	6.20	0.04
Null	g0~h2 sigma~1	HN	5	564.78	7.94	0.02
Prey (all)	g0~h2 sigma~1	HN	6	566.59	9.74	0.01

Detection = structure of detection sub-model
Detectfn = detection function
HN = half normal detection function describing the decline in capture probability as an animal moves away from the activity centre
k = number of parameters
AICc = Aikaike's Information Criterion adjusted for small sample size
ΔAICc = difference in AICc score from best-ranking model (AICc =0)
w = model weight

Table 2. 3. Candidate models with ecological and anthropogenic covariates explaining variation in the density parameter for spatially-explicit capture recapture models based on lion (*Panthera leo*) detections from dry season camera trap surveys in the south-western Okavango Delta, Botswana. Values in bold indicate factors that are significant.

Models					Estimates			
					NDVI		D_hdis	
	k	*AICc*	*ΔAICc*	*w*	*β (SE)*	*CI*	*β (SE)*	*CI*
NDVI	6	556.85	0.00	0.52	**0.58 (0.17)**	**0.23 - 0.92**		
D_hdis	6	558.32	1.48	0.25			**0.61 (0.21)**	**0.21 - 1.02**
NDVI +D_hdis	7	558.52	1.67	0.22	0.41 (0.24)	-0.05 - 0.88	0.30 (0.27)	-0.23 - 0.82
Null	5	564.78	7.94	0.01				

k = number of model parameters
AICc = Aikaike's information criterion adjusted for small sample size
ΔAICc = change in AICc weight between top model and other candidate models
w = weight of candidate models.
NDVI = normalized difference vegetation index
D_hdis = distance to human disturbance, which is distance to the veterinary fence and distance to village within the wildlife management areas
β = beta estimates for covariates
SE = standard error of beta estimates
CI = 95 % confidence interval

Table 2. 4. Summed AICc weights for covariates the set of best explanatory models describing density of lions (*Panthera leo*) across the south-western Okavango Delta, Botswana. NDVI = normalized difference vegetation index, and D_hdis = distance to disturbance associated with human settlements.

Covariate	Summed AICc weight
NDVI	0.74
D_hdis	0.47

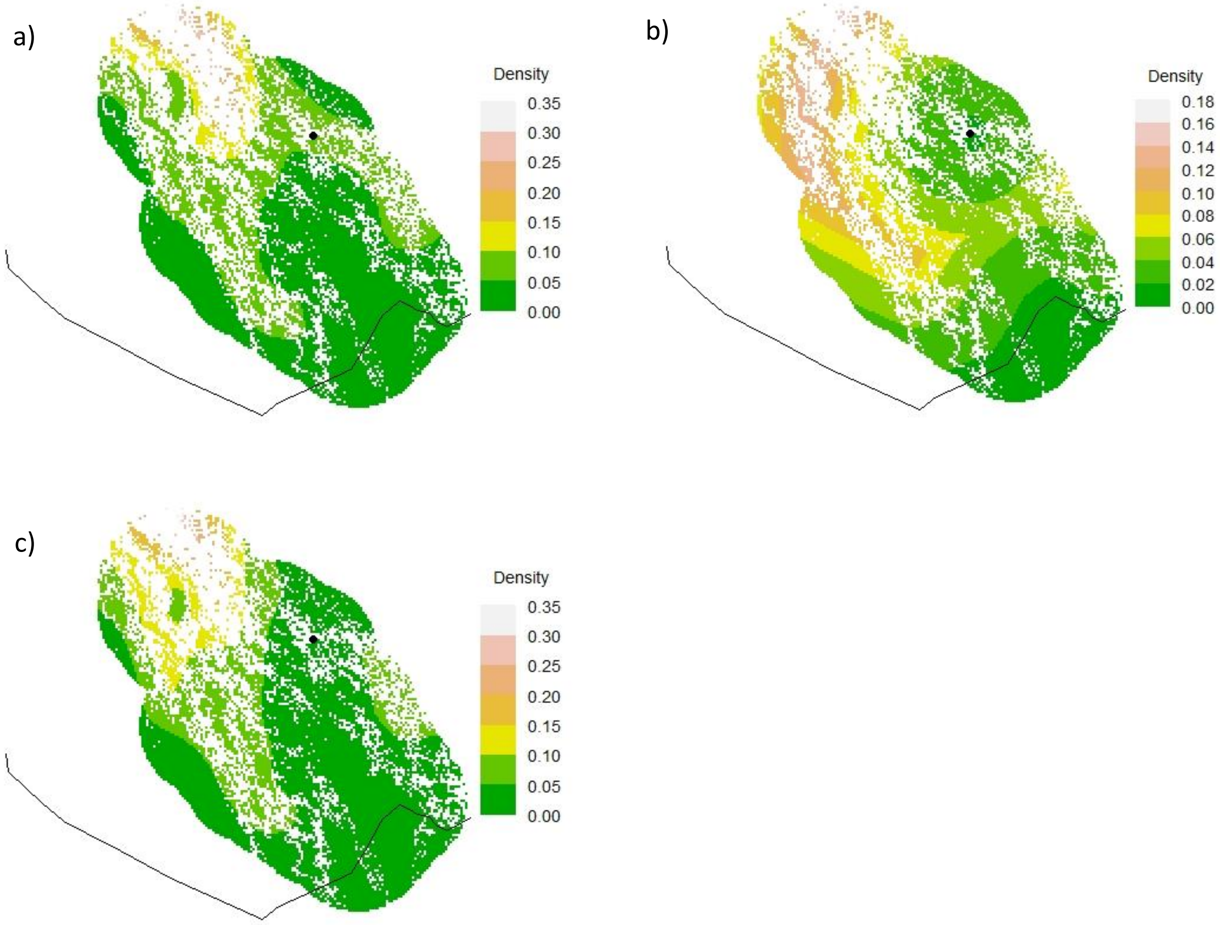

Figure 2. 2. Predictive density surfaces for lion (*Panthera leo*) across wildlife management areas in the south-western Okavango Delta related to estimates produced by a) only normalized difference vegetation index (NDVI), b) only human disturbance and c) NDVI and human disturbance combined. The dot in the north-eastern corner represents a residential village.

The predictive density surface for the NDVI model shows that lion densities are generally higher in the north of the wildlife management area, which is dominated by floodplain habitats (Figure 2. 2a). Densities are lower further south in the concession, particularly on the large sandveld tongue, but are slightly higher along the floodplain systems to the east and west of this tongue (Figure 2. 2a). The predictive surface based on human disturbance alone, shows low-density areas around villages and the southern buffalo fence (Figure 2. 2b), however, when combining the two factors, the density surface shows that lion density follows patterns of NDVI, but is much lower than would be expected based on NDVI alone along the fence line and around the resident village (Figure 2. 2c).

Discussion

Camera trapping, together with advances in spatially-explicit capture-recapture (SECR) analyses, have significantly improved our ability to produce cost effective, reliable and repeatable density estimates (Braczkowski et al., 2020). Higher quality imagery has also enabled the application of SECR to lions, which lack distinct pelage markings, but which can nevertheless be distinguished individually using whisker-spot patterns and permanent scars. In this study, we have shown that camera trapping can be used to produce robust estimates of lion densities in a seasonally flooded landscape. Furthermore, when coupled with ecological and anthropogenic predictors, the factors driving differences in density across the landscape can be identified, giving managers a snap-shot view into the short-term factors influencing habitat quality for lions (Mosser et al., 2009). In the south-western Okavango Delta, vegetation productivity was the best ecological predictor of lion density, but this was clearly constrained by human disturbance along the wildlife management area boundary fence and villages. Understanding what drives differences in density is important for informing future conservation action and threats to large cats. The spatial variation in density across the study area, which is heterogeneous, also shows the value of robust estimation methods which can account for spatial heterogeneity, and shows the danger of extrapolating lion numbers across broad areas based on spatially limited survey sites.

Modelling detection and movement

An important step in the modelling process is selecting a detection sub-model which reduces potential bias in estimates of density. The spatial scale parameter is calculated based on the average distance between detections throughout the study and can be converted to a 95% home range estimate by assuming movement conforms to a circular bivariate normal distribution (Sollmann et al., 2011). In this study, latent mixture models showed no heterogeneity in the scale of the movement parameter, but did indicate heterogeneity in detection rates, with 10% of the population having a significantly higher detection rate than the rest. Generally, large carnivores are expected to exhibit sex-differentiated movement behaviour where males often have large ranges than females (Bertram, 1975; Loveridge et al., 2009; Sandell, 1989; Sollmann et al., 2011, see also Chapter 3). However, this assumption may be confounded by other factors such as social behaviour or social status. In lions for example, female adults with dependent cubs and sub-adults of both sexes live in cohesive groups and will thus exhibit similar movement patterns (Schaller, 1972). Similarly, pride males generally defend the territory of the pride and thus spatially overlap with females in their territories (Funston et al., 1998), and under conditions in which female densities are high, males may use smaller ranges than when female density is low (Benhamou et al., 2014; Funston et al., 1998). Lion social behaviour may thus explain the apparent lack in heterogeneity of space use as detected by camera traps, between the sexes in this study.

Social status may also be important in determining rates of detection for lions. Of the males captured during the study, approximately 50% were sub-adults or non-residents at the time. As a small proportion of the population showed high recapture rates, it is likely that the heterogeneity in detection rates resulted from a small number of resident adult males being captured frequently. Resident pride males expend considerable energy scent-marking to maintain territorial boundaries and may alternate between sub-groups of females in the same pride, causing them to patrol the area more often (Funston et al., 1998; Mosser & Packer, 2009; Schaller, 1972). As large carnivores often use roads as paths of least resistance (Forman & Alexander, 1998), and as our sampling was focused largely on roads, resident male lions were more likely to be detected. On the contrary, young males or females with young cubs may want to avoid detection by adult males (Elliot et al., 2014; Funston et al., 1998), and therefore may avoid routes the latter frequent which would lead to lower relative detection probabilities. However, it is important to note that the division of observed data into latent groups does not necessarily mean that the groups have biological meaning (Balme et al., 2019; Drewry et al., 2013; Pledger, 2000). Other recent studies on large carnivores have shown that sex is not necessarily the most important factor influencing movement and detection heterogeneity and that sex differences in behaviour may not be as important as other factors such as social behaviour and territorial status related to age (Balme et al., 2019; Hickey & Sollmann, 2018). Similarly, in Strampelli et al. (2022), in only one of three survey models was sex an important determinant of differences in the movement parameter. Finite mixture models should therefore be tested as potential alternatives for sex-varying models when conducting SECR analyses on large carnivores, particularly for social species like lions which may share ranges and where social status may confound general patterns of space use based solely on sex.

Lastly, in social animals, the detectability of individuals may be influenced by detectability of the group and ignoring this influence on detection probability could lead to over-estimating precision (Hickey & Sollmann, 2018). Solutions to this have been investigated in two ways: a two-step hierarchical estimation method which takes both group and individual heterogeneity in capture into account, or through the incorporation of measures of aggregation and group cohesion when estimating detection (Bischof et al., 2020; Hickey & Sollmann, 2018). For this study, we did not include either of these measures for accounting for group size as: 1) lions exhibit fission-fusion social behaviour, where group composition and structure change over time in accordance with prevailing social or ecological conditions (Kotze et al., 2018), which would result in low cohesion and 2) with camera trap surveys, the detection of one individual does not enhance detection of other members of the group. This is contrary to indirect capture methods such as spoor or DNA from scat, where detection of one will likely lead to detection of others in the group (Bischof et al., 2020). Furthermore, Bischof et al. (2020) show the bias in density estimation is low for group sizes smaller than eight, which was the case in our study. As such, we are confident that group structure did not significantly bias density estimates in this study. However, we suggest that further empirical studies are conducted on a range of social species to understand the circumstances under which social structure may affect detection (see Emmet et al., 2021), and how this may differ with various methods of data collection.

Modelling density

The population size estimated for the area, taking heterogeneity in detection into account, was 119 lions, or a density of 4.7 lions per 100 km^2. This is slightly lower than average lion densities estimated in the eastern Okavango Delta using call-up station surveys (Cozzi et al., 2013), which averaged 5.8 lions per 100 km^2, but higher than estimates by Rich et al. (2019) of 1.2 lions per 100 km^2 in that same area from camera trap data. The HRCIW for the estimate of 34.5% is slightly higher than the recommended 30% in terms of precision (see

Dröge et al. 2020). With mark-recapture studies, precision increases as recaptures increase (Efford, 2004). As mean camera trap nights was only 53.6 per camera, perhaps increasing the length of the survey to ensure all cameras are out for a longer period (but within the 90 day limit which is considered to represent population closure; Nichols & Karanth, 2002) may increase recaptures and improve precision. Densities, however, should be interpreted with caution, particularly when comparing to other studies. In the Okavango Delta, the amount of available dry land changes both annually and inter-annually (Bennitt et al., 2014; Burger, 2020; Fynn et al., 2015). For this study, we defined areas flooded for longer than 5 months (which is the time it takes for the flood to traverse the system) over a three-year period leading up to the study period as ‘non-habitat’ (Efford, 2019b). Densities are therefore representative of ‘functional’ habitat available (Efford, 2019b) which is highly variable in a flooded system. More detailed resource selection functions using GPS location data from collars may better estimate the use of flooded areas and what should be defined as non-habitat. Furthermore, it is important to note that the result is not a ‘density surface’ per se, but a density of ‘activity centres’ for individuals across the landscape (Royle et al., 2013). This can be equated to a resource selection function which examines how covariates affect space usage at the scale of the home range, which in this case is defined by the movement around the predicted activity centre (Royle et al., 2013). Areas of low ‘density’ do not necessarily indicate an absence of lions, but may identify areas which lions actively avoid, or represent infrequently used areas of the home range. Further reference to ‘density’ is therefore interpreted as ‘density’ of activity centres or areas of high use (see Chapter 4).

In this study, lion density was best predicted by vegetation productivity, likely due to its indirect effect on prey abundance (Fynn et al., 2015; Murray-Hudson et al., 2006). Vegetation productivity is determined by environmental covariates such as rainfall, soil and climate, and in savanna systems, is most limited in the dry season (Coe et al., 1976). In the Okavango Delta, a seasonally flooded wetland, both the water and nutrients deposited by the annual flood pulse results in ‘green-flush’ of grazing which is an important resource during the dry season (Bartlam-Brooks et al., 2013; Bennitt et al., 2014; Murray-Hudson et al., 2006). Floodplains, and the surrounding riparian forest, therefore, have higher vegetation productivity, and dry season prey abundance in comparison to drier habitats such as mopane (*Colophospermum mopane*) woodland, which are only productive during the rainy season (Bartlam-Brooks et al., 2013; Cozzi et al., 2013; Rich et al., 2017). The predictive density models show that dry season NDVI had a positive relationship with lion density across the landscape, in accordance with our predictions, and that this pattern generally follows the pattern of the floodplain systems in the WMA. Densities of lions are much higher in the north, where habitat is dominated by open floodplains and islands, than in the south, which is a large sandveld tongue dominated by mopane and Kalahari apple-leaf (*Philonoptera nelsii*) woodland. This is concurrent with findings from other studies of prey and lion density in the Okavango Delta (Cozzi et al., 2013; Rich et al., 2019).

Contrary to our expectations, the prey encounter rate did not rank high among predictive ecological variables. However, prior studies have indicated that even where prey is regularly encountered, it is prey accessibility, or prey catchability which is more important (Balme et al., 2007; Funston et al., 1998, Hopcraft et al., 2005). Prey catchability is often measured by indices such as tree cover or bush cover, as vegetation structure provides better opportunities for ambush predators to hunt successfully (Davidson et al., 2012). It is also important to keep in mind that encounter rates are not a substitute for abundance, and that caution must be used when interpreting these indices from camera trap data (Sollman et al., 2013b, Rich et al., 2017). In this study, tree cover was highly correlated with dry season NDVI, likely due the concentration of riparian forest along floodplain edges on islands, and where the green flush of grazing occurs because of the flood. This riparian forest may also provide cover for lions to rest and ambush prey during the day (Elliot, 2013; Midlane et al., 2014), and this may have contributed to the significant positive relationship between NDVI and lion density. Distance to water was not as influential as we expected, which is also consistent with other studies in the Okavango (Rich et al., 2017). Unlike in other mesic ecosystems where water availability constrains herbivore movement in the dry season (Redfern et al., 2003, Valeix et al., 2010), water is ubiquitous in the Okavango Delta in the dry season due to flooding. It is therefore likely that herbivore distribution and abundance is driven more by dry season food quality than water availability.

In the Okavango Delta, the density of lion activity centres increased as distance from human settlements increased. These results are consistent with other studies on lions which show that large carnivores actively avoid areas where there is higher human activity and disturbance (Everatt et al., 2014; Kiffner et al., 2009). In protected areas, this avoidance manifests as ‘edge effects’ which can have a significant negative influence on large carnivore populations deep into the protected area, keeping the carrying capacity well below the maximum potential (Everatt et al. 2019b; Lindsey et al., 2017). Lions suffer from both exploitative and interference competition from humans (Everatt et al., 2015, 2019b) and we suggest that both may be at work along the borders of the Okavango Delta. A recent study on bushmeat poaching on the western edge of the Okavango Delta indicated that significant quantities of bushmeat are removed annually (Rogan et al., 2017). This reduction in wild prey effectively decreases the prey base for lions, which could lead to lions using these areas less frequently. There are also high levels of human-lion conflict along the buffalo fence, where lions cross into community-owned concessions and predate on livestock (LeFlore et al., 2019; Weise et al., 2019b; Whitesell, 2019). This livestock depredation often leads to retaliatory killing – in the same study of bushmeat poaching prevalence, hunters admitted to killing a total of 21 lions (and wounding 3) across the western Okavango Delta in a period of only 12 months (Rogan pers.comment). This conflict is further exacerbated in the dry season, when domestic cattle often cross into the wildlife management areas because of poor fence maintenance or in years where grazing is scarce (Weise et al., 2019a). Ultimately, human-caused mortality as well as competition for prey species as a result of bushmeat harvesting can have a significantly negative influence on the population structure, social organisation, movement behaviour and density of lions living on the edge of wildlife management areas and may contribute to the observed lower density of home ranges along the buffalo fence (Davidson et al., 2011; Loveridge et al., 2007, 2010).

Conclusion and recommendations

Lions are not only a priority for maintaining healthy ecosystems (Dalerum et al., 2008; Wallach et al., 2015), but add significant value to tourism experiences in and around the Okavango Delta (Mladenov et al., 2007). To effectively conserve lions, reliable counting methods are necessary to monitor population trends (Braczkowski et al., 2020; Dröge et al., 2020), and understand the anthropogenic and natural drivers of variation in density across the landscape. This study showed that camera trapping can be used to survey large areas systematically for lions and provide relatively precise estimates. When it comes to scaling up however, the total size of the area needs to be considered. As alluded to in Strampelli et al. (2022), to cover the entire Okavango Delta landscapes at a similar sampling effort would have high budgetary and logistical costs. However, given that wide-scale surveys for the Okavango have not been attempted for almost two decades (Winterbach et al., 1998), for the Okavango, and for areas for which almost no population data is available, this investment may be worth it. Furthermore, information gained from such surveys can be used to inform either i) how the area could be stratified in future to allow for continued smaller surveys that are representative of ecoregions across the Okavango, or ii) be continued in areas of the Okavango where there is little tourism presence while incorporating citizen science efforts in core tourism areas (see Rafiq et al., 2019). However, caution would need to be applied with extrapolations for ecoregions given the heterogeneity of the Okavango and the extent to which changing flood conditions may influence lion abundance, survival and the size of core areas available to resident lions in different parts of the Okavango (see Kotze et al., 2020; Chapter 4). Lastly, it is recommended that surveys for the Okavango take place in the hot dry season, or in the window after the rains and pre-flood, when most areas are more accessible by vehicle. This will reduce the chances of missing some prides or sub-groups that may occupy islands during the flood season that cannot be easily accessed for surveying.

This survey showed that lion densities are greater along floodplain systems which have high levels of vegetation productivity in the dry season (Bartlam-Brooks et al., 2013; Bennitt et al., 2014; Burger, 2020; Murray-Hudson et al., 2014), and decrease in density towards areas with high levels of human activity along the Okavango's boundaries. However, this too should be interpreted with caution when extrapolating to the rest of the system, as in some areas lions may have higher densities closer to the fence as the floods preclude using areas closer to the Delta's core (see Chapter 4). From a conservation perspective, the effect of reduced density closer to the fence in this survey, indicating that edge effects do exist, may be the result of more systemic issues such as retaliatory killings (LeFlore et al., 2019; Weise et al., 2019b; Whitesell, 2019) and the reduction in the natural prey base through poaching (Rogan et al., 2017) that need to be addressed across the Okavango's wildlife management areas. Opportunities for improved livelihoods, as well as improved livestock husbandry practices need to be a conservation priority to minimize bushmeat harvesting and reduce negative interactions between people and lions if negative edge effects on protected area boundaries are to be mitigated (Rogan et al., 2017; van Rooyen, 2016). Alternatively, the development of community-owned ecotourism enterprises could buffer edge effects, as well as provide communities with economic incentives to conserve wildlife, rather than just carrying the costs of coexistence, which could ultimately benefit both people and lions (Blackburn et al., 2016; Goldman et al., 2010; Osano et al., 2013). While the Okavango is currently one of the largest free-ranging populations in the Kavango-Zambezi Transfrontier Conservation Area and in Africa (IUCN SCSG, 2006), continued monitoring efforts are a priority to ensure the viability of this population.

References

Alexander, J. S., Gopalaswamy, A. M., Shi, K., Riordan, P., & Margalida, A. (2015). Face value: Towards robust estimates of snow leopard densities. *PloS ONE*, 8, 1–17.

Balme, G., Hunter, L., & Slotow, R. (2007). Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, 74, 589–598.

Balme, G., Rogan, M., Thomas, L., Pitman, R., Mann, G., Whittington-Jones, G., Midlane, N., Broodryk, M., Broodryk, K., Campbell, M., Alkema, M., Wright, D., & Hunter, L. (2019). Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. *Population Ecology*, 61, 256–267.

Bartlam-Brooks, H. L. A., Bonyongo, M. C., & Harris, S. (2013). How landscape scale changes affect ecological processes in conservation areas: External factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta. *Ecology and Evolution*, 3, 2795–2805.

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

Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S. K., Sillero-Zubiri, C., Hunter, L., Linsdsey, P., & Macdonald, D. W. (2022). Threat analysis for more effective lion conservation. *Oryx*, 56, 108-115.

Bauer, H., & van der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, 38, 26–31.

Becker, M., Watson, F. G. R., Droge, E., Mcrobb, R., Watson, F., Kanyembo, B., Murdoch, J., & Kakumbi, C. (2018). Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores*, Biological Conservation,* 158*,* 23-36.

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, 90, 171–180.

Bennitt, E., Bonyongo, M. C., & Harris, S. (2014). Habitat selection by African buffalo (*Syncerus caffer*) in response to landscape-level fluctuations in water availability on two temporal scales. *PloS ONE*, 9, 1–14.

Bertram, B. C. R. (1975). The social system of lions. *Scientific American,* 232, 54-65.

Bischof, R., Dupont, P., Milleret, C., Chipperfield, J., & Royle, J. A. (2020). Consequences of ignoring group association in spatial capture–recapture analysis. *Wildlife Biology*, 1, 1-10.

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

Bonyongo, M. C., & Harris, S. (2007). Grazers species-packing in the Okavango Delta, Botswana. *African Journal of Ecology,* 45*,* 527–534.

Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64, 377–385

Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., & Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *PloS ONE*, 11, e0153973.

Bouley, P., Poulos, M., Branco, R., & Carter, N. H. (2018). Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biological Conservation*, 227, 233–242.

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., Biggs, D & Allan, J. R. (2020). Restoring Africa's Lions: Start with good counts. *Frontiers in Ecology and Evolution*, 8, 138.

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PloS ONE*, 11, 1–15.

Burger, K. (2020). *The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta.* PhD Thesis. Johannesburg: University of the Witwatersrand.

Burnham, K. P., & Anderson, D. R. (2004). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (2nd ed.). Springer: New York.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J. R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D. W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D. J. L., Sunquist, M., Tilson, R., & Wan Shahruddin, W. N. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4, 75–79.

Cassidy, L., Fynn, R., & Sethebe, B. (2013). Effects of restriction of wild herbivore movement on woody and herbaceous vegetation in the Okavango Delta Botswana. *African Journal of Ecology*, 51, 513–527.

Celesia, G. G., Townsend Peterson, A., Kerbis Peterhans, J. C., & Gnoske, T. P. (2010). Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48, 58–71.

Chandler, R., & Hepinstall-Cymerman, J. (2016). Estimating the spatial scales of landscape effects on abundance. *Landscape Ecology*, 31, 1383–1394

Chapman, S., & Balme, G. (2010). An estimate of leopard population density in a private reserve in KwaZulu-natal, South Africa, using camera-traps and capture-recapture models. *African Journal of Wildlife Research*, 40, 114–120.

Chardonnet, P. (2002). *Conservation of the African lion: contribution to a status survey*. International Foundation for the Conservation of Wildlife.

Coe, M. J., Cumming, D. H., & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22, 341-354.

Cozzi, G., Broekhuis, F., McNutt, J. W., & Schmid, B. (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.

Cusack, J. J., Dickman, A. J., Kalyahe, M., Rowcliffe, J. M., Carbone, C., MacDonald, D. W., & Coulson, T. (2017). Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: a comparison of spatiotemporal approaches. *Oikos*, 126, 812–822.

Dalerum, F., Somers, M. J., Kunkel, K. E., & Cameron, E. Z. (2008). The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation*, 17, 2939–2949.

Das, S., Dutta, S., Sen, S., A. S., J., Babu, S., Kumara, H. N., & Singh, M. (2014). Identifying regions for conservation of sloth bears through occupancy modelling in north-eastern Karnataka, India. *Ursus*, 25, 111–120.

Davidson, Z., Valeix, M., Loveridge, A. J., Madzikanda, H., & Macdonald, D. W. (2011). Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation*, 144, 114–121.

Davidson, Z., Valeix, M., Loveridge, A., Hunt, J., Johnson, P., Madzikanda, H., & Macdonald, D. (2012). Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy*, 93, 677–685.

Drewry, J. M., van Manen, F. T., & Ruth, D. M. (2013). Density and genetic structure of black bears in coastal South Carolina. *Journal of Wildlife Management*, 77, 153–164.

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution,* 10, 3276-3292.

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion-conservation stronghold. *Diversity and Distributions*, 25, 870–879.

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 106, 598–610.

Efford, M. (2019a). *Density surfaces in secr 4.1*.

Efford, M. (2019b). *Habitat masks in the package secr*.

Efford, M. G. (2018). *Spatially-explicit capture-recapture models. R package version 3.1.5.* (3.5.1).

Efford, M. G., & Boulanger, J. (2019). Fast evaluation of study designs for spatially explicit capture–recapture. *Methods in Ecology and Evolution,* 10, 1529-1535.

Elliot, N. B. (2013). *The Ecology of Dispersal in Lions* (Panthera leo). PhD Thesis. University of Oxford.

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, 95, 2860–2869.

Emmet, R. L., Augustine, B. C., Abrahms, B., Rich, L. N., & Gardner, B. (2021). A spatial capture–recapture model for group-living species. *Ecology*, e03576.

Everatt, K. T., Andresen, L., & Somers, M. J. (2014). Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PloS ONE*, 9, e99389.

Everatt, K. T., Andresen, L., & Somers, M. J. (2015). The influence of prey, pastoralism and poaching on the hierarchical use of habitat by an apex predator. *African Journal of Wildlife Research*, 45, 187

Everatt, K. T., Kokes, R., & Lopez Pereira, C. (2019a). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, 28, 4099–4114.

Everatt, K. T., Moore, J. F., & Kerley, G. I. H. (2019b). Africa’s apex predator, the lion, is limited by interference and exploitative competition with humans. *Global Ecology and Conservation*, *20*, e00758.

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29, 207–231.

Frank, L., Maclennan, S., Hazzah, L., Bonham, R., & Hill, T. (2006). Lion killing in the Amboseli-Tsavo Ecosystem, 2001-2006, and its implications for Kenya’s lion population. *National Parks*, May, 1–9.

Funston, P. J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., Durant, S., Packer, C., Mosser, A., & Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281, 56–65.

Funston, P. J., Mills, M. G. L., Biggs, H. C., & Richardson, P. R. K. (1998). Hunting by male lions: Ecological influences and socioecological implications. *Animal Behaviour*, 56, 1333–1345.

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, 23, 559-581.

Gavin, T. A. (1991). Why Ask “Why”: The Importance of Evolutionary Biology in Wildlife Science. *The Journal of Wildlife Management*, 55, 760.

Goldman, M. J., de Pinho, J. R., & Perry, J. (2010). Maintaining Complex Relations with Large Cats: Maasai and Lions in Kenya and Tanzania. *Human Dimensions of Wildlife*, 15, 332–346.

Graler, B., Pebesma, E., & Heuvelink, G. (2016). Spatio-temporal Interpolation using gstat. *The R Journal*, 8, 204–218.

Gumbricht, T., McCarthy, J., & McCarthy, T. (2000). Portraying the geophysiology of the Okavango Delta, Botswana. In *Proceedings of the 28th International Symposium on Remote Sensing of the Environment*, *Cape Town, South Africa, ICRSE* (Vol. 4, pp. 10-13).

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, 267, 309–322.

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, 139, 219–229.

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

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

Henschel, P., Petracca, L. S., Hunter, L. T. B., Kiki, M., Sewadé, C., Tehou, A., & Robinson, H. S. (2016). Determinants of distribution patterns and management needs in a Critically Endangered lion *Panthera leo* population. *Frontiers in Ecology and Evolution*, *4*, 110.

Hickey, J. R., & Sollmann, R. (2018). A new mark-recapture approach for abundance estimation of social species. *PloS ONE*, 13, e0208726.

Hiemstra, P. H., Pebesma, E. J., Twenhöfel, C. J. W., & Heuvelink, G. B. M. (2009). Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. *Computers and Geosciences*, 35, 1711–1721.

Hobbs, N. T., & Hanley, T. A. (1990). Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of Wildlife Management*, 515–522.

Hopcraft, G. J. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74, 559–566.

Inman, V., & Lyons, M. (2020). *Automated Inundation History Mapping over Large Areas using Landsat and Google Earth Engine*. https://www.preprints.org/manuscript/202003.0038.

IUCN SCSG. (2006). Regional conservation strategy for the lion *Panthera leo* in Eastern and Southern Africa. *IUCN SSC Cat Specialist Group*.

Karanth, K. U. (1995). Estimating tiger (*Panthera tigris*) populations from camera-trap data using capture-recapture models. In *Biological Conservation*, 71, 333-338.

Karanth, K. U. (2011). India's tiger counts: the long march to reliable science. *Economic and Political Weekly*, 22–25. https://www.jstor.org/stable/41152336. Accessed June 2019.

Karanth, K. U., Chundawat, R. S., Nichols, J. D., & Kumar, N. S. (2004). Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. *Animal Conservation*, 7, 285–290.

Karanth, K. U., Gopalaswamy, A. M., Kumar, N. S., Vaidyanathan, S., Nichols, J. D., & Mackenzie, D. I. (2011). Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology*, 48, 1048–1056.

Kelly, M. J., Karen Laurenson, M., Fitzgibbon, C. D., Anthony Collins, D., Durant, S. M., Frame, G. W., Bertram, B. C. R., & Caro, T. M. (1998). Demography of the serengeti cheetah (*Acinonyx jubatus*) population: The first 25 years. *Journal of Zoology*, 244, 473–488.

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: What limits lions *Panthera leo* in katavi national park, western Tanzania? *Oryx*, 43, 52–59.

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E. K., & Marshal, J. P. (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.

Kotze, R., Marshal, J. P., Winterbach, C. W., Winterbach, H. E. K., & Keith, M. (2021). Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment. *African Journal of Ecology*, 59, 63–73.

LeFlore, E. G., Fuller, T. K., Tomeletso, M., & Stein, A. B. (2019). Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation*, 18, e00592.

Li, J., Wang, D., Yin, H., Zhaxi, D., Jiagong, Z., Schaller, G. B., Mishra, C., McCarthy, T. M., Wang, H., Wu, L., Xiao, L., Basang, L., Zhang, Y., Zhou, Y., & Lu, Z. (2014). Role of Tibetan buddhist monasteries in snow leopard conservation. *Conservation Biology*, 28, 87–94.

Lichtenfeld, L. L., Trout, C., & Kisimir, E. L. (2015). Evidence-based conservation: predator-proof bomas protect livestock and lions. *Biodiversity and Conservation*, 24, 483–491.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A. E., Kasiki, S., Loveridge, A., Macdonald, D. W., Mandisodza, R., Mgoola, W., Miller, S. M., Nazerali, S., Siege, L., Uiseb, K., & Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation*, 209, 137–149.

Loveridge, A. J, & Canney, S. (2009). African lion distribution modelling project. *Horsham, UK*:*WildCRU.*

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). African lions on the edge: reserve boundaries as “attractive sinks”: In D. W. Macdonald & A. J. Loveridge (Eds.), *Biology and Conservation of Wild Felids* (p. 183). Oxford University Press.

Loveridge, A. J., Searle, A. W., Murindagomo, F., & Macdonald, D. W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, *134*(4), 548–558.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W. (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.

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, 54, 815–825.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, 172, 101-108.

Mladenov, N., Gardner, J. R., Flores, N. E., Mbaiwa, J. E., Mmopelwa, G., & Strzepek, K. M. (2007). The value of wildlife-viewing tourism as an incentive for conservation of biodiversity in the Okavango Delta, Botswana. *Development Southern Africa*, 24, 409–423.

Mosser, A., Fryxell, J. M., Eberly, L., & Packer, C. (2009). Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, 12, 1050–1060.

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78, 359-370.

Murray-Hudson, M., Wolski, P., Cassidy, L., Brown, M. T., Thito, K., Kashe, K., & Mosimanyana, E. (2015). Remote Sensing-derived hydroperiod as a predictor of floodplain vegetation composition. *Wetlands Ecology and Management*, 23, 603–616.

Murray-Hudson, M., Wolski, P., Murray-Hudson, F., Brown, M. T., & Kashe, K. (2014). Disaggregating hydroperiod: components of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands*, 34, 927–942.

Murray-Hudson, M., Wolski, P., & Ringrose, S. (2006). Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. *Journal of Hydrology*, 331, 73–84.

Nichols, J., & Karanth, K. (2002). Statistical concepts: estimating absolute densities of tigers using capture-recapture sampling. In *Monitoring tigers and their prey: A manual for wildlife researchers, managers and conservationists in tropical Asia* (pp 121-137). Bangalore, India: Centre for Wildlife Studies.

Norton, P. (1990). How many leopards? A criticism of Martin and de Meulenaer's population estimates for Africa. *South African Journal of Science*, 86, 218.

O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.

Ogutu, J. O., Piepho, H.-P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara-Serengeti ungulates in relation to land use changes. *Journal of Zoology*, 278, 1–14.

Osano, P. H., Said, M. Y., de Leeuw, J., Ndiwa, N., Kaelo, D., Schomers, S., Birner, R., & Ogutu, J. O. (2013). Why keep lions instead of livestock? Assessing wildlife tourism-based payment for ecosystem services involving herders in the Maasai Mara, Kenya . *Natural Resources Forum*, 37, 242–256.

Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical Inference from capture data on closed animal populations. *Wildlife Monographs*, 62*,* 3-135.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., & Sinclair, A. R. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, 307, 390–393.

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, 106, 497–508.

Pledger, S. (2000). Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics*, 56, 434–442.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A., Meloro, C., Wich, S. A., McNutt, J. W. & Hayward, M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, 29, R681-R682.

R Core Team. (2019). *R: A language and environment for statistical computing* (3.6.1). R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., van As, J., & VanderPost, C. (2006). Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences*, 68, 310–337.

Ramesh, T., Kalle, R., Rosenlund, H., & Downs, C. T. (2017). Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecology and Evolution*, 7, 1964–1973.

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology,* 84, 2092-2107.

Rich, L. N., Miller, D. A. W., Muñoz, D. J., Robinson, H. S., McNutt, J. W., & Kelly, M. J. (2019). Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data. *Biological Conservation,* 233*,* 12-20.

Rich, L. N., Miller, D. A. W., Robinson, H. S., McNutt, J. W., & Kelly, M. J. (2017). Carnivore distributions in Botswana are shaped by resource availability and intraguild species. *Journal of Zoology*, 303, 90–98.

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

Riggio, J. S. (2011). *The African Lion (*Panthera leo leo)*: A continent-wide species distribution study and population analysis*. PhD Thesis. Duke University.

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

Rogan, M. S., Lindsey, P. A., Tambling, C. J., Golabek, K. A., Chase, M. J., Collins, K., & McNutt, J. W. (2017). Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, 210, 233–242.

Royle, J. A., Chandler, R. B., Sun, C. C., & Fuller, A. K. (2013). Integrating resource selection information with spatial capture-recapture. *Methods in Ecology and Evolution*, 4, 520–530.

Royle, J. A., Karanth, K. U., Gopalaswamy, A. M., & Samba Kumar, N. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, 90, 3233-3244.

Royle, J. A., & Young, K. V. (2008). A hierarchical model for spatial capture recapture data. *Ecology*, 8, 2281–2289.

Sandell, M. (1989). The Mating Tactics and Spacing Patterns of Solitary Carnivores. In J. L. Gittleman (Ed.), *Carnivore Behavior, Ecology, and Evolution* (pp. 164–182). Springer US.

Saunders, N. J. (1994). Predators of culture: Jaguar symbolism and Mesoamerican elites. *World Archaeology*, 26, 104–117.

Schaller, G. (1972). *The Serengeti Lion: A study of predator-prey relations*. University of Chicago Press.

Silveira, L., Jácomo, A. T. A., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: A comparative evaluation. *Biological Conservation*, 114, 351–355.

Smallwood, K. S., & Fitzhugh, E. L. (1993). A rigorous technique for identifying individual mountain lions *Felis concolor* by their tracks. *Biological Conservation*, 65, 51–59.

Sogbohossou, E. A., Kassa, B. D., Waltert, M., & Khorozyan, I. (2018). Spatio-temporal niche partitioning between the African lion (*Panthera leo leo*) and spotted hyena (*Crocuta crocuta*) in western African savannas. *European Journal of Wildlife Research*, 64.

Soisalo, M. K., & Cavalcanti, S. M. C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129, 487–496.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56, 740–749.

Sollmann, R., Furtado, M. M., Gardner, B., Hofer, H., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2011). Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation*, 144, 1017–1024.

Sollmann, R., Mohamed, A., & Kelly, M. J. (2013a). Camera trapping for the study and conservation of tropical carnivores. *Raffles Bulletin of Zoology*, *28*, 21–42.

Sollmann, R., Mohamed, A., & Samejima, H. (2013b). Risky business or simple solution– Relative abundance indices from camera-trapping. *Biological Conservation*, 159, 405–412.

Stander, P. E. (1998). spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology,* 25, 378–385.

Strampelli, P., Andresen, L., Everatt, K. T., Somers, M. J., & Rowcliffe, J. M. (2018). Leopard *Panthera pardus* density in southern Mozambique: Evidence from spatially explicit capture-recapture in Xonghile Game Reserve. *Oryx*, 1–7.

Strampelli, P., Searle, C. E., Smit, J. B., Henschell, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., & Dickman, A. J. (2022). Camera trapping and spatially explicit capture-recapture for the monitoring and conservation management of lions: Insights from a globally important population in Tanzania. *Ecological Solutions and Evidence*, 3, e12129.

Treves, A., & Karanth, K. U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, 17, 1491–1499.

Tumenta, P. N., Kok, J. S., Van Rijssel, J. C., Buij, R., Croes, B. M., Funston, P. J., De Iongh, H. H., & Udo de Haes, H. A. (2010). Threat of rapid extermination of the lion (*Panthera leo leo*) in Waza National Park, Northern Cameroon. *African Journal of Ecology*, 48, 888-894.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements:

Waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337–351.

van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*, 206, 97–112.

van Rooyen, J. (2016). *Livestock production and animal health management systems in communal farming areas at the wildlife-livestock interface in southern Africa*. PhD Thesis. University of Pretoria.

Voeten, M. M., & Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, 120, 287–294.

Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., Chifunte, C., Midlane, N. & Simukonda, C. (2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications*, 31, e02298.

Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J., & Shanas, U. (2015). What is an apex predator? *Oikos*, 124, 1453–1461.

Weise, F. J., Fynn, R. W. S., Stein, A. B., Tomeletso, M., Somers, M. J., & Périquet, S. (2019a). Seasonal selection of key resources by cattle in a mixed savannah-wetland ecosystem increases the potential for conflict with lions. *Biological Conservation*, 237, 253–266.

Weise, F. J., Hauptmeier, H., Stratford, K. J., Hayward, M. W., Aal, K., Heuer, M., Tomeletso, M., Wulf, V., Somers, M. J., & Stein, A. B. (2019b). Lions at the gates: Trans-disciplinary design of an early warning system to improve human-lion coexistence. *Frontiers in Ecology and Evolution*, *7*, 1–19.

Whitesell, C. A. (2019). *Movements of lions and other carnivores in relation to domestic and wild prey in northwestern Botswana*. PhD Thesis. University of California Davis.

Williams, V. L., Newton, D., Loveridge, A. J., & Macdonald, D. W. (2015). Bones of Contention : An Assessment of the South African Trade in African Lion *Panthera leo* Bones and Other Body Parts. *TRAFFIC, Cambridge, UK & WildCRU, Oxford, UK.*

Winterbach, C. W., Winterbach, H., Rutina, L., & Kat, P. W. (1998) Results of the coordinated dry season lion survey for the Okavango Delta, 1998. *Tau Constultants, Unpublished report. Maun, Botswana.*

Winterbach, H. E., Winterbach, C. W., & Somers, M. J. (2014). Landscape suitability in Botswana for the conservation of its six large African carnivores. *PloS ONE*, 9, e100202.

Wolski, P., Murray-Hudson, M., Thito, K., & Cassidy, L. (2017). Keeping it simple: Monitoring flood extent in large data-poor wetlands using MODIS SWIR data. *International Journal of Applied Earth Observation and Geoinformation*, 57, 224–234.

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

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

Chapter 3

Changes in landscape structure and configuration influence home range size in lions (*Panthera leo*) under different flood conditions in a seasonally-flooded wetland

Abstract

Home ranges summarize the relationships between movement of individuals and the temporal and spatial distribution of resources and are useful indices for quantifying relationships between organisms and their environment. Carnivore home ranges are largely influenced by availability of prey, and factors determining interspecific and intraspecific differences have been well-detailed. There has been little work to date, however, on the relationship between home range size and indices of landscape structure and configuration, as these are often considered at much larger spatial scales, or as more important for large herbivores. We used movement data from the African lion (*Panthera leo*) in a seasonally flooded environment, the Okavango Delta, to investigate the relationship between home range size and indices of landscape and habitat structure under varying flood conditions, while taking sex differences into account. At maximum flood, male and female home range sizes did not differ, and home range sizes were larger where there was increased fragmentation of land. This supports the prediction of the resource dispersion hypothesis that states territory increases with increased dispersion of resources. At minimum flood, however, they showed divergent strategies typical of felids: female home range size decreased with increasing land connectivity, increasing habitat heterogeneity and increasing prey abundance, suggesting area minimization to meet energetic needs. Male home range sizes were significantly larger during this season, and inversely related to habitat heterogeneity and proportion of riparian woodland. As habitat heterogeneity equates with greater prey diversity in the Okavango, we suggest that males are maximizing access to

females by selecting high quality habitat sought out by females. Both extended wet and extended dry periods could reduce carrying capacity for lions by fragmenting dry land or decreasing habitat heterogeneity, both of which would necessitate larger home ranges.

Introduction

Home ranges are defined as areas in which individuals can meet their needs, including the acquisition of resources such as food, mates, breeding sites and resting sites, as well as balance interactions with potential competitors or predators (Broekhuis et al., 2013; Burt, 1943; Gardiner et al., 2019; Johnson, 1980; Jones & Davidson, 2016; Valeix et al., 2009). As individuals must adjust their movement behaviour to match the spatial and temporal availability of these resources and risks, the home range, which encapsulates movements over discrete time periods, is an appropriate metric to quantify the influence of resource fluctuations on species in a particular environment (Gardiner et al., 2019; Jones & Davidson, 2016; Snider et al., 2021). Ultimately, home range size and distribution will affect the carrying capacity for a particular habitat or protected area; understanding the scope of the temporal and spatial variation that influences home ranges is thus relevant to solving conservation issues such as preservation, restoration and adaptative management in response to habitat modifications (Barlow et al., 2011; Duncan et al., 2015; Jones & Davidson, 2016; Morales et al., 2010; Snider et al., 2021). It is thus not surprising that the factors influencing home range size have been well studied across a range of species of conservation concern (Gittleman & Harvey, 1982; Herfindal et al., 2005a; Loveridge et al., 2009; Snider et al., 2021; Trewhella et al., 1988).

For carnivores, home range sizes are largely influenced by the availability of prey resources, particularly their abundance and distribution across the landscape (Duncan et al., 2015; Gittleman & Harvey, 1982). According to predictions of the resource dispersion hypothesis (RDH), home range sizes will increase as resources become more dispersed, and the richness of resources within a patch will influence the number of conspecifics patches can accommodate, with higher richness translating into larger groups (MacDonald, 1983). Aside from resource availability, interspecifically, factors such as size, metabolic needs and diet breadth all play a role (Gittleman & Harvey, 1982), while intraspecifically, intrinsic factors such as density and social structure, and extrinsic factors such as habitat type, quality and local climatic conditions which influence the spatial and temporal distribution of resource availability, may factor into home range size determination (Duncan et al., 2015).

Lastly, home range size may be influenced by individual variation, including factors such as breeding status, age and sex (Hiller et al., 2015; Mangipane et al., 2018; Rauset et al., 2015). For carnivores in particular, differences in home range size between sexes have been linked to differences in priority with regards to resource acquisition (Clutton-Brock, 1989; Sandell 1989). According to optimal foraging theory, there are two main strategies for resource acquisition; area minimization, where individuals seek to use the smallest area possible to meet their energetic needs, and resource maximization, where individuals attempt to maximize access to resources across the landscape (Mitchell & Powell, 2004, 2007). Across the order Carnivora, females generally adopt the former approach, selecting resources economically so that energy can be geared towards reproduction, while males adopt the latter, also seeking to increase reproductive success by maximizing access to females (Kotze et al., 2012; Loveridge et al., 2009; Marker & Dickman, 2005). Depending on prevailing ecological conditions, however, individuals may switch between these strategies (Mitchell & Powell, 2004).

To date, the influence of landscape configuration and heterogeneity on home range size of large carnivores has received little attention (Gardiner et al., 2019; Kie et al., 2002). Most studies, including those on metapopulation management, consider the influence of habitat patch size between sub-populations, and how landscape configuration influences connectivity between patches to allow for processes such as dispersal and persistence of sub-populations (Crooks et al., 2011; Hearn et al., 2018; Kramer-Schadt et al., 2004; Wiegand et al., 2005). At the population level, the influence of habitat fragmentation on the resilience of different species has been investigated largely in the context of adaptation to habitat loss because of urbanization (Crooks, 2002; Haidir et al., 2021; Hearn et al., 2018; Linkie et al., 2006). These approaches, however, do not account for response of individuals to habitat structure and the role of landscape configuration and composition in determining the size of the home range (but see Hiller et al., 2015; Mangipane et al., 2018; Snider et al., 2021).

Conversely, there is a growing body of literature on the role of landscape structure, composition and heterogeneity in determining home range size for large herbivores (Bartlam-Brooks et al., 2013; Kie et al., 2002; Saïd & Servanty, 2005). These studies have shown that landscape metrics such as edge habitat, habitat heterogeneity and patch size and configuration of preferred habitat explain large proportions of variation in herbivore home range size (Bartlam-Brooks et al., 2013; Kie et al., 2002; Lovari et al., 2017). In roe deer for example, edge density within home ranges was negatively correlated with home range size, as roe deer prefer edge habitats for browsing (Lovari et al., 2017; Morellet et al., 2011; Saïd & Servanty, 2005). Even within the same ecosystem, metrics related to habitat composition can reveal differences in selection of home ranges in relation to habitat. In the Okavango Delta, for example, zebra (*Equus quagga*) in the central Delta had smaller home ranges than those on the periphery, and this difference was largely attributed to indices of higher habitat heterogeneity in the central Okavango (Bartlam-Brooks et al., 2013). As prey distribution and abundance are known to influence home ranges of carnivores (Herfindal et al., 2005; Loveridge et al., 2009; Marker & Dickman, 2005; Schaller, 1972), it is likely that carnivore home range sizes would be similarly affected by landscape structure.

To determine the potential influence of landscape indices such as habitat structure and heterogeneity on home range sizes for large carnivores, I used data from the African lion (*Panthera leo*) in the Okavango Delta, a seasonally flooded wetland in north-western Botswana. The annual flood pulse results in significant seasonal contractions of land availability, and over longer time scales, shifts habitat composition based on flood characteristics such as duration and frequency (Murray-Hudson et al., 2014, 2015; Thito et al., 2016). Lions must therefore adapt their home ranges on a seasonal basis in response to local flood conditions and maintain home ranges that will account for shifts in habitat in the long-term. Lions live in social groups called prides, composed of related adult females and their offspring, as well as accompanying pride males (Schaller, 1972; van Orsdol et al., 1985). Prides maintain high site fidelity in home range use on an annual basis, and successful defence of the home range plays a large role in reproductive success (Packer & Pusey, 1987). As with other large carnivores, home range sizes are closely tied to prey abundance during the ‘lean season’ when prey abundance is at its lowest (Bertram, 1975; Loveridge et al., 2009; Spong, 2002). When prey is more dispersed (Mbizah et al., 2019; Zehnder et al., 2018), lion home ranges expand to meet their metabolic needs. Lions, too, exhibit divergent strategies in space use based on sex, where females prioritize access to food resources, and males try to maximize access to females (Loveridge et al., 2009; Schaller, 1972).

I therefore used lion home range data from areas characterized by high variation in seasonal flood levels, to examine the influence of landscape structure on lion home range size, comparing these indices across maximum and minimum flood conditions. Firstly, I examined landscape indices related to the availability of dry land in each season, focusing on indices measuring fragmentation and connectivity of dry land. Secondly, I examined the influence of landscape indices related to habitat proportions and heterogeneity, which can be used as proxies for habitat quality. In both cases I took differences between sexes into account and included a prey variable due to its influence on lion space use. I hypothesized that home range size would increase during the maximum flood season as lions must travel further to find smaller patches of dry land (Midlane, 2013), while during the minimum flood season, home ranges would be smaller. With regards to habitat selection in both seasons, I hypothesized that higher habitat heterogeneity, and higher proportions of open woodlands and riparian woodlands, would be negatively related to home range size in both seasons (Mangipane et al., 2018). I also hypothesized that there would be clear sex differences in home range size between males and females in both seasons, and that female home range size would be more strongly influenced by prey availability than males (Loveridge et al., 2009).

Methods

Study area

This study took place in the Okavango Delta in north-western Botswana, a seasonally inundated wetland surrounded by the arid Kalahari ecosystem. The annual flood pulse, which typically arrives in April, is the result of seasonal rainfall in an upstream catchment in the Angolan highlands (Ramberg et al., 2006). From the highlands, the flood water travels down the Okavango River, through the Caprivi strip in Namibia, ending in a large alluvial fan in Botswana (Gumbricht et al., 2000; Ramberg et al., 2006). The flood pulse arrives in Botswana during the dry season, producing a green flush of vegetation that acts as a key bridging resource, particularly for large herbivores, when forage quality in an otherwise arid system is typically at its lowest (Fynn et al., 2015; Yoganand & Owen-Smith, 2014). This ebb and flow of floodwater produces a diversity of habitat types, the compositions of which are largely driven by flood characteristics across both short and long-term temporal scales such as depth, duration and frequency (Murray-Hudson et al., 2015; Ramberg et al., 2006). Habitat diversity is also influenced by small changes in elevation in an otherwise flat landscape; low areas become inundated and form the seasonal floodplains, while slightly elevated areas make up the islands in between channels (Ellery et al., 1993; McCarthy et al., 2012). Islands vary in size and are generally larger towards the Delta's drier periphery (Ramberg et al., 2006). Riparian woodlands with water-dependent trees make up island fringes, and riparian woodlands transition into open or bushed woodland towards the island centres which may also have short grasslands or saline centres (Ellery et al., 1993). Larger islands which are never flooded, and have a lower water table, are characterized by sandveld vegetation communities such as *Colophospermum mopane, Lonchocarpus nelsii* or *Vichella* woodlands and mixed bushland (Ellery et al., 1993; Ramberg et al., 2006).

Study animals

I used data from 14 collared lions from the southern (n=9), western (n=2) and northern Okavango Delta (n=3); areas characterized by large variation in seasonal flooding patterns. All individuals use in the analysis were resident males (n=7) and resident females (n=7), and all were adults with the exception of a one male in the southern Delta (3 years old) that remained resident with the females in his cohort and did not yet disperse over the study period. Collared lions belonged to various research projects across the Okavango Delta that had been fitted with global-positioning system (GPS) enabled collars between 2013 and 2016, using Botswana registered veterinarians and with permission from the Botswana Department of Wildlife and National Parks (permit numbers EWT 8/36/4 XVIV(92), EWT 8/36/4 XX(V (30) and EWT 8/36/4 XXXIII (36)). Collars were manufactured by Vectronics Aerospace GmbH (Berlin, Germany) or Africa Wildlife Tracking (Pretoria, South Africa) and data collection schedules varied: in the southern Okavango (n=9), collars recorded 18 locations a day (two-hourly in the day and hourly at night), in the western delta (n=2) collars recorded 12 locations a day at two-hourly intervals, and in the northern Okavango (n=2) 6 points of data on a four-hourly schedule were collected each day. Data was screened for outlying points by checking distances between points and removing those that were biologically implausible (D’Eon et al., 2002). In the northern and western Delta, lions were collared to monitor conflict prevalent on the borders of the wildlife management areas, and as such information on pride structures was not collected due to their shy nature and tendency to avoid people. Similarly, in the southern Delta, a few of the residents collared lived in swampy areas that could only be accessed for a few months of the year. The density of lions is highest in the southern part of the study area, followed by the western and then the northern regions of the Okavango (Loveridge et al., *unpublished data*).

Data analysis

Home Range Analysis

To investigate the effects of flooding and habitat structure on lion home range sizes, we used geolocations from lions that coincided with the maximum (June to August) and minimum (March to May) flood conditions for the year 2014 to 2016, as determined through data collected by the Okavango Research Institute, to construct home ranges. We calculated home range sizes using kernel density estimates (KDE) and used the 95% isopleth to represent the home range. KDE uses a utilization distribution, which accounts for intensity of use in different areas, and as such is less influenced by outliers and data points on the home range periphery than other methods such as minimum convex polygon (Worton, 1989). This allows for a more accurate depiction of home range use, and inclusion of areas not utilised is therefore less likely (Hemson et al., 2005; Powell, 2000). We used the *href* smoothing factor, which takes sample size and standard deviation between points for each input dataset into account and is more likely to appropriately smooth kernels for large sample sizes, as suggested by Hemson et al., (2005). All home range analyses were conducted in R (R Core Team, 2021) using the package *adeHabtiatHR* (Calenge, 2006). I used Mann-Whitney U tests to compare home range sizes between males and females in each flood season, and Wilcoxon Matched-Pairs tests to compare seasonal differences in home range size for males and females respectively.

Habitat and landscape structure

To examine the influence of maximum and minimum flood conditions, I then created monthly flood maps, depicting dry versus wet pixels, using Landsat 8 imagery with a 30m x 30m resolution as described in Inman and Lyons (2020), and used the month with the highest and lowest flood extent to depict flood conditions for maximum and minimum seasons respectively. To compare differences in habitat and landscape structure of home ranges between the maximum and minimum flood seasons, I used the package *landscapemetrics* (Hesselbarth et al., 2019) in R (R Core Team, 2021), which measures landscape metrics as defined in the software Fragstats (McGarigal et al., 2012) to derive indices related to landscape configuration. Using inundation maps of dry and wet pixels, I measured 4 metrices which described landscape structure: number of patches of dry land (NP), as a measure of fragmentation in dry land caused by flooding; largest patch index (LPI), which measures the relative size of the largest patch of dry land; division (DIVISION), which increases as patches become more fragmented; and mean radius of gyration (GYRATE_MN), which measures patch extent across the landscape (see Table 3. 1.). For indices related to habitat structure, we used a 30m x 30m habitat map created by Collins et all. (2019), and measured the relative proportion of three habitat types, namely riparian woodland (RIP), open woodland (OWL) and open grassland (OGL), as well as mean shape index (SHAPE_MN) which measures patch complexity and is an index of habitat heterogeneity (see Table 3. 1. for detailed definitions). For each home range, I ensured that land and habitat indices were extracted from the corresponding year.

Prey

Lastly, as lion home range size is often correlated with prey biomass (Loveridge et al., 2009; Schaller, 1972; van Orsdol et al., 1985) I used a camera trap based prey abundance index estimated across the Okavango (Loveridge et al., *unpublished),* which briefly modelled prey encounter rates (using generalised additive modelling) of lion preferred prey species, independently recorded across multiple camera trap surveys, with a suite of habitat and anthropogenic covariates and per prey body size (small prey <100kg, medium prey >100kg and large prey > 250kg). Prey included in the analyses were selected based on observations in the field in the southern Delta of lion kills between 1997 and 2002 (Christiaan

Winterbach, pers. obs). Small prey thus included all mongoose species, springhare (*Pedets capensis*), baboon (*Papio ursinus*), warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*), red lechwe (*Kobus leche*), reedbuck (*Redunca arundinum*) and tsessebe (*Damaliscus lunatus*), medium prey included kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*) and blue wildebeest (*Connochaetes taurinus*), and large prey included zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), roan antelope (*Hippotragus equinus*) and buffalo (*Syncerus caffer*). The three modelled abundance layers (per body size) were then summed and this provided an indication of general prey availability in the area, with the overall mean abundance being extracted at each home range polygon. For all prey, prey abundance was highest in the western study area, followed by the southern and then northern study area (Loveridge et al. *unpublished data*).

Statistical Analysis

I tested for collinearity between all predictor variables before analysis, and found that that there were no correlations (Pearson's r<|0.7|). All covariates were therefore retained for further analysis. I tested the relationship between home range size and each index using Pearson's correlation tests in R (R Core Team, 2021).

Table 3. 1. Landscape indices used to describe the distribution of land patches at maximum and minimum flood, and the heterogeneity of habitats within home ranges at maximum and minimum flood for African lion (*Panthera leo*) home ranges in the Okavango Delta Botswana. Index descriptions were obtained from the landscapemetrics package (Hesselbarth et al., 2019).

Landscape Index	**Description**
Number of patches (NP)	Aggregation metric which describes the level of fragmentation of a particular class. NP = 1 for 1 patch and increases with number of patches of dry land.
Division	Aggregation metric related to the probability that two random cells are not part of the same land patch. Indicates to some extent the dispersion of land across the landscape, in contrast to number of patches. Value lies between 0, for only one patch present, and 1, if every patch of land is as small as one pixel and separated by water.
Largest patch index (LPI)	Area and edge metric which describes the dominance of the amount of land; it measures the percentage of the home range covered by the largest patch of land. Values vary between 0 and 100, and approaches 0 as the largest patch decreases and 100 if the land patch covers the whole home range
Mean radius of gyration	Area and edge metric, measures the extent of the landscape patch across the home range. The value is 0 if every patch is a single cell, but increases when a

	land patch (like an island) is large and compact, or elongated and less compact but still extends far across the home range. It can be interpreted as a measure of the traversability across the home range if the lion is confined to a single patch.
Mean shape index (MSI)	Shape metric, which is a measure of shape complexity, where the value is 0 if all patches are square and increases as patch shape becomes more complex. This is used as a heterogeneity index for habitats within the home range.

Results

Median home range sizes for females (225.45 km^2, IQR 158.60km^2; Table 3. 2.) in the maximum flood season were not significantly different (Z = 1.72 , p = 0.097; Figure 3. 2.) from those of males (349.17 km^2, IQR = 159.11 km^2) (Figure 3. 1. and 3. 2.). Conversely, female home ranges (Median = 186.17 km^2, IQR = 72.37 km^2; Table 3. 2.) were significantly smaller (Z = 3.13, p = 0.002, Figure 3. 2.) than male home ranges (366.03km^2, IQR = 234.97 km^2) during the minimum flood season (Figure 3. 1. and 3. 2.). There were no significant inter-seasonal differences in home range size for females (Z = -1.35, p = 0.22) or males (Z = 1.18, p = 0.30; Figure 3. 1.).

Table 3. 2. Home range sizes (95% kernel density isopleth) for male and female lions in the Okavango Delta during minimum flood conditions (Mar-May) and maximum flood conditions (Jun-Aug). The comparisons are drawn between maximum and minimum flood within the same year, with data from individuals drawn from the years 2014 to 2016.

ID	Sex	Study area	Minimum flood HR (km^2)	Maximum Flood HR (km^2)
F1	Female	South	186.71	109.99
F2	Female	South	86.10	104.99
F3	Female	South	213.93	275.01
F4	Female	South	203.22	344.42
F5	Female	North	186.31	401.62
F6	Female	North	228.88	192.25
F7	Female	West	62.69	225.45
M1	Male	South	366.06	349.16
M2	Male	West	540.93	576.39
M3	Male	South	323.64	357.19
M4	Male	South	246.41	146.36
M5	Male	North	789.94	635.42
M6	Male	South	552.30	322.59
M7	Male	South	299.65	292.76

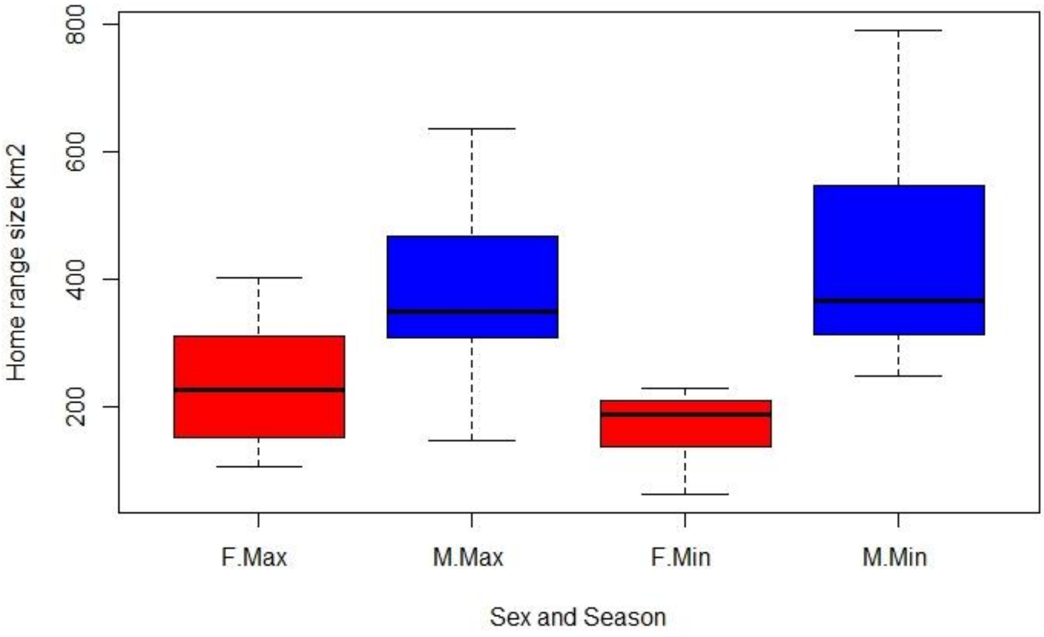

Figure 3. 1. Differences in male (M – blue) and female (F – red) home range size for African lions (Panthera leo) in the Okavango Delta Botswana. Seasons depicted are the maximum flood season (June to August) and minimum flood season (March to May) from data collected between 2014 and 2016.

As there were no significant differences between male and female home range sizes during the maximum flood season, I pooled these data when examining the relationship between home range size and landscape metrics. For landscape metrics related to dry land availability, only number of patches was significantly positively correlated with home range size at maximum flood, and home range size was not significantly influenced by division or largest patch index (Table 3. 3.). For metrics related to habitat, there was a marginally significant negative relationship between home range sizes and proportion of riparian woodland (Table 3. 3.). However, none of the other habitat types, including open woodland or open grassland, nor mean shape index, significantly influenced home rang size (Table 3. 3.). Lastly, prey availability did not have an influence on home range size at maximum flood (Table 3. 3.).

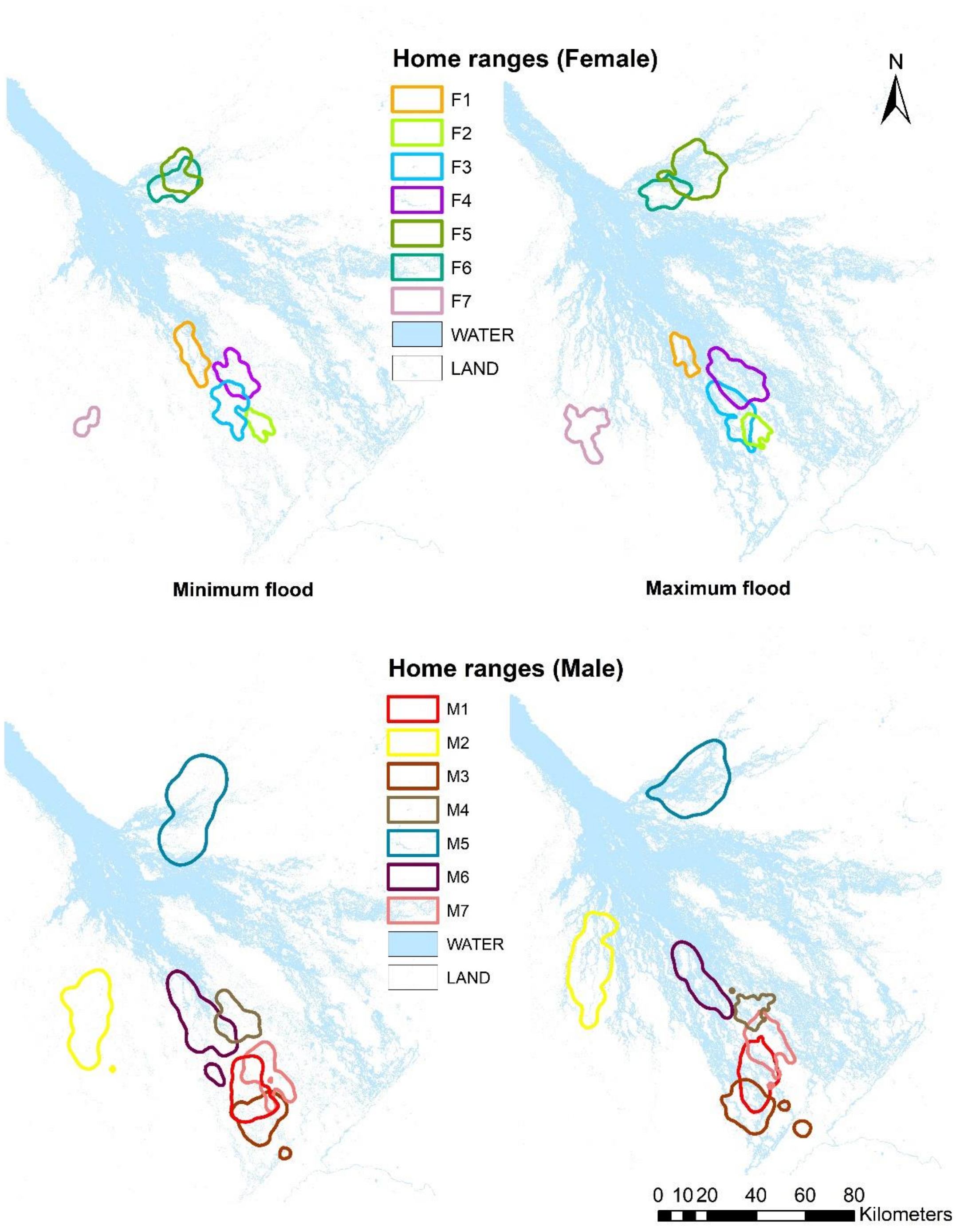

Figure 3. 2. Home ranges (95% kernel density isopleths) for male and female African lions (*Panthera leo*) in the Okavango Delta, Botswana, under minimum (left, March - May) and maximum (right, June - August) flood conditions. Data was collected between 2014 and 2016.

As there were significant differences between home range size of males and females during minimum flood season, I measured correlations between habitat and landscape metrics and home range sizes separately for each sex. For females, minimum flood season home range size was negatively influenced by radius of gyration (Table 3. 3.), and no longer influenced by the number of patches. For habitat variables, female home range size was not significantly influenced by any particular habitat type but was significantly negatively correlated with mean shape index and mean prey availability (Table 3. 3.). Male home range size during the flood minimum was not significantly influenced by any indices associated with availability of dry land (Table 3. 3.) but was negatively correlated with mean shape index (Table 3. 3.). Male home range size showed a strong negative correlation with proportion of riparian woodland (Table 3. 3.) but there was no significant relationship between male home range size and mean prey availability (see Table 3. 3.).

Table 3. 3. Correlations between home range size in male and female African lions (*Panthera leo*) in the Okavango Delta, Botswana, and various landscape indices related to available land and habitat during maximum (June to August) and minimum (March to May) flood conditions. Home ranges during maximum flood were not significantly different in size, and all home ranges were therefore pooled in this season. Indices in bold and italics are significant, * indicates marginally significant.

	Maximum flood			**Minimum flood**					
Sex	Combined			Female			Male		
	r	df	p	r	df	p	r	df	p
Land indices									
Number of patches	***0.749***	***12***	***0.044***	0.583	5	0.170	0.658	5	0.108
Division	0.270	12	0.350	0.646	5	0.117	0.204	5	0.660
Largest patch index	-0.274	12	0.343	-0.566	5	0.185	-0.144	5	0.758
Radius of gyration	-0.439	12	0.116	***-0.927***	***5***	***0.003***	0.197	5	0.672
Habitat indices									
Riparian woodland	-0.516	12	0.059*	0.002	5	0.996	***-0.834***	***5***	***0.020***
Open woodland	-0.092	12	0.753	-0.649	5	0.115	0.130	5	0.781
Open grassland	0.116	12	0.692	-0.663	5	0.105	-0.227	5	0.624

Mean shape index	-0.020	12	0.947	***-0.793***	***5***	***0.033***	***-0.767***	***5***	***0.044***
Prey indices									
Mean prey availability	0.215	12	0.460	***-0.784***	***5***	***0.037***	0.104	5	0.825

Discussion

This study investigated the influence of indices of landscape structure and composition on home range size in a large carnivore, the African lion *(Panthera leo*) in a seasonally flooded environment - the Okavango Delta. Changes in the number of land patches, which can be interpreted as the degree of fragmentation of dry land, was the most important factor in determining home range size for both sexes when the flood was at its peak. At minimum flood, however, male and female home range sizes were driven by different factors, as expected; female home range was negatively correlated with prey biomass and habitat shape complexity, while male home range size was negatively correlated with habitat complexity and proportion of riparian woodland. The degree to which land patches were connected across the home range also influenced female home range size at minimum flood, with higher connectivity leading to smaller home ranges. These results reveal that landscape structure and composition, particularly in heterogeneous environment in which seasonal fluctuation is extreme, should not be ignored when examining home range size, and may even explain a large proportion of the variation observed in home range size estimations (Kie et al., 2002; Mangipane et al., 2018).

In accordance with my expectations, when floods were at their maximum extent, lion home range size was positively correlated with number of patches; therefore, higher fragmentation of habitat through flooding necessitated larger home ranges. Similar patterns have been observed in other wetlands in Kafue National Park, Zambia (Midlane, 2013) and Waza National Park, Cameroon (Tumenta et al., 2013). As there were no other factors correlated with home range size in this season, and there were likewise no differences in home range size between males and females, this suggests that when floods are at their maximum, resulting landscape fragmentation is the most important factor influencing home range size, and that this is independent of sex. Increasing home range size in response to habitat fragmentation, or in this case the dispersion of dry land, corroborates the first prediction of the RDH (Macdonald, 1983; Macdonald & Carr, 1989). This adaptation to fragmentation has been observed in other carnivore species such wolves (*Canis lupus*) in Italy, which increase home range size in response to habitat fragmentation caused by roads (Marcinelli et al., 2018). This pattern is however, in contrast to patterns observed for jaguars in the seasonal wetlands of Brazil, where home range sizes of jaguars (*Panthera onca*), were smaller during the flood season, owing to the spatial clustering of prey on islands (Crawshaw & Quigley, 1991). In the Pantanal however, with over 80% of the region flooded each year and significantly higher rainfall, the permanently dry forested islands are likely more predictable refuges for prey on an inter-annual basis (Cavalcanti & Gese, 2009; Nunes da Cunha et al., 2007), making the dispersion of prey more predictable.

During the minimum flood season, males had significantly larger ranges than females. This observed difference is likely related to different drivers of resource selection between the sexes when lion movements are not physically constrained by flood water. The differences in sex-specific drivers of home range size are also consistent with observations for lions in other systems, and the patterns observed here lend further support that while females try to optimize access to prey, males may instead attempt to optimise access to females (Loveridge et al., 2009; Midlane, 2013). For females, both the expected negative correlation between prey availability and home range size for females, and the negative correlation between patch complexity and home range size provides support for the employment of area minimization as the predominant home range strategy for females in this environment (Mitchell & Powell, 2004). Habitat heterogeneity in the Okavango Delta, which can occur over relatively small areas, is also associated with higher levels of herbivore species richness (Bonyongo, 2004; Bonyongo & Harris, 2007). Lion’s preferred prey range includes both medium and large herbivores, and studies on prey species such as buffalo (*Syncerus caffer*) and zebra (*Equus quagga*), for example, indicate that these species also prioritize habitat heterogeneity when selecting home ranges to minimize energetic requirements of maintaining access to a multitude of habitats necessary to fulfil their resource needs across all seasons (Bartlam-Brooks et al., 2013; Bennitt, 2012).

The negative correlation between radius of gyration, which is a measure of extent of a patch across a particular area, and female home range size in the minimum flood season, was also in accordance with our expectations. In the upper parts of the Delta, where island sizes are smaller (Gumbricht et al., 2004; McCarthy et al., 2012), females are more likely to occupy islands which can still be easily traversed at all times of the year. This minimizes energy requirements that may be associated with traversing water bodies and defending a series of smaller islands, which are likely to experience higher fluctuations in size and where changes are less predictable than larger, more permanent islands. Permanent islands are also likely to have established vegetation succession and are thus more likely to have more stable and diverse prey populations (Ramberg et al., 2006).

The negative correlation between male home range size and mean patch index is also likely because of the 'quality of habitat', but in the case of males, this quality may be more closely linked to density of females as opposed to density of prey. In contrast to the effect of prey on female home range size, there is a lack of relationship between male home range size and prey abundance in this study at minimum flood. Owing to the difficulty of accessing different pride home ranges at different times of the year, it was difficult to collect reliable information on pride sizes for collared animals. As such, this study could not directly confirm the degree to which home range size was influenced by female density. However, if – as predicted in the RDH – patch richness determines group size (MacDonald, 1983; Macdonald & Carr, 1989), males are likely trying to maximize access to females by incorporating areas of high-quality habitat that would translate into higher female density in the long-term (Loveridge et al., 2009; Mosser et al., 2009). In Hwange National Park, for example, male home range size decreased as pride density within their home ranges increased (Loveridge et al., 2009). This suggests that males may be trying to maximize access to females rather than prey, and these differences in drivers between male and female home range have also been observed in other felids such as leopards (*Panthera pardus;* Snider et al., 2021) and tigers (*Panthera tigris;* Sunquist & Sunquist, 1989). The lack of difference inter-seasonally within sex was contrary to our expectations, but is likely to ensure site fidelity of home ranges across all seasons and so minimize energy expended to increase or decrease home range significantly under different flood conditions.

As lions are territorial, which by Burt's (1943) definition is the exclusive defence of part or all of the home range against conspecifics, it is possible more complex territorial behaviour of lions not accounted for in this study, could also have significant impact on determining home range sizes. In the western and northern study sites for example, lions experience higher levels of human disturbance in the form of retaliatory killing (Weise et al., 2019a, 2019b; Whitesell, 2019). The resulting perturbance to the lion population may result in lower densities of conspecifics, which could lead to larger home ranges, particularly for males, as chances of encountering competitors is decreased (Davidson et al., 2011; McComb & Packer, 1994). In Hwange National Park, for example, an increase in the number of males, and interestingly, in accompanying coalition size, led to smaller home ranges for males during a phase of population recovery from excessive offtake (Davidson et al., 2011; Loveridge et al., 2010). Similarly, female home range decreased as female density increased (Davidson et al., 2011). In Hwange, even within prides, increases in pride size led to larger home ranges (Loveridge et al., 2009). However, in a similar wetland in Kafue National Park group size did not affect home range size (Midlane 2013). Complex interactions between group sizes, territorial behaviour and density of conspecifics, and their influence on home range sizes for lions in the Okavango is thus an important area of future research.

Lastly, when examining the influence of various habitat types, male home range size was negatively correlated with riparian woodland, which based on resource selection results of Chapter 4, I expected would also influence female home range size. Woodlands, however, may be valuable as a resource for males for other reasons. For example, in and around Hwange National Park, Zimbabwe, Elliot (2013) showed that male lions selected resting sites that i) were close to water and ii) gave them high visibility. In the Okavango, riparian woodlands offer both advantages as they are adjacent to prey-rich floodplains, and termite mounds found in woodlands are often used by lions as vantage points in an otherwise flat landscape (pers. observation). It is also possible that in the Okavango Delta, where average daytime temperatures in October are around 35˚C (Ramberg et al., 2006), shade, cover and easy access to water during the day is important for thermoregulation of adult males with large manes. Lastly, riparian woodlands may offer good cover for ambush hunting (Davidson et al., 2012; Hopcraft et al., 2005), an important consideration for male lions whose large manes make them conspicuous.

While there are clear patterns in relationships between home range sizes and landscape indices, there are several other possibilities that could be investigated with more data. For example, in Kafue National Park, Zambia, Midlane (2013), compared home range size differences between lions whose home ranges were predominantly located in floodplain habitat, and those predominantly located in woodland, and found that there were distinct differences in habitat selection. Similarly, Bartlam-Brooks et al. (2013) found that strategies of home range use differed between zebra that lived in the central Delta compared to those which lived in the peripheral Delta, and that sizes and habitat selection patterns were different between these two groups. For lions, it is also possible that home range size differences between lions that occupy floodplains in the central Delta differ in size to those on the periphery due to prey depletion on the boundaries of the Okavango. In Chapter 2, I demonstrate how lion density is lower near the boundary of the wildlife management area and in close proximity to people, and how this may be linked to prey density in these areas. As predicted by the RDH, where resources are more dispersed, home ranges may be larger to improve resource access (Macdonald, 1983). Prevalent bushmeat harvesting along the wildlife management boundaries (Rogan et al., 2017) may similarly reduce prey availability, and by extension lion density (Chapter 2) and result in larger home range sizes for lions closer to the peripheries of the wildlife management areas. Such impacts have been observed for carnivores in other prey depleted systems; for example, in Kafue National Park, pack size was smaller and home range size considerably larger wild dogs for (*Lycaon pictus*) than other ecosystems, largely as a result of prey depletion (Goodheart et al., 2021).

Conclusions

Landscape structure clearly has an important effect on ranging behaviour in lions in the Okavango Delta and landscape structure in heterogeneous habitats should not be overlooked at this scale when investigating ecological relationships between species and their environments (Snider et al., 2021). Especially in the absence of prey data, or in temporally and spatially dynamic environments, landscape indices that describe habitat heterogeneity, and those that describe degree of fragmentation or connectivity, may be valuable proxies of resource availability for large carnivores in the long-term, especially for species which maintain high site fidelity. The changes in landscape structure provided interesting insight into the different drivers of home range size between seasons. During the maximum flood season, home range sizes did not differ between sexes, and in general were negatively correlated with fragmentation of dry land, which supports the first prediction of the RDH that territories will are larger where resources being more widely dispersed (MacDonald, 1983). While most studies have corroborated this relationship between lion home range size and the seasonal dispersion of prey (Hopcraft et al., 2005; Valeix et al., 2012; Zehnder et al., 2018), this study is the first which relates it to the availability of dry land. During minimum flood however, females appear to follow an area minimization strategy, using the minimum area necessary to meet their energetic needs as home range size shrinks with higher prey biomass and habitat heterogeneity, and as land patches across the landscape have higher connectivity (Mitchell & Powell, 2004, 2007). However, the significantly larger home ranges of males in this season, and lack of association with prey, suggests that males may be trying to maximize access to females. While we could not test this directly using group sizes, as female home range size is inversely related to habitat heterogeneity, and male home range size follows the same pattern, males may be using high quality habitat to maximize access to females. This may in part support the second prediction of the RDH that patch richness increases group size (MacDonald, 1983), as areas of higher heterogeneity can support more lions (see Chapter 2).

The negative correlation between home range sizes for lions and increasing habitat fragmentation may have important conservation implications for lions in years with extended periods of high flood. As the extent of Okavango Delta is spatially constrained, both by the southern buffalo fence and by the contrast of wetland to Kalahari ecotypes (Bartlam-Brooks et al., 2013; Dures et al., 2020) an increase in home range size requirements during years of high flood will ultimately decrease the carrying capacity for lions. This is corroborated by previous studies in the south-western Okavango Delta, which show that as dry land decreases, and competition increases, cub survival decreases, and this leads to population decline (Kotze et al., 2021). As such, fluctuations in population size are to be expected under different flood scenarios, and points to the importance of landscape changes caused by flooding as a key driver of lion population ecology in the Okavango Delta (Kotze et al., 2018, 2021). However, it is also important to note that decreased flood levels would decrease habitat heterogeneity (Bartlam-Brooks et al., 2013; Murray-Hudson et al., 2006), as well as reduce the proportion of key habitats for lions such as riparian woodland

(Chapter 4; Gule et al., 2021) leading to a similar need to expand home ranges, although at longer time scales. Maintaining natural flood patterns, which produce a balance between these two scenarios (Bartlam-Brooks et al., 2013; Bennitt et al., 2019), will therefore be key to maintain the lion population at its full potential.

References

Barlow, A. C. D., Smith, J. L. D., Ahmad, I. U., Hossain, A. N. M., Rahman M, & Howlader A. (2011). Female tiger *Panthera tigris* home range size in the Bangladesh Sundarbans: the value of this mangrove system for the species' conservation. *Oryx*, 45, 125–128.

Bartlam-Brooks, H. L. A., Bonyongo, M. C., & Harris, S. (2013). How landscape scale changes affect ecological processes in conservation areas: External factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta. *Ecology and Evolution*, 9, 2795–2805.

Bennitt, E. (2012). *The ecology of African buffalo (*Syncerus caffer*) in the Okavango Delta*. PhD Thesis. University of Bristol

Bennitt, E., Hubel, T. Y., Bartlam-Brooks, H. L. A., & Wilson, A. M. (2019). Possible causes of divergent population trends in sympatric African herbivores. *PloS ONE*, 14, e0213720.

Bertram, B. C. R. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology*, 177, 463–482.

Bonyongo, C. (2004). *The ecology of large herbivores in the Okavango Delta, Botswana*. PhD Thesis. University of Bristol.

Bonyongo, M. C., & Harris, S. (2007). Grazers species-packing in the Okavango Delta, Botswana. *African Journal of Ecology* , 45, 527–534.

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

Burger, K. (2020). *The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta*. PhD Thesis. University of the Witwatersrand.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Mammalogy*, 24, 346–352.

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.

Cavalcanti, S. M. C., & Gese, E. M. (2009). Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 90, 935–945.

Clutton-Brock, T. H. (1989). Female transfer and inbreeding avoidance in social mammals. *Nature*, 337, 70–72.

Collins, K., Moyo, L., & Thompson, M. (2019). Okavango catchment vegetation, land-cover and land-use classification derived from Sentinel-2 satellite imagery. *Unpublished report. GeoTerra Image, Pretoria, South Africa.*

Crawshaw, P. G., & Quigley, H. B. (1991). Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology*, 223, 357–370.

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16, 488–502.

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2642–2651.

D’Eon, R., Serrouya, R., Smith, G., & Kochanny, C, O. (2002). GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, 430–439.

Davidson, Z., Valeix, M., Loveridge, A., Hunt, J., Johnson, P., Madzikanda, H., & Macdonald, D. (2012). Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy*, 93, 677–685.

Davidson, Z., Valeix, M., Loveridge, A. J., Madzikanda, H., & Macdonald, D. W. (2011). Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation*, 144, 114-121.

Duncan, C., Nilsen, E. B., Linnell, J. D. C., & Pettorelli, N. (2015). Life-history attributes and resource dynamics determine intraspecific home-range sizes in Carnivora. *Remote Sensing in Ecology and Conservation*, 1, 39–50.

Dures, S. G., Carbone, C., Savolainen, V., Maude, G., & Gottelli, D. (2020). Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation,* 23, 502-515.

Ellery, W. N., Ellery, K., & McCarthy, T. S. (1993). Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions. *African Journal of Ecology* 31, 118–134.

Elliot, N. B. (2013). *The Ecology of Dispersal in Lions* (Panthera leo). PhD Thesis. University of Oxford.

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, 23, 559–581.

Gardiner, R., Proft, K., Comte, S., Jones, M., & Johnson, C. N. (2019). Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. *Ecology and Evolution*, 9, 14005-14014.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10, 57–63.

Goodheart, B., Creel, S., Becker, M. S., Vinks, M., Schuette, P., Banda, K., Sanguinetti, C., Rosenblatt, E., Dart, C., Kusler, A., Young-Overton, K., Stevens, X., Mwanza, A. & Simukonda, C. (2021). Low apex carnivore density does not release a subordinate competitor when driven by prey depletion. *Biological Conservation*, 261, 109273.

Gule, T. T., Tsheboeng, G., Dlamini, W. M., Mabaso, S. D., & Cassidy, L. (2021). Change detection of riparian woodland vegetation in the Okavango Delta, Botswana. *Remote Sensing Applications: Society and Environment*, 22, 100497.

Gumbricht, T., Mccarthy, J., & Mccarthy, T. (2000). Portraying the geophysiology of the Okavango Delta , Botswana. In *Proceedings of the 28th International Symposium on Remote Sensing of the Environment*, *Cape Town, South Africa, ICRSE* (Vol. 4, pp. 10-13).

Gumbricht, T., McCarthy, J., & McCarthy, T. S. (2004). Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. *Earth Surface Processes and Landforms*, 29, 15–29.

Haidir, I. A., Kaszta, Ż., Sousa, L. L., Lubis, M. I., Macdonald, D. W., & Linkie, M. (2021). Felids, forest and farmland: identifying high priority conservation areas in Sumatra. *Landscape Ecology*, 36, 475–495.

Hearn, A., Cushman, S., Goossens B, Macdonald E, Ross J, Hunter L T B, Abram N K, & Macdonald D W. (2018). Evaluating scenarios of landscape change for Sunda clouded leopard connectivity in a human dominated landscape. *Biological Conservation*, 222, 232–240.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., & Macdonald, D. W. (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.

Herfindal, I., Linnell, J. D. C., Odden, J., Nilsen, E. B., & Andersen, R. (2005). Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology*, 265, 63–71.

Hesselbarth, M., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, 42, 1648–1657.

Hiller, T. L., Belant, J. L., & Beringer, J. (2015). Sexual size dimorphism mediates effects of spatial resource variability on American black bear space use. *Journal of Zoology*, 296, 200–207.

Hopcraft, G. J. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74, 559–566.

Inman, V., & Lyons, M. (2020). *Automated Inundation History Mapping over Large Areas using Landsat and Google Earth Engine*. https://www.preprints.org/manuscript/202003.0038

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.

Jones, M. E., & Davidson, N. (2016). Applying an animal-centric approach to improve ecological restoration. *Restoration Ecology*, 24, 836–842.

Kie, J. G., Bowyer, R. T., Nicholson, M. C., Boroski, B. B., & Loft, E. R. (2002). Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology*, 83, 530–544.

Kotze, R., Bennett, N. C., Cameron, E. Z., Low de Vries, J., Marneweck, D. G., Pirk, C. W. W., & Dalerum, F. (2012). Temporal patterns of den use suggest polygamous mating patterns in an obligate monogamous mammal. *Animal Behaviour*, 84, 1573-1578.

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E. K., & Marshal, J. P. (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.

Kotze, R., Marshal, J. P., Winterbach, C. W., Winterbach, H. E. K., & Keith, M. (2021). Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment. *African Journal of Ecology*, 59, 63–73.

Kramer-Schadt, S., Revilla, E., Wiegand, T., & Breitenmoser, U. (2004). Fragmented landscapes, road mortality and patch connectivity: Modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, 41, 711–723.

Linkie, M., Chapron, G., Martyr, D. J., Holden, J., & Leader-Williams, N. (2006). Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology*, 43, 576–586.

Lovari, S., Serrao, G., & Mori, E. (2017). Woodland features determining home range size of roe deer. *Behavioural Processes*, *140*, 115–120.

Loveridge et al. *unpublished.* Estimates of lion (*Panthera leo*) density for the Okavango Delta, Botswana.

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). African lions on the edge: reserve boundaries as “attractive sinks”: In D. W. Macdonald & A. J. Loveridge (Eds.), *Biology and Conservation of Wild Felids* (p. 183). Oxford University Press.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W. (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. (1983). The ecology of carnivore social behaviour. *Nature*, 301, 379–384.

Macdonald, D. W., & Carr, G. M. (1989). Food security and the rewards of tolerance. In *Comparative socioecology: the behavioural ecology of humans and animals* (pp. 75–99). Blackwell Scientific Oxford.

Mangipane, L. S., Belant, J. L., Hiller, T. L., Colvin, M. E., Gustine, D. D., Mangipane, B. A., & Hilderbrand, G. v. (2018). Influences of landscape heterogeneity on home-range sizes of brown bears. *Mammalian Biology*, 88, 1–7.

Marcinelli, S., Botiani L, & Ciucci, P. (2018). Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy. *Canadian Journal of Zoology*, 96, 828–838.

Marker, L. L., & Dickman, A. J. (2005). Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *African Journal of Wildlife Research*, 35, 105–115.

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (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, T., Humphries, M., Mahomed, I., le Roux, P., & Verhagen, B. T. (2012). Island forming processes in the Okavango Delta, Botswana. *Geomorphology*, 179, 249–257.

McGarigal, K., Cushman, S. A., & Ene, E. (2012). FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. *Computer software program produced by* *the authors at the University of Massachusetts, Amherst. http://www. umass.edu/landeco/research/fragstats/fragstats. html*, *15*.

Midlane, N. (2013). *The conservation status and dynamics of a protected African lion* Panthera leo *population in Kafue National Park, Zambia*. PhD Thesis. University of Cape Town.

Mitchell, M. S., & Powell, R. A. (2004). A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, 177, 209–232.

Mitchell, M. S., & Powell, R. A. (2007). Optimal use of resources structures home ranges and spatial distribution of black bears. *Animal Behaviour*, 74, 219–230.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H., & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2289–2301.

Morellet, N., Moorter, B. v., Cargnelutti, B., Angibault, J-M., Lourtet, B., Merlet, J., Ladet, S., & Hewison, M. (2011). Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landscape Ecology*, 26, 999–1010.

Murray-Hudson, M., Wolski, P., & Ringrose, S. (2006). Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. *Journal of Hydrology*, 331, 73–84.

Murray-Hudson, M., Wolski, P., Cassidy, L., Brown, M. T., Thito, K., Kashe, K., & Mosimanyana, E. (2015). Remote Sensing-derived hydroperiod as a predictor of floodplain vegetation composition. *Wetlands Ecology and Management*, 23, 603–616.

Murray-Hudson, M., Wolski, P., Murray-Hudson, F., Brown, M. T., & Kashe, K. (2014). Disaggregating hydroperiod: Components of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands*, 34, 927–942.

Nunes da Cunha, C., Junk, W. J., & Leitão-Filho, H. F. (2007). Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology. *Amazoniana*, 19, 159–184.

Packer, C., & Pusey, A. E. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, 101, 275–310.

Powell R. A. (2000). Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences*, 442*,* 65–110.

R Core Team. (2021). *R: A language and environment for statistical computing* (3.6.1). R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., van As, J., & VanderPost, C. (2006). Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences*, 68, 310–337.

Rauset, G. R., Low, M., & Persson, J. (2015). Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology*, 96, 3153–3164.

Rogan, M. S., Lindsey, P. A., Tambling, C. J., Golabek, K. A., Chase, M. J., Collins, K., & McNutt, J. W. (2017). Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, 210, 233–242.

Saïd, S., & Servanty, S. (2005). The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, 20, 1003–1012.

Sandell, M. (1989). The Mating Tactics and Spacing Patterns of Solitary Carnivores. In J. L. Gittleman (Ed.), *Carnivore Behavior, Ecology, and Evolution* (pp. 164–182). Springer US.

Schaller, G. (1972). *The Serengeti Lion: A study of predator-prey relations*. University of Chicago Press.

Snider, M. H., Athreya, V. R., Balme, G. A., Bidner, L. R., Farhadinia, M. S., Fattebert, J., Gompper, M. E., Gubbi, S., Hunter, L. T. B., Isbell, L. A., Macdonald, D. W., Odden, M., Owen, C. R., Slotow, R., Spalton, J. A., Stein, A. B., Steyn, V., Vanak, A. T., Weise, F. J., Wilmers, C. C., & Kays, R. (2021). Home range variation in leopards living across the human density gradient. *Journal of Mammalogy*, 102, 1138–1148.

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.

Sunquist, M. E., & Sunquist F C. (1989). Ecological constraints on predation by large felids. In *Carnivore Behavior, Ecology and Evolution* (pp. 283–301). Springer.

Thito, K., Wolski, P., & Murray-Hudson, M. (2016). Mapping inundation extent, frequency and duration in the Okavango Delta from 2001 to 2012. *African Journal of Aquatic Science*, 41, 267–277.

Trewhella, W. J., Harris, S., & McAllister, F. E. (1988). Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): A Quantitative Analysis. *The Journal of Applied Ecology*, 25, 423.

Tumenta, P. N., Van't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo De Haes, H. A., de Iongh, H. H., & Zachos, F. E. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, 78, 461–469.

Valeix, M., Loveridge, A. J., & Macdonald, D. W. (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., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90, 23–30.

van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*, 206, 97–112.

Weise, F. J., Fynn, R. W. S., Stein, A. B., Tomeletso, M., Somers, M. J., & Périquet, S. (2019a). Seasonal selection of key resources by cattle in a mixed savannah-wetland ecosystem increases the potential for conflict with lions. *Biological Conservation*, 237, 253–266.

Weise, F. J., Hauptmeier, H., Stratford, K. J., Hayward, M. W., Aal, K., Heuer, M., Tomeletso, M., Wulf, V., Somers, M. J., & Stein, A. B. (2019b). Lions at the gates: Trans-disciplinary design of an early warning system to improve human-lion coexistence. *Frontiers in Ecology and Evolution*, 7, 1–19.

Whitesell, C. A. (2019). *Movements of lions and other carnivores in relation to domestic and wild prey in northwestern Botswana*. PhD Thesis. University of California Davis.

Wiegand, T., Revilla, E., & Moloney, K. A. (2005). Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology*, 19, 108–121.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164–168.

Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: Key resources concept expanded. *Ecography*, 37, 969–982.

Zehnder, A., Henley, S., & Weibel, R. (2018). Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability. *Zoology*, 128, 46–54.

Chapter 4

Temporal effects of flooding regimes on cores and corridors of a large carnivore population: lions (*Panthera leo*) in the Okavango Delta

Abstract

For large carnivores, the loss of natural habitat and the fragmentation of existing populations because of anthropogenic threats such as land conversion or climate change represent a challenge to their conservation. To mitigate these threats, many are turning to the development of corridor models for conservation planning, which can identify important population cores and provide information on how these can be linked through protection of corridors. However, many of these plans ignore temporal variation in habitat selection and prevailing ecological conditions at different times of the year, which can result in erroneous conclusions regarding a landscape's permeability. I used data from African lion (*Panthera leo*) to compare seasonal differences in predicted core lion areas in the Okavango, the connectivity between them and connectivity to surrounding areas under different flood regimes. Lion movement data was used to develop resistance surfaces showing the permeability of the landscape at maximum and minimum flood, which serve as proxies for high and low flood phases. Resistance surfaces were then used to calculate cumulative resistance kernels, which can be used to identify core population areas, and least-cost path analyses which can highlight the connectivity between the different cores, and examined how this differed between high and low flood. During low flood conditions, connectivity in the Okavango is high and there are large areas of core lion habitat available across the Okavango. However, during high floods, connectivity within the Okavango is markedly reduced, the core lion areas of the southern and central Okavango shrink, and the western core disappears. During high flood phases, lions in the southern and western delta are more isolated and pushed towards the edges of the protected area. Lions are thus more susceptible to

anthropogenic threats like retaliatory killing by livestock owners and bushmeat harvesting during high flood periods. There is little connectivity in both seasons to the south, south-east and west of the Okavango, mostly because of higher human densities and associated agricultural and urban activities that disrupt lion movement and ecology. Improved connectivity to and from the Okavango can build resilience in the delta's lion population and reduce further genetic differentiation as a result of movement restrictions imposed by flooding and human densities.

Introduction

Accelerated habitat loss from human activities and climate change are among the top threats to the conservation of megafauna across the globe (Bellard et al., 2012; Ripple et al., 2014, 2015; Woodroffe, 2000). With most of the world's megafauna now restricted to core protected areas (PAs), there is a pressing need to ensure that corridors between protected areas and areas of natural habitat outside of PAs be maintained, or restored, as anthropogenic development increases (Rudnick et al., 2012). Connectivity, which is defined as the facilitation or hindrance of movement across features of a landscape (Taylor et al., 1993), and its role in allowing individuals to move between different populations or even sub-populations, has become increasingly important in conservation planning (Ash et al., 2021; Cushman et al., 2013; Kaszta et al., 2020; Rabinowitz and Zeller, 2010; Zeller et al. 2012; 2016). Maintenance of connectivity 'corridors' which facilitate this movement increases genetic diversity and makes smaller populations more robust to disease and other stochastic events that might affect population viability, ultimately reducing the risk of local extinctions (Brook et al., 2002; Frankham, 2005). Far-ranging species such as large carnivores, which occur at low densities and pose a risk to human lives and livelihoods, are particularly vulnerable to extinction risk caused by habitat loss and isolation (Cohen & Newman, 1991). Securing effective corridors is thus one of the main tools in the conservation approach to halt or reverse further declines in large carnivore numbers while ensuring future population viability (Cushman et al., 2018; Kaszta et al., 2020; Moqanaki & Cushman, 2017).

Conservation planning for corridors typically relies on the parameterization of a resistance surface which is representative of the ease with which organisms can traverse the landscape (Cushman et al., 2013; Taylor et al., 1999; Zeller et al., 2012). To be realistic, the development of these resistance surfaces requires an estimation of how environmental variables affect animal movement choices, their survival probability and their lifetime reproductive success (Ash et al. 2021; Cushman et al. 2013; Zeller et al. 2012). Previously, methods such as expert opinion (Clevenger et al., 2002; Rabinowitz & Zeller, 2010), species presence (Zeller et al., 2011), habitat suitability models (Huck et al., 2010; LaRue & Nielsen, 2008) or genetic markers (Cushman et al., 2006; Wasserman et al., 2010) were used to devise resistance surfaces. However, these methods are largely subjective or lack a direct link between animal movement and the spatial and temporal aspects of their environments in their parameterization (Cushman et al., 2013). As connectivity is unique to each scenario based on species as well as landscape, incorporating biological data based on actual animal movements has led to improvement of the parameterization process, leading to empirically informed functional connectivity models (Elliot et al., 2014a; Osipova et al., 2019; Richard & Armstrong, 2010). This improvement has been largely due to developments in global-positioning system (GPS) collar technology, which has enabled the use of actual movement data in relation to their environments (Zeller et al., 2014, 2016).

One of the most common methods for developing resistance surfaces from animal movement data is through resource selection functions (RSF; Chetkiewicz et al., 2006; Chetkiewicz & Boyce, 2009; Zeller et al., 2012). RSFs, using either point, step or paths derived from GPS collar data, compare environmental or anthropogenic covariates at used locations to the covariates at unused locations within an animal's movement range to determine their preference or avoidance of features within their environment (Manly et al., 2002). Resource selection probability surfaces are then assumed to be inversely related to resistance, and these resistance surfaces then form the basis of connectivity modelling (Carvalho et al., 2016; Chetkiewicz & Boyce, 2009; Reding et al., 2013; Zeller et al., 2016). While many RSF studies take spatial heterogeneity into account, temporal heterogeneity is less studied (Kaszta et al., 2021). Many resistance surfaces developed to inform corridor planning are based on only one season, which largely ignores the temporal variation that can exist in resource availability, selection, and by extension, landscape permeability, at different times of the year (Cushman & Lewis, 2010; Kaszta et al., 2021; Osipova et al., 2019). Ignoring the temporal variation in species-environment relationships induced by seasonality, particularly in more arid environments, has the potential to undermine the conservation application of identified corridors and their long-term resilience (Kaszta et al., 2021; Osipova et al., 2019). Incorporating this 'non-stationarity' in species movement is thus an important part in ensuring the functionality of prioritized conservation corridors in the face of rapid development and in the assignment of scarce conservation resources (Kaszta et al., 2020, 2021; Moqanaki & Cushman, 2017).

The Okavango Delta is a seasonally inundated wetland in the Kalahari-desert of north-western Botswana (Gumbricht et al., 2004). In this ecosystem, flooding patterns vary not only on a seasonal and inter-annual basis determined primarily on seasonal rainfall in the catchment of Angola, (McCarthy et al., 2000; Murray-Hudson et al., 2015), but also on a multi-decadal climatic cycle which sees the system oscillate between periods of extended high or low floods (McCarthy et al., 2000; Murray-Hudson et al., 2014). These short and long-term fluctuations provide a good testing ground for how connectivity can vary temporally in both contexts. As African lions have large home ranges, are capable of dispersing long distances, and require connectivity of sub-populations to maintain population viability in open systems (Cushman et al., 2018; Elliot et al., 2014a), they were an ideal study species to examine spatial and temporal variation in connectivity across the Okavango Delta.

The Okavango Delta is a stronghold for the African lion (*Panthera leo*) and is one of the key source populations for the Kavango-Zambezi Transfrontier Conservation Area (KAZA; Riggio et al., 2013; Bauer et al., 2015), making its continued viability as a lion core population a conservation priority. Recent genetic analysis across KAZA have revealed declining genetic diversity across the region (Dures et al., 2019), and within the Okavango Delta itself, the lion population has relatively unique genetic markers, pointing to a degree of isolation from the other Kalahari populations (Dures et al., 2020). The prevailing flooding patterns have been cited as one of the main factors leading to the observed genetic patterns (Dures et al., 2020); however, the extent to which flooding impedes or promotes movement under different flooding regimes has not been investigated.

I therefore used high resolution movement data from resident lions across the Okavango Delta, from 2013 to 2016, to develop seasonal resistance surfaces during low and high flood conditions. My main objectives were to: 1) determine how resource selection varied seasonally, with seasons defined by maximum and minimum flood, 2) examine temporal differences in connectivity between maximum and minimum flood scenarios, and 3) combine both high and low flood scenarios to examine which core populations and corridors remained consistent regardless of seasonal inundations. I expected that 1) the direction and size of relationships between lions and different environmental factors would depend on season, but that lions would consistently avoid human dominated areas; 2) under high flood conditions, there would be increasing isolation of the core lion population in the central Delta, and increasing isolation of the western Okavango Delta from the eastern Okavango Delta, with a concomitant decrease in size of core lion populations, 3) connectivity and size of eastern core populations would be less variable than connectivity and size of central, southern and western populations because the former experiences less extreme inter-annual variation in flood extent

Methods

Study Area

The Okavango Delta (Figure 4. 1.) is characterized by a single dry season flood pulse, which originates in the highlands of Angola following seasonal austral summer rains (McCarthy et al., 2005; Ramberg et al., 2006). This rainwater takes about four months to reach Botswana, travelling down the Okavango River and its tributaries through Namibia (Gumbricht et al., 2000, 2004), reaching the panhandle between March and May, and taking an additional four months to move through the system, terminating in an alluvial fan that can vary in extent from 4,000 km^2 to 18,000 km^2 (Gumbricht et al., 2000; Murray-Hudson et al., 2014). In addition to rainfall conditions in Angola, the extent of the flood is also determined by the recharging of the water table from local rainfall as well as the extent of the previous flood (Murray-Hudson et al., 2014, 2015). As a result, there can be large inter-annual variation in flood extent (Thito et al., 2016; Wolski & Murray-Hudson, 2006). The inter-annual variation, however, varies across the surface of the Delta. Typically, tributaries to the eastern side of the Okavango Delta experience less inter-annual variation in flooding and have a more consistent distribution of permanently flooded areas, while areas to the west of Chief's Island (Figure 4. 1.) experience significant expansions and contractions of seasonally inundated area on an annual basis (Gumbricht et al., 2000; Wolski and Murray-Hudson, 2006). On longer time-scales, climatic patterns influence inundation extent, and the Okavango thus oscillates through a series of 'wet' and 'dry' periods during which flood levels are consistently higher or lower, that can last between one and four decades (Mazvimavi & Wolski, 2006; Murray-Hudson et al., 2014; Tyson et al., 2002). This study period (2013 to 2017) falls within what would be considered a 'drying period'.

The Okavango is divided into four major ecoregions; the Panhandle which is the conduit for water into the alluvial fan, permanent wetland located in both the upper and the more distal regions of the fan, seasonal wetlands, often referred to as floodplains, and dry islands (e.g., Chief's Island) (Gumbricht et al., 2000). Seasonal inundation is the main driver of plant diversity, and results in clear patterns of vegetation zonation, which shift according to both the long- and short-term flood conditions (Murray-Hudson et al., 2014, 2015). As the Okavango Delta is so flat, even small changes in elevation result in large variations in vegetation types over relatively small distances (Ramberg et al., 2006). Directly adjacent to channels are seasonal sedgelands, followed by seasonal floodplains interspersed with islands; while these typically start as termite mounds, they can gradually grow over time as sediments accumulate and vegetation takes hold (Gumbricht et al., 2000; McCarthy et al., 2005; Murray-Hudson et al., 2014). Most islands are characterized by riparian woodlands along the edge, with larger islands gradually transition to having more saline centres (McCarthy et al. 2005) with more permanent sandveld islands characterized by Mopane (*Colophospermum mopane*) and Acacia (*Vichellia sp.*) woodlands and dry grassland habitats (Ramberg et al., 2006). This mosaic of vegetation types produces heterogeneity that allows for a higher diversity and density of plant and animal life than the more arid surrounding Kalahari regions (Ramberg et al., 2006), but that themselves are also influenced by varying flood conditions (Bennitt et al., 2014; Bonyongo & Harris, 2007; Kotze et al., 2021).

Data collection

Lion movement data within the Okavango Delta were recorded using Global Positioning System (GPS) enabled collars and collected from various long-term research projects between 2013 and 2016. Data were obtained from the southern Okavango Delta (n = 4 adult females and n= 5 adult males), the western Okavango Delta (n = 2 adult females and n=3 adult males) and the northern Okavango Delta (n = 2 adult females and n = 3 adult males). Collars used were produced either by Vectronics Aerospace GmbH or Africa Wildlife Tracking (AWT). All collars were fitted under the supervision of a Botswana registered veterinarian, and with prior approval from the Botswana Department of Wildlife and National Parks (permit numbers EWT 8/36/4 XVIV(92), EWT 8/36/4 XX(V (30) and EWT 8/36/4 XXXIII (36)). Most of the collars (n =14) collected data at two-hour intervals, while the others (n = 5) collected data at four-hour intervals, for an average of 20 months for each individual (range 3.5 - 28 months). Information on GPS accuracy was not recorded; however, data were screened for outlying points using distance covered between locations as an indication of biologically plausible movements (D'Eon et al., 2002).

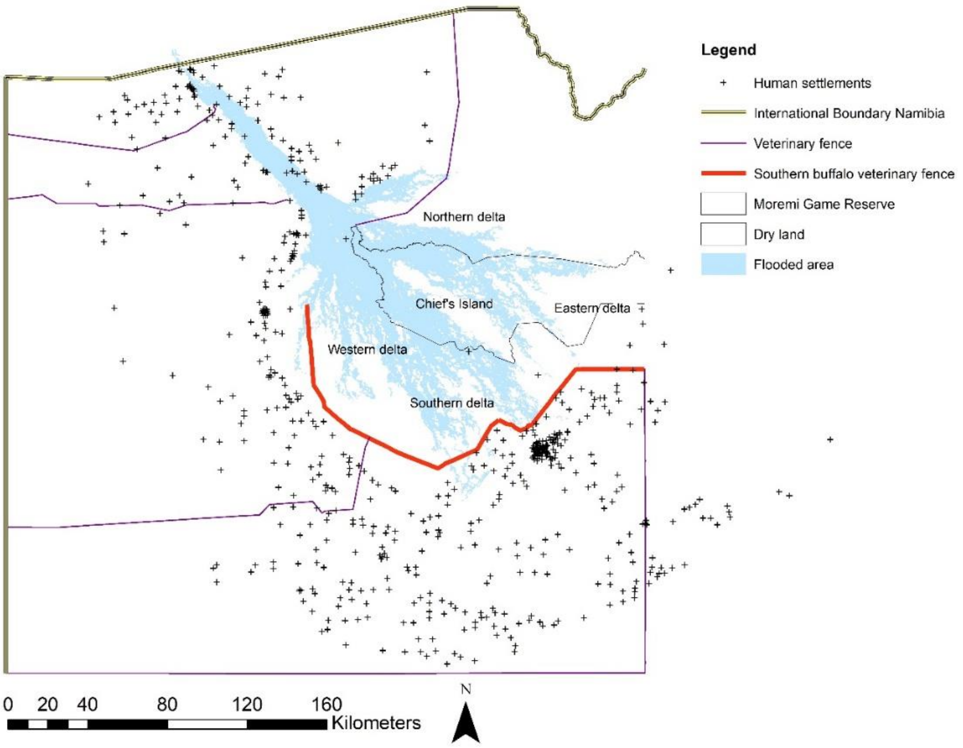

Figure 4. 1. A map of the Okavango Delta showing the extent of the flood water relative to the four different regions of the delta, the Moremi Game Reserve with Chiefs Island near its centre and all human settlements including cattle posts, villages and small towns.

Data analysis

Data preparation

To investigate lion habitat-use across the landscape, I developed resource selection probability functions at the home range scale (Johnson, 1980). As resource selection patterns may vary with season (Anderson et al., 2005; Boyce, 2006), and I was interested in the temporal patterns of connectivity in relation to flooding, 'seasons' were defined based on flood levels. Information on flood minima and maxima were obtained from the Okavango Research Institute's long term flood monitoring database (http://okavangodata.ub.bw/ori/monitoring/flood_maps/). I then selected three-month intervals that consistently contained the maxima and minima across the years of study, using June to August as the months for maximum flood, and March to May as the months for minimum flood for each year. All covariates were extracted according to these time scales.

Resource selection functions followed a used-available design (Manly et al., 2002), which compares used locations within seasonal movement ranges to a selection of 'available' locations within that range. Home ranges were constructed using minimum convex polygons based on all available telemetry locations (Bohnett et al., 2020; Carvalho et al., 2016), to capture the full range of movement for each individual, and particularly exploratory movements that under other analyses would not be considered part of the home range. Available locations were distributed randomly across each individual's range, buffered by the median daily distance moved (6.5 km), following suggestions by Johnson et al. (2002) that available habitat should take an animal's movement capabilities beyond the selected home range boundary into account (Boyce et al., 2003; Hoffman & O'Riain, 2012). Due to the large number of locations available for each animal, and the relatively small home ranges in a resource-rich environment, one randomly selected available location for each used location was deemed sufficient to represent unused habitat within the buffered home range.

Several ecological and landscape covariates, hypothesized to influence lion movement, were characterized for each used and random location. To account for the surrounding environment in resource selection, a 500m buffer was placed around each random and used point. This buffer size was deemed appropriate to reflect surrounding habitat at the home range scale for a large carnivore (Pitman et al., 2017; Reding et al., 2013), and preliminary analyses revealed that this scale performed better for the covariates of choice than smaller scales. Similarly, larger scales were computationally intensive, and caused significant overlap of buffers of adjacent points which could increase spatial autocorrelation (Northrup et al., 2013). Covariates were selected based on available literature on factors influencing lion resource selection (Elliot et al., 2014a; Elliot et al., 2014b; Loveridge et al., 2017). Habitat composition was defined for each point as the percentage of each habitat type occurring in each buffer radius. Habitat types were extracted from a landcover map developed for the Okavango Delta (Collins et al., 2019), and habitat types were collapsed into three broad habitat categories, viz., open grassland (including non-flooded floodplain communities), riparian woodland and open woodland, including dry woodland (dominated by *Mopane, Combretum* or *Vichellia*) and sandveld (dominated by *Philenoptera*). In addition to habitat proportion, I examined the linear distance between points and habitat edges to determine whether points selected were influenced by the spatial location of landscape features or if they select for ecotones (Carvalho et al., 2016). I therefore measured the Euclidean distance between each point and the nearest habitat edge as a scale independent factor in habitat selection.

To examine the influence of flooded areas on lion movement, I produced monthly flood maps for the flood season using methodology outlined in Inman and Lyons (2020). Monthly inundation maps, depicting dry versus wet pixels, were produced from Landsat 8 imagery with a 30m x 30m resolution. For the minimum and maximum flood season, I selected the monthly inundation map which had the lowest flood levels for that period to ensure that inferences drawn from flood layers were conservative (Dures et al., 2020). As water is an important resource that may attract both predator and prey (Mosser et al., 2009; Valeix et al., 2010a), I used distance to water as a scale-independent index of selection for areas closer to water.

Other environmental variables included tree cover, which previous studies indicate is important for hunting by increasing prey catchability (Hopcraft et al., 2005) and is also selected by adults for resting (Elliot, 2013). Information on tree cover was obtained from

Moderate Resolution Imaging Spectroradiometer (MODIS) products created by Hansen et al. (2013) indicating percentage canopy cover (NSASA LP DAAC https://lpdaac.usgs.gov/) at 30m resolution, and this percentage was averaged within the 500m buffer around each random and selected point. Secondly, as prey species, and by extension lions, may congregate in areas of high vegetation productivity, I also calculated the average seasonal Normalized Difference Vegetation Index (NDVI), which was derived from Landsat 8 Level 2 imagery (https://earthexplorer.usgs.gov/) with a spatial resolution of 30m (see Chapter 2). Monthly NDVI values were averaged across the three months of each season to produce a seasonal NDVI average for the analysis, and then averaged within each 500m buffer for random and selected points.

Lastly, to examine the influence of anthropogenic covariates, I included the distance to human settlements and human-modified landscape (Elliot et al., 2014a; Loveridge et al., 2017). Human-modified landscape, such as agricultural fields, were extracted from the vegetation map (Collins et al., 2019) and human settlement data (i.e., cattle posts, villages and towns) were derived from the Botswana National Census (Statistics Botswana, 2014). To account for the likely sphere of human influence around settlements, I drew a 500m buffer around each cattle post, settlement, village and fields, and combined polygons where these overlapped (van der Weyde et al., 2021). This resulted in large polygons in areas with a high concentration of settlements like villages and large towns, and smaller polygons around isolated cattle posts.

Resource selection functions

To compare landscape covariates between used and available points, I used generalized linear models with mixed effects (GLMM), with a binomial variable to indicate used (“1”) versus available (“0”) points (Cushman & Lewis, 2010; Elliot et al., 2014a). To account for individual heterogeneity in point selection, and to account for unequal sample size, the individual identity of each animal was used as a random factor in all analyses (Gillies et al., 2006). Furthermore, to ensure that all covariates were comparable on a similar scale, covariate values were centred and standardized (Schielzeth, 2010). Covariates were tested for collinearity using variance inflation factors, and covariates that were considered highly correlated (VIF > 3, Zuur et al., 2010) were removed from the subsequent analyses. Global models were then constructed using remaining explanatory variables, and model dredging was applied using the package *MuMIn* (Barton, 2019) to examine all possible model combinations. Models whose AICc values were less than two units from the best model, were considered parsimonious (Burnham & Anderson, 2004), and where multiple models were selected, model averaged estimates were calculated. GLMMs were performed using the package *lme4* (Bates et al., 2014) and model-averaged estimates calculated using the package *MuMIn* (Barton, 2019). All analyses were conducted in R (R Core Team, 2019).

Resistance Mapping

The final resource function for each season was used to produce a 30m x 30m resolution map of the study area depicting probability of use (Harju et al., 2013). As 2016 was the lowest year of flood for the study period, covariates from the low and high flood seasons from this year's maps were used as a conservative representation of low and high flood conditions. For each habitat type predictor variable, a new raster was created setting the habitat type to 1 and all other grid cells to 0. To take into the account the effect of scale for each habitat type, we used the focal statistics tool in ArcGIS Pro to calculate the proportion of habitat type surrounding each grid cell, in accordance with the 500m buffer size, and produced new rasters where grid cells reflected these proportions. Similarly, new rasters were produced for NDVI and tree cover, sampling average values of each within 500m buffers. When calculating NDVI and tree cover values, any water pixels within the buffer zone were set to null to avoid aquatic plant productivity and aquatic plant cover from throwing off land-based values (Gumbricht et al., 2000). For scale-independent factors, I created Euclidean distance rasters where each pixel was classified based on the Euclidean distance to the feature or habitat of interest. All rasters were then re-scaled so that coefficient values from the RSF model matched the values of the covariates in the created rasters (Boswell, 2017). The resource selection function probability surfaces were created for each season by applying the best model or model-averaged parameter estimates to each grid cell so that:

$$P(x) = \exp(\beta_0 + \beta_1 x_{1j} + \ldots + \beta_n x_{nj}) / (1 + (\exp(\beta_0 + \beta_1 x_{1j} + \ldots + \beta_n x_{nj}))$$

where P(x) represents relative probability of selection, β represents each coefficient estimate for each covariate and x the value extracted for each covariate n in the model at each grid cell *j* (Harju et al., 2013). All water pixels which were previously set to null were then added in with a selection value of 0.

Model validation

For model validation, 30% of the original points were withheld from the original analysis as test data for each season. These points were then mapped onto the resource selection function layer, and model fit was validated using the Boyce index from the package *ecospat* in R (R Core Team, 2019). This Boyce index is appropriate for evaluating models with presence only data and calculates the ratio of predicted points to points expected from a random distribution based on habitat suitability values from the created resource selection function probability surface (Khalyani et al., 2019). This produces a Spearman rank correlation coefficient, with values nearer to 1 representing good model fit (Hirzel et al., 2006).

Resistance surfaces and corridor mapping

As selection is considered the inverse of cost paths (Chetkiewicz & Boyce, 2009; Roever et al., 2010), the inverse of the selection map was used to create resistance maps for each season and scaled so that:

$$\text{Cost} = 100*(1-P(x)).$$

This created a resistance raster ranging from 0 to 100, with 0 being the highest selectivity and lowest cost to movement and 100 representing the lowest selectivity and highest cost to movement.

To determine the level of connectivity within the Okavango Delta, I calculated factorial least-cost paths (LCP) networks (see Cushman et al., 2009) using the developed resistance surfaces. Factorial LCPs calculate the extent and intensity of corridors between all combinations of source and destination nodes, determining least cost paths along pixels between each possible pair of nodes (Cushman et al., 2013; Cushman & Landguth, 2012). “Intense” corridors are then identified as areas with multiple least-cost paths passing through the same points in a landscape (Elliot et al., 2014a). To create potential source nodes, I used recent camera trap survey data from the Okavango Delta (Loveridge et al., *unpublished*) to estimate the density of lions in each area surveyed and estimated the number of source points based on rough polygons of sampled areas. For areas outside of the Okavango Delta, I estimated densities based on local knowledge of the area. Lastly, for a realistic distribution of source points, I created a binary random raster layer of the same extent and raster resolution as the resistance surfaces and subtracted the habitat suitability layer. Positive values in the resultant layer were taken to represent pixels with the highest probability of lion presence, and source points were thus generated within these cells to mimic the occurrence of individual lions across the landscape (Haidir et al., 2021).

Identification of cores and corridors

Using cumulative resistance kernel and least-cost path analysis (Compton et al., 2007; Cushman et al., 2009), I aimed to identify core areas and dispersal corridors for lions in low and high flood seasons within and around the Okavango Delta using UNICOR software (Landguth et al., 2012). Cumulative resistance kernels identify areas where relative frequency and density of movement, based on resistance values for each pixel across the landscape, is highest, thereby highlighting areas of core habitat and high connectivity (Kaszta et al., 2018). Factorial least cost paths, however, use an increased dispersal threshold to identify key or narrow linkages across the landscape where movement might be more limited, but can act as potential dispersal corridors (Haidir et al., 2021). As with most species the dispersal threshold is unknown (Haidir et al., 2021) and may vary according to local conditions, I thus used empirical dispersal values of 250,000 and 1,000,000 cost units for resistant kernel and least cost path approaches respectively, following Elliot et al. (2014a). These values represent a dispersal distance of 80km through relatively low resistance landscape patches, which is a dispersal threshold four times larger than local connectivity (Cushman et al., 2018; Elliot et al. 2014a). Least cost path density layers were then smoothed using a 5 km radius focal mean. To increase computational efficiency in UNICOR (Landguth et al., 2012), while still maintaining a sufficient level of detail, resistance surfaces were resampled to a resolution of 90m before running the above analyses.

As landscape connectivity may vary drastically between different flood seasons, we aimed to identify which focal core areas were most important for lions across the Okavango Delta, regardless of season (Haidir et al., 2021; Kaszta et al., 2021). To do this, we identified a threshold of the minimum 80th percentile of the cumulative resistant kernel layer based on information from each flood season. Cumulative resistance kernel density estimates were then reclassified according to this threshold to create a binary layer for each season, with above-threshold areas classified as ‘1’ and representing core areas, and below-threshold values classified as ‘0’. Binary layers representing each season were then overlaid and summed so that overlapping core areas would produce a value of 2, representing priority lion core areas in the Okavango Delta that are consistent across seasons. Similarly, to identify dispersal corridors which remained resilient to changes in flood conditions, the 40th percentile of the minimum least-cost path layers were used as a threshold for each flood season, and binary layers created, as with core areas, with corridors above threshold being classified as ‘1’ and all others as ‘0’. Seasonal binary layers were once again summed, and corridors with a value of ‘2’ were considered resilient to flood changes. Lastly, I calculated i) the size of areas occupied by lions according to kernel density estimates in both flood seasons, ii) the size of the core areas identified in both seasons, iii) the difference in size of core areas between both seasons, and iv) the size of the final overlapping core areas (Kaszta et al. 2019; Cushman et al. 2016).

Results

For the minimum flood season, proportion of open grassland showed a high degree of collinearity, and so was excluded from further analysis. The multivariate analyses resulted in four parsimonious models (ΔAICc<2), which were averaged to produce the final selection model (Table 4. 1.). The model-averaged coefficients showed that lions selected for habitats with higher proportions of open woodland and riparian woodland, and selected areas close to the edge of these habitat types and further away from open grassland (Table 4. 1.). Lions appeared to avoid areas with very high tree cover, and although non-significant, showed a weak positive relationship with NDVI and selected for areas closer to water (Table 4. 1.). Lastly, lions showed a strong avoidance of human settlements.

For the maximum flood season, in addition to proportion of grassland, tree cover was also excluded from further models due to collinearity. The global model was retained as the best model (ΔAICc = 0, model weight =1) with no other competing models. The directionality and strength of selection remained similar for habitat types across both seasons, with the exception of open woodland and distance to open woodland which switched from selection to avoidance in the high flood season (Table 4. 1.). Lions also seemed to select more strongly for areas closer to floodwater, but in contrast to the low flood season, showed selection for areas with lower NDVI values (Table 4. 1.). Across both seasons, lions maintained a strong avoidance of areas close to human settlements (Table 4. 1.) and avoided use of a large sandveld tongue in the south-western Delta, which is relatively arid in relation to surrounding floodplain areas and is characterized by deep Kalahari sand and *Colophospermum mopane* and *Philonoptera nelsii* communities. Using the 30% test data, both minimum and maximum flood resource selection function probability surfaces were highly predictive, with Boyce index values of 0.884 and 0.887 respectively.

Table 4. 1. Resource selection function results for minimum flood level (March – May) and maximum flood level (June – August) for lions (*Panthera leo*) in the Okavango Delta, Botswana. *** indicates covariates which were highly significant. Minimum flood values are based on model-averaged estimates for the four top models (Appendix 1), while model estimates for maximum flood area based on the top model, which was the global model.

	Minimum flood				Maximum flood			
	Estimate	SE	z value	p-value	Estimate	SE	z value	p-value
Intercept	1.186	0.771	1.539	0.124	0.277	0.164	1.688	0.091
HUM_dis	0.313	0.025	12.458	< 2e-16 ***	0.706	0.023	30.212	< 2e-16 ***
OGL_dis	0.161	0.012	12.969	< 2e-16 ***	0.121	0.012	9.859	< 2e-16 ***
OWL_prop	0.061	0.013	4.676	2.90E-06 ***	-0.138	0.012	-11.237	< 2e-16 ***
OWL_dis	-0.059	0.013	4.629	3.70E-06 ***	0.105	0.012	8.585	< 2e-16 ***
RIP_prop	0.087	0.015	5.951	< 2e-16 ***	0.187	0.012	15.261	< 2e-16 ***
RIP_dis	-0.212	0.016	13.049	< 2e-16 ***	-0.272	0.018	-15.344	< 2e-16 ***
TREE_avg	-0.084	0.017	4.836	1.30E-06 ***				
WAT_dis	-0.009	0.013	0.717	0.473	-0.164	0.014	-11.564	< 2e-16 ***
NDVI_avg	0.001	0.007	0.14	0.889	-0.237	0.012	-19.177	< 2e-16 ***

HUM_dis = distance to village, cattlepost or agricultural field
OGL_dis = distance to edge of open grassland
OWL_prop = proportion of open woodland within 500m radius
OWL_dis = distance to edge of open woodland
RIP_prop = proportion of riparian woodland in 500m radius
RIP_dis = distance to edge of riparian woodland
TREE_avg = average percentage tree cover in 500m radius
WAT_dis = distance to water
NDVI_avg = average NDVI value in 500m radius

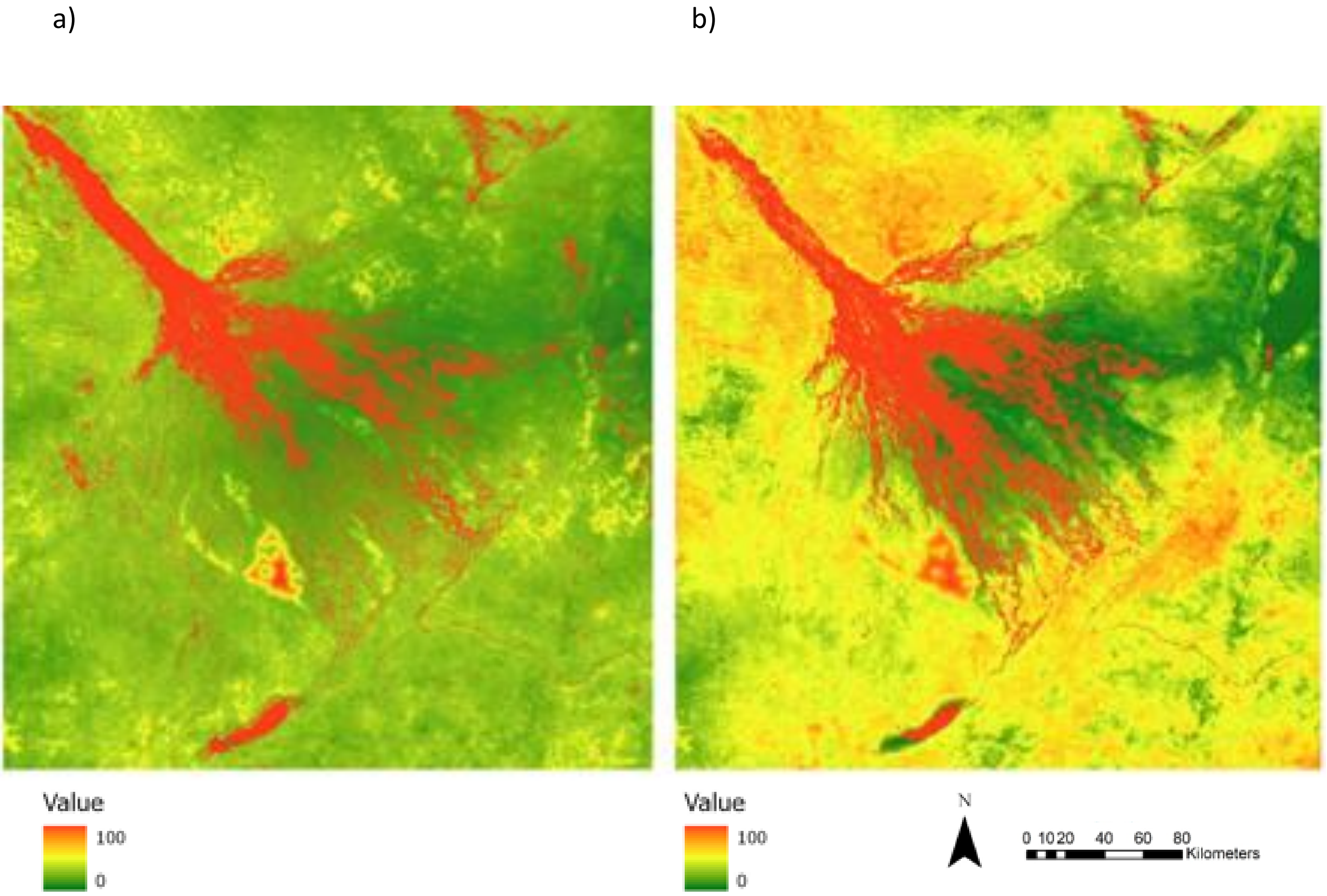

Figure 4. 2. Resistance surface maps created for the a) minimum flood season (March- May) and b) maximum flood season (June to August) for the year 2016 based on movement data from lions (*Panthera leo*) in the Okavango Delta, Botswana. Green indicates low resistance to movement while red indicates high resistance to movement.

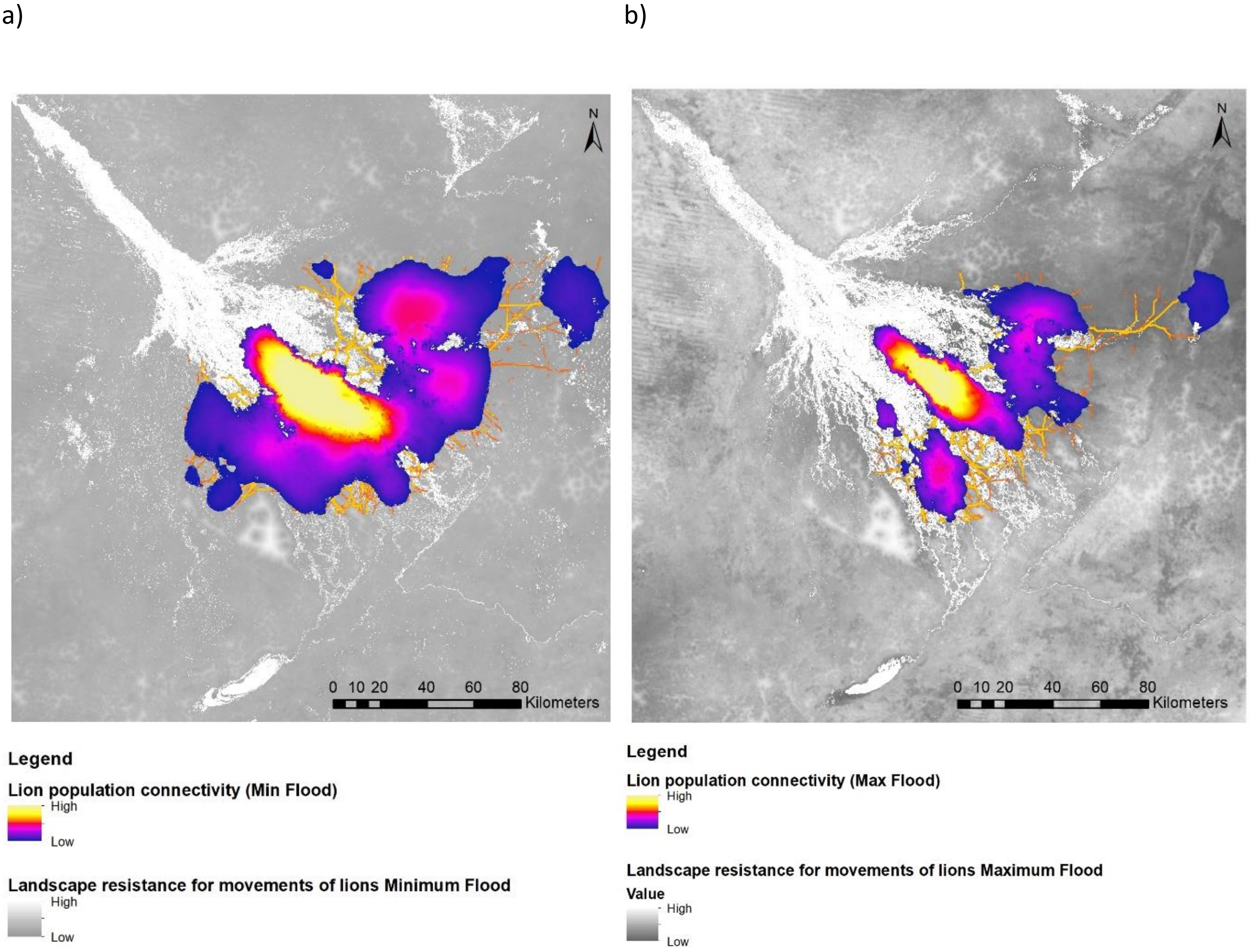

Figure 4. 3. Core areas created from kernel density estimates showing areas of high connectivity (kernels) and least cost path corridors (orange lines) during conditions of minimum flood (March - May; a) and maximum flood (June – August; b) for 2016 for lions (*Panthera leo*) in the Okavango Delta Botswana.

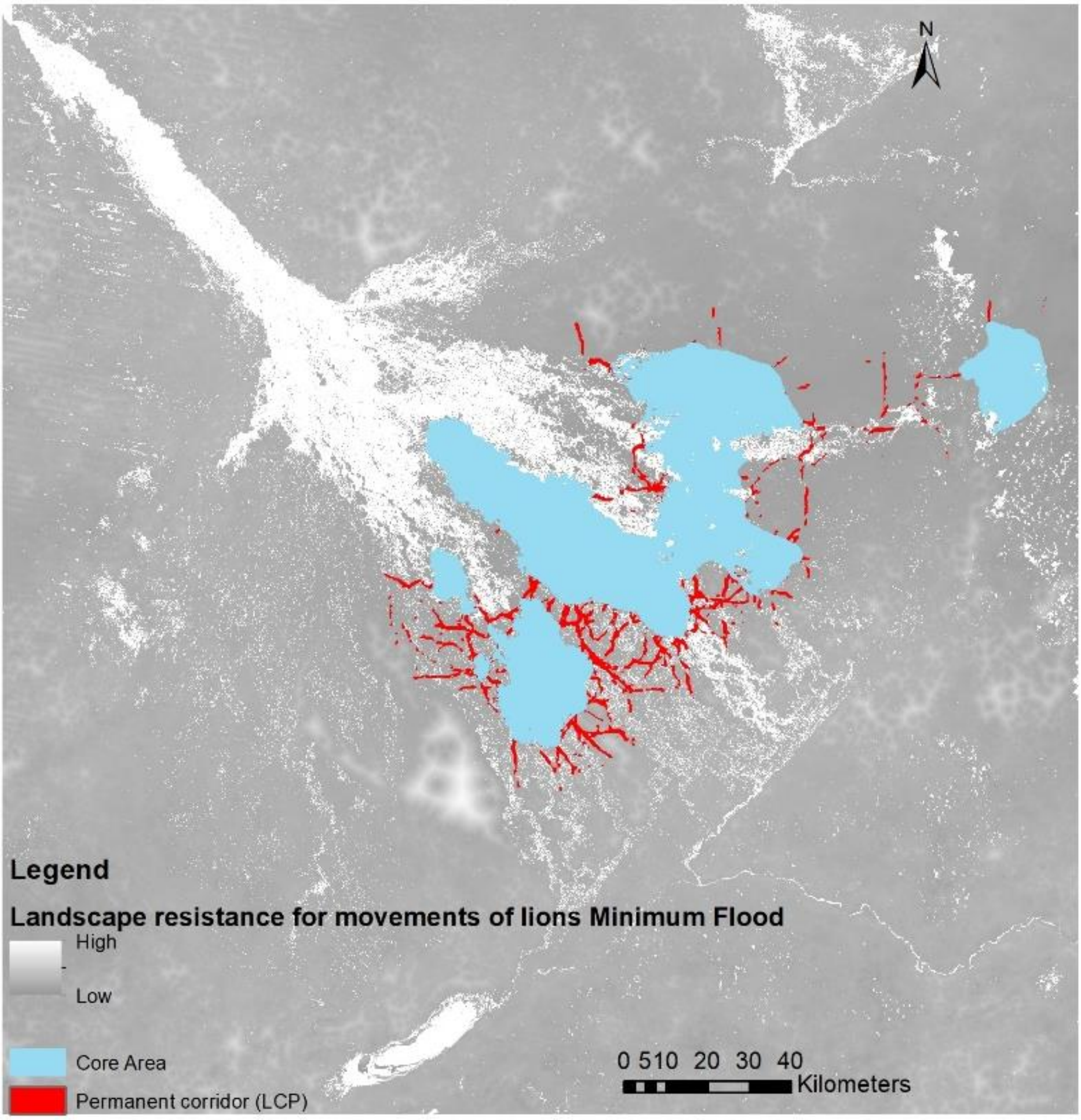

Figure 4. 4. Permanent core areas and corridors for lions (*Panthera leo*) resulting from combining kernel density estimate and least cost path corridor information from both minimum (March – May) and maximum flood conditions (June – August) for the Okavango Delta, Botswana, in 2016. Only core areas and corridors present in both seasons are represented. These are projected onto the minimum flood map for illustration.

Resistance to movement in the minimum flood season was much lower than resistance during the maximum flood season (Figure 4. 2). When examining connectivity, there are large seasonal differences in the core habitat areas estimated from kernel densities as well as the linkages between these estimated from least cost path analysis under minimum and maximum flood conditions (Figure 4. 3.). Based on kernel density estimates, during minimum flood, lions occupy an area of approximately 38 293 km^2. Of this area, 8936 km^2 is considered core habitat (Figure 4. 3.). Chief's Island consists of highly connected habitat, with medium connectivity to the western and southern Delta. There are an additional two core patches to the east, with a small core detected in the Mababe Depression (Figure 4. 3a). During the high flood, the areas occupied by lions decreases to 24,634km^2, with the combined cores shrinking by a total of 55% to only 4038km^2 (Figure 4. 3b). The core area of Chief's Island decreases significantly, and there is increasing fragmentation across the landscape, with the western core connectivity kernel disappearing completely. The small southern core remains the only other core area west of Chief's Island, with only narrow linkages to Chief's Island and the west remaining. The eastern cores are also significantly smaller, with the number of narrow corridors linking this area to Chief's Island significantly reduced (Figure 4. 3b). Lastly, when combining results from both core areas to identify permanent core and corridors, only 3802 km^2 of core area remains, with core areas clearly limited by conditions observed during the maximum flood extent (Figure 4. 4.). Fragmentation is significantly increased in areas to the west of Chief's Island, while in the east, some connection is maintained between Chief's Island core areas and the core areas in the east (Figure 4. 4.). Similarly, linkages remain to the small core in the Mababe depression (Figure 4. 4.). Most noticeably, for all scenarios, predicted corridors do not extend beyond the west, south and south east of the Okavango's periphery (Figure 4. 3., 4. 4.).

Discussion

Recent research has shown the importance of including data from different temporal scales when examining resource use in areas characterised by marked seasonal variation in resource availability and quality (Osipova et al., 2019; Kaszta et al., 2021). In the Okavango Delta, the seasonal flood pulse is the driving force for much of the ecological change observed, resulting in dramatic shifts in productivity and connectivity between different parts of the Okavango. My findings reveal that on average, during high flood phases, there are significant restrictions in movement density and connectivity across the Okavango Delta itself; most notably, in the western regions. On the edges of the Okavango, narrow corridor linkages persist in both seasons, but many of these are truncated by the buffalo fence, with little movement predicted to the west, south and south-east of the Delta where the density of human settlements is highest.

Seasonal resource selection

During both flood seasons, lions selected areas close to woodland edge, and areas with higher proportions of woodland in their home ranges. Riparian woodlands are directly adjacent to floodplains, and include evergreen trees such as *Garcinia livinsgtonei, Diospyros mespiliformis, Ficus sp.,* and stands of *Croton megalobotrys* (Ellery et al., 1993). Herbivores such as buffalo *(Syncerus caffer)*, tsessebe *(Damaliscus lunatus*), zebra (*Equus quagga*) and warthog (*Phacochoerus africanus*) utilize these woodlands for shade during the hot summer months, as well as for the high-quality grazing following localised rainfall, while in the dry season, multiple species use the floodplains adjacent to the woodlands for the high-quality grazing produced by receding floods (Bartlam-Brooks et al., 2013a; Bennitt et al., 2014; Bonyongo, 2005). Similarly, lions make use of the woodlands as resting places (pers. obs.), and as an ideal place for ambush hunting (Hopcraft et al., 2005; Midlane et al., 2014). The availability of prey, as well as the potential cover provided due to vegetation structure for hunting, may thus explain the selection for riparian woodland and riparian woodland edge year-round, and for males, proportion of riparian woodland is inversely related to home range size (Chapter 3). Similar patterns of higher preference for areas with more prey species were evident in Hwange National Park, Zimbabwe, where lions spent a large proportion of their time in bushed grasslands where prey were most abundant (Davidson et al., 2012), while in Selous Game Reserve, Tanzania, lions also selected habitats with higher prey abundances (Spong, 2002).

Contrary to my prediction, there was only a weak association between lion resource selection and NDVI in the low flood season, and a negative relationship in the dry, high flood season. It is possible that this reflects the scale of selection; while at a broad scale, lions may select for areas with higher NDVI values that are associated with greater prey abundance

(Chapter 2), at smaller home range scales, they may select for vegetation structure which influences prey catchability (Davidson et al., 2012; Hopcraft et al., 2005). Therefore, even though many large and medium-sized prey may follow the ‘green-up’ of vegetation (Bartlam-Brooks et al., 2013a; Bennitt et al., 2014), lions need to select for habitat types within these areas that increase their hunting success. This may additionally explain why lions avoid open grasslands and patches of bare earth as well as the edges of these habitats. The trade-off between prey abundance and prey catchability has also been observed in other large ambush hunters such as leopards (*Panthera pardus;* Balme et al., 2007). Additionally, as the dry season progresses, distance to water in such an arid environment becomes more of a constraining factor than vegetation quality for prey species (Burger, 2020; Redfern et al., 2003). Lions may therefore follow prey such as zebra and buffalo back to newly flooded areas as ephemeral pans dry out (Bartlam-Brooks et al., 2013b; Bennitt et al., 2014), which can confound any relationship with NDVI. In other studies, selection for areas close to water, particularly during the dry season, is a key determinant of habitat selection for lions in arid and semi-arid environments (Valeix et al., 2010b). This hypothesis is corroborated by the indication that lions select for areas close to water, with stronger selection for this resource in the dry season.

While the direction of the relationship between lion resource selection and most environmental variables remained consistent across both seasons, the relationship with open woodlands, which are dominated by *Colophospermum mophane, Philonoptera nelsii* and *Vichellia sp.,* changed markedly with lions preferring them during the low flood season. Once again, this is likely driven by the distribution of large to medium-sized prey with species like zebra and buffalo being attracted to this habitat because of the high nutrient content of the clay soils, or in the case of *Vichellia* habitats, due to associated nitrogen capture, which when combined with localised rainfall stimulates grass growth and thus provides nutritious forage (Bartlam-Brooks et al., 2013b; Bennitt et al., 2014; Burger, 2020). During this season, water is also likely available in the woodlands in the form of ephemeral pans. Lions are therefore likely to shift their habitat selection to open woodlands during the low flood season (which also coincides with the rain), and away from these back to the floodplains during the dry season. Lastly, lions appeared to avoid the use of the large sandveld tongue, depicted in the resistance maps in the south-western Delta. This area is relatively resource poor, has low water availability and consists of deep Kalahari sands (pers. observation), which likely incur large energetic costs for crossing for little reward. Large herbivore species such as buffalo and zebra, that were collared in this area at a similar time, also showed avoidance of the sandveld tongue throughout the year (see Burger 2020), and only moved along its edges.

Connectivity and cores

Connectivity between different core lion populations was highest in the minimum flood season, as expected. During this period, core areas are more connected, and there is less overall resistance to movement across the landscape. However, as flood levels increase, movement corridors are drastically impacted, particularly in the western Okavango Delta. While the isolation is only for part of the year in low-flood phases, decade-long high flood phases, where even minimum flood levels remain high, may have large impacts on lion core populations in the southern and western delta. As flood levels increase, lions in these areas will have to increase home range size to accommodate land fragmentation (Chapter 3) and as a result, lions on the periphery will be pushed towards the buffalo fence. This could increase the risk of negative interactions with people (e.g., livestock depredation), elevating the risk of anthropogenically caused injury and mortality and increasing competition for prey with bushmeat harvesters along the Okavango's edge (Rogan et al., 2017; Whitesell, 2019). As lion populations naturally decline during periods of high flood in areas of the Okavango which experience extensive inter-annual changes in seasonal flooding (Kotze et al., 2021), this could result in additive lion mortalities that will further depress population sizes in these areas (see Vinks et al., 2021), with limited opportunity for replenishment from the eastern and central delta. Current density estimates (Chapter 2) indicate that lion densities are lower closer to the buffalo fence, suggesting that these areas already function as population sinks (Kristan, 2003; Loveridge et al., 2010). Conservation efforts, such as reducing negative interactions between lions and both livestock and people, in addition to limiting bushmeat harvesting, should thus be prioritised to minimize the edge effects on the southern and western Okavango lion populations, which are particularly vulnerable to edge effects in years of high flood.

The lack of significant corridors outside of the Delta, with the exception of movement east towards the Mababe Depression, and to some degree to the north towards the Linyanti swamps, reinforce the finding that the ecological conditions caused by flooding, and accompanying habitat selection of resident lions, has resulted in the unique genetic distinction between Okavango lions and those in the surrounding Kalahari region (Dures et al., 2020). The genetic similarities between various core populations observed are well explained by the kernel density and predicted corridor results; lions on Chief's Island have a genetic makeup that indicates very little admixture from surrounding Kalahari lions, sharing a larger proportion of genetic similarities with the western and southern populations respectively (Dures et al., 2020). Conversely, on the eastern and northern side of the Okavango Delta, which are least impacted by flooding, and where there are comparatively fewer human settlements, there is an increased mix of genetic markers from dryland lions (Dures et al., 2020). While Dures et al. (2020) suggested that the presence of human activity did not significantly explain the observed genetic structure, our study showed that at the home range scale, lions consistently avoid areas of human settlements regardless of season. Differences in scale at which these factors were investigated (landscape versus home range) may be responsible for this discrepancy, but it could also have resulted from a mismatch between resistance surfaces inferred based only on genetic data, and resistance surfaces parameterized by movement data (Cushman et al., 2014; Cushman & Lewis, 2010). Where possible, as shown in this study, the two methods should be used to complement one another; resistance surfaces which are developed from movement data can more realistically depict geographic distance, leading to more accurate depictions of the mechanisms which lead to observed genetic differentiation (Coulon et al., 2004; Reding et al., 2013).

A limitation of this study is that the data obtained were mostly from resident adult males and females, with only one male of dispersal age collared. Resistance surfaces and resulting dispersal corridors can be markedly different across demographic groups for lions due to differing resource selection, territorial status and risk perception (Elliot et al., 2014a; Elliot et al., 2014b). While the physical restrictions to movement resulting from flooding are likely accurately depicting connectivity within the Okavango, it is possible that movement outwards has been underestimated by the parameterization of resistance surfaces primarily using territorial adults. This may be the reason for the mismatch between corridors predicted by Cushman et al. (2018) between the Okavango Delta and habitats to the south and east, which was based on a larger scale analysis of the entire KAZA landscape and parameterized by behaviour of dispersers from the neighbouring Hwange system. However, it is also possible that in the models by Cushman et al. (2018) the exclusion of information from local demographic processes such as mortality rates of dispersers, or the exclusion of local movement data may have led to an underestimation of the degree to which human dominated areas along the Okavango act as barriers to dispersal. The spatial variation in mortality risk (Cushman et al., 2016; Elliot et al., 2014a; Loveridge et al., 2017), as well as variation in other population demographic processes such as the frequency of dispersal, local dispersal behaviour, fluctuating population density, and individual behaviour are all factors which could potentially influence connectivity (Ash et al., 2020; Kaszta et al., 2019). Given the unique influence that flooding exerts on many demographic processes in this system (Kotze et al., 2018, 2021), further study on dispersal behaviour of sub-adult or dispersing males is important to refine connectivity modelling to and from the Okavango Delta.

Conclusions and conservation implications

This study highlights the importance of examining landscape resistance based on real biological movement data when parameterizing resistance surfaces and adds to recent studies which emphasise the importance of accounting for multiple temporal scales when planning corridors for conservation to ensure that corridors are functional (Cushman et al., 2014; Kaszta et al., 2021; Osipova et al., 2019; Uroy et al., 2021). The combined model in this study, which takes overlap of cores and connectivity in both seasons into account, largely explains the mechanisms by which genetic patterns described by Dures et al. (2020) may have emerged. The genetic similarities between the central, western and southern Okavango are likely due to the periodic isolation of these lions from other parts of the Okavango by flood waters, and their isolation from lion populations in the Kalahari to the south and Namibia to the west due to high human densities. While the current lion population in the Okavango Delta is currently estimated at more than 500 individuals (Loveridge et al. *unpublished data*), which is large enough to maintain a healthy, genetically viable, outbred population (Björkland, 2003), this study identified how temporal shifts in core lion areas and connectivity may make lion prides in different parts of the Okavango, particularly in the south and west, vulnerable to anthropogenic pressure. Mitigating edge effects caused by retaliatory killing of lions and bushmeat harvesting in these areas will be important to ensure the resilience of these cores during high flood phases. Furthermore, improving connectivity to other lion populations in the south and west can also build resilience of Okavango lions to stochastic events, improve the region's genetic diversity (Curry et al., 2021; Dures et al., 2019) and potentially buffer effects of climate change through creation of a stable metapopulation in KAZA with natural source and sink dynamics.

To date, most of the predicted effects of climate change and water extraction on flooding in the Okavango have been modelled in the context of flow patterns, flood extent and associated habitat conversion (Andersson et al., 2006; Milzow et al., 2010; Murray-Hudson et al., 2006). This study, however, can also be used as an example of the potential changes in population dynamics at the highest trophic level for future 'drier' or 'wetter' scenarios. Currently, 'drier' scenarios based on climate change projections and potential for upstream water extraction through agriculture or mining, are more likely, and the potential effects could be compared to our low flood models. While it appears that lower floods favour lions by increased connectivity within and around the Okavango, consistent low floods will have negative consequences in the long-term. Lions clearly favour habitats such as riparian woodland (see also Chapter 2), which are associated with the nutrient-rich floodplains and are sustained by the water table (Ellery et al. 1993; Milzow et al. 2010), and prolonged low floods will reduce the cover of these habitats (Gule et al., 2021; Milzow et al., 2010; Murray-Hudson et al., 2006). The associated decline in herbivore populations which depend on the seasonal floodplains (Bartlam-Brooks et al., 2013b; Burger, 2020), the extents of which also decline during dry phases, will inevitably reduce the carrying-capacity for lions. As with many seasonally flooded systems, biodiversity of the Okavango is reliant on the continued natural oscillations in seasonal floods (Beilfuss et al., 2010; Fynn et al., 2015; Keddy et al., 2009). While we can try to ameliorate the impacts of climate change through adaptive management, reducing the impact of anthropogenic water extraction by fostering sustainable management plans for the catchment and upstream Okavango River will be key for preservation of the Okavango and its lions (Keddy et al., 2009; Tomas et al., 2019).

References

Anderson, D. P., Turner, M. G., Forester, J. D., Zhu, J., Boyce, M. S., Beyer, H., & Stowell, L. (2005). Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management*, 69, 298–310.

Andersson, L., Wilk, J., Todd, M. C., Hughes, D. A., Earle, A., Kniveton, D., Layberry, R., & Savenije, H. H. G. (2006). Impact of climate change and development scenarios on flow patterns in the Okavango River. *Journal of Hydrology*, 331, 43–57.

Ash, E., Cushman, S. A., Macdonald, D. W., Redford, T., Kaszta, Z., Winitchai Rd, S., Nai, S., & Thai, P. (2020). How important are resistance, dispersal ability, population density and mortality in temporally dynamic simulations of population connectivity? A case study of tigers in Southeast Asia. *Land*, 9, 415.

Balme, G., Hunter, L., & Slotow, R. (2007). Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, 74, 589–598.

Bartlam-Brooks, H. L. A., Beck, P. S. A., Bohrer, G., & Harris, S. (2013a). In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, 118, 1427–1437.

Bartlam-Brooks, H. L. A., Bonyongo, M. C., & Harris, S. (2013b). How landscape scale changes affect ecological processes in conservation areas: External factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta. *Ecology and Evolution*, 3, 2795–2805.

Barton, K. (2019). Multi-model inference. R package version 1.43. 6. 2019.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

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

Beilfuss, R. D., Bento, C. M., Haldane, M., & Ribaue, M. (2010). Status and distribution of large herbivores in the Marromeu Complex of the Zambezi Delta, Mozambique. *Unpublished report. WWF, Maputo, Mozambique.*

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.

Bennitt, E., Bonyongo, M. C., & Harris, S. (2014). Habitat selection by African buffalo (*Syncerus caffer*) in response to landscape-level fluctuations in water availability on two temporal scales. *PloS ONE*, 9, 1–14.

Björkland, M. (2003). The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics*, 4, 515–523.

Bohnett, E., Hulse, D., Ahmad, B., & Hoctor, T. (2020). Multi-level, multi-scale modelling and predictive mapping for jaguars in the Brazilian Pantanal. *Open Journal of Ecology*, 10, 243–263.

Bonyongo, C. M. (2005). Habitat utilization by impala (*Aepyceros melampus*) in the Okavango Delta. *Botswana Notes & Records*, 37, 227–235.

Bonyongo, M. C., & Harris, S. (2007). Grazers species-packing in the Okavango Delta, Botswana. *African Journal of Ecology,* 45*,* 527–534.

Boswell, R. (2017). Seasonal resource selection and habitat treatment use by a fringe population of Greater sage-grouse. *All Graduate Plan B and Other Reports*, *1192*.

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions*, 12, 269–276.

Boyce, M. S., Mao, J. S., Merrill, E. H., Fortin, D., Turner, M. G., Fryxell, J., & Turchin, P. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, 10, 421–431.

Brook, B. W., Tonkyn, D. W., O'Grady, J. J., & Frankham, R. (2002). Contribution of inbreeding to extinction risk in threatened species. *Conservation Ecology*, 6.

Burger, K. (2020). *The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta.* PhD Thesis. University of the Witwatersrand.

Burnham, K. P., & Anderson, D. R. (2004). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (2nd ed.). Springer: New York.

Carvalho, F., Carvalho, R., Mira, A., & Beja, P. (2016). Assessing landscape functional connectivity in a forest carnivore using path selection functions. *Landscape Ecology*, 31, 1021–1036.

Chetkiewicz, A. C. B., Cassady, C., Clair, S., Boyce, M. S., Chetkiewicz, C. B., Cassady, C., Clair, S., & Boyce, M. S. (2006). Corridors for conservation : integrating pattern and process. *Annual Review of Ecology, Evolution, and Systematics,* 37, 317–342.

Chetkiewicz, C. L. B., & Boyce, M. S. (2009). Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology*, 46, 1036–1047.

Clevenger, A. P., Wierzchowski, J., Chruszcz, B., & Gunson, K. (2002). GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology*, 16, 503–514.

Cohen, J. E., & Newman, C. M. (1991). Community area and food-chain length: theoretical predictions. *American Naturalist*, 138, 1542–1554.

Collins, K., Moyo, L., & Thompson, M. (2019). Okavango catchment vegetation, land-cover and land-use classification derived from Sentinel-2 satellite imagery. *Unpublished report. GeoTerra Image, Pretoria, South Africa.*

Compton, B. W., Mcgarigal, K., Cushman, S. A., & Gamble, L. R. (2007). A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conservation Biology*, *21*(3), 788–799.

Coulon, A., Cosson, J. F., Angibault, J. M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S., & Hewison, A. J. M. (2004). Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. *Molecular ecology*, 13, 2841-2850

Curry, C. J., Davis, B. W., Bertola, L. D., White, P. A., Murphy, W. J., & Derr, J. N. (2021). Spatiotemporal genetic diversity of lions reveals the influence of habitat fragmentation across Africa. *Molecular Biology and Evolution*, 38, 48–57.

Cushman, S.A, McKelvey, K.S. & Schwartz, M. K. (2009). Use of empirically derived source-destination models to map regional conservation corridors. *Conservation Biology*, 23, 368-376.

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., & Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS ONE*, 13, e0196213.

Cushman, S. A., Elliot, N. B., Macdonald, D. W., & Loveridge, A. J. (2016). A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecology*, 31, 1337–1353.

Cushman, S. A., & Landguth, E. L. (2012). Multi-taxa population connectivity in the Northern Rocky Mountains. *Ecological Modelling*, 231, 101–112.

Cushman, S. A., & Lewis, J. S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology*, 25, 1613–1625.

Cushman, S. A., Lewis, J. S., & Landguth, E. L. (2014). Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modelling methods. *Diversity*, 6, 844–854

Cushman, S. A., McKelvey, K. S., Hayden, J., & Schwartz, M. K. (2006). Gene flow in complex landscapes: Testing multiple hypotheses with causal modelling. *American Naturalist*, *168*(4), 486–499.

Cushman, S. A., Mcrae, B., Adriaensen, F., Beier, P., Shirley, M., & Zeller, K. (2013). Biological corridors and connectivity. *Key Topics in Conservation Biology, 2*, 384–404.

Davidson, Z., Valeix, M., Loveridge, A., Hunt, J., Johnson, P., Madzikanda, H., & Macdonald, D. (2012). Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy*, 93, 677–685.

D'Eon, R., Serrouya, R., Smith, G., & Kochanny, C. O. (2002). GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, 430–439.

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion-conservation stronghold. *Diversity and Distributions*, 25, 870–879.

Dures, S. G., Carbone, C., Savolainen, V., Maude, G., & Gottelli, D. (2020). Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation,* 23, 502-515.

Ellery, W. N., Ellery, K., & McCarthy, T. S. (1993). Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions. *African Journal of Ecology*, 31, 118–134

Elliot, N. B. (2013). *The Ecology of Dispersal in Lions* (Panthera leo). PhD Thesis. University of Oxford.

Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014a). The devil is in the dispersers: Predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51, 1169–1178.

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014b). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, 95, 2860–2869.

Frankham, R. (2005). Genetics and extinction. *Biological Conservation*, 126, 131–140.

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, 23, 559–581.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E., & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, 75, 887–898.

Gule, T. T., Tsheboeng, G., Dlamini, W. M., Mabaso, S. D., & Cassidy, L. (2021). Change detection of riparian woodland vegetation in the Okavango Delta, Botswana. *Remote Sensing Applications: Society and Environment*, 22, 100497.

Gumbricht, T., McCarthy, J., & McCarthy, T. (2000). Portraying the geophysiology of the Okavango Delta, Botswana. In *Proceedings of the 28th International Symposium on Remote Sensing of the Environment*, *Cape Town, South Africa, ICRSE* (Vol. 4, pp. 10-13)

Gumbricht, T., McCarthy, J., & McCarthy, T. S. (2004). Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. *Earth Surface Processes and Landforms*, 29, 15–29.

Haidir, I. A., Kaszta, Ż., Sousa, L. L., Lubis, M. I., Macdonald, D. W., & Linkie, M. (2021). Felids, forest and farmland: identifying high priority conservation areas in Sumatra. *Landscape Ecology*, 36, 475–495.

Hansen, M. C., Potapov, P. v., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, 342.

Harju, S. M., Olson, C. v., Dzialak, M. R., Mudd, J. P., & Winstead, J. B. (2013). A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). *PloS ONE*, 8 e82271.

Hirzel, A. H., le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, 199, 142-152.

Hoffman, T. S., & O’Riain, M. J. (2012). Landscape requirements of a primate population in a human-dominated environment. *Frontiers in Zoology*, 9, 1-17.

Hopcraft, G. J. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74, 559–566.

Huck, M., Jedrzejewski, W., Borowik, T., Miłosz-Cielma, M., Schmidt, K., Jedrzejewska, B., Nowak, S., & Mysłajek, R. W. (2010). Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. *Acta Theriologica*, 55, 177–192.

Inman, V., & Lyons, M. (2020). *Automated Inundation History Mapping over Large Areas using Landsat and Google Earth Engine*. https://www.preprints.org/manuscript/202003.0038

Johnson, C. J., Parker, K. L., Heard, D. C., & Gillingham, M. P. (2002). A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications*, 12, 1840–1860.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.

Kaszta, Ż., Cushman, S. A., & Macdonald, D. W. (2020). Prioritizing habitat core areas and corridors for a large carnivore across its range. *Animal Conservation*, 23, 607–616.

Kaszta, Ż., Cushman, S. A., Sillero-Zubiri, C., Wolff, E., & Marino, J. (2018). Where buffalo and cattle meet: modelling interspecific contact risk using cumulative resistant kernels. *Ecography*, 41, 1616–1626.

Kaszta, Ż., Cushman, S. A., & Slotow, R. (2021). Temporal non-stationarity of path-selection movement models and connectivity: an example of African elephants in Kruger National Park. *Frontiers in Ecology and Evolution*, 9, 553263.

Kaszta, Ż., Cushman, S., Hearn, A., Burnham, D., Macdonald, E., Goossens, B., Nathan, S., & Macdonald, D. (2019). Integrating Sunda clouded leopard (*Neofelis diardi*) conservation into development and restoration planning in Sabah (Borneo). *Biologcial Conservation*, 235, 63-76.

Keddy, P. A., Fraser, L. H., Solomeshch, A. I., Junk, W. J., Campbell, D. R., Arroyo, M. T. K., & Alho, C. J. R. (2009). Wet and Wonderful: The World's Largest Wetlands Are Conservation Priorities. *BioScience*, 59, 39–51.

Khalyani, A., Gould, W. A., Falkowski, M. J., Muscarella, R., Uriarte, M., & Yousef, F. (2019). Climate change increases potential plant species richness on Puerto Rican uplands. *Climatic Change,* 156, 15–30.

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E. K., & Marshal, J. P. (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.

Kotze, R., Marshal, J. P., Winterbach, C. W., Winterbach, H. E. K., & Keith, M. (2021). Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment. *African Journal of Ecology*, 59, 63–73.

Kristan, W. B. (2003). The role of habitat selection behavior in population dynamics: Source-sink systems and ecological traps. *Oikos*, 103, 457–468.

Landguth, E. L., Hand, B. K., Glassy, J., Cushman, S. A., & Sawaya, M. A. (2012). UNICOR: A species connectivity and corridor network simulator. *Ecography*, 35, 9–14.

LaRue, M. A., & Nielsen, C. K. (2008). Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. *Ecological Modelling*, 212, 372–381.

Loveridge et al. *unpublished.* Estimates of lion (*Panthera leo*) density for the Okavango Delta, Botswana.

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). African lions on the edge: reserve boundaries as “attractive sinks”: In D. W. Macdonald & A. J. Loveridge (Eds.), *Biology and Conservation of Wild Felids* (p. 183). Oxford University Press.

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, 54, 815–825.

Manly, B. F. J., Mc Donald, L. L., Thomas, D. L, McDonald, T.L., & Erickson, W. P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. Kluwer, Boston.

Mazvimavi, D., & Wolski, P. (2006). Long-term variations of annual flows of the Okavango and Zambezi Rivers. *Physics and Chemistry of the Earth, Parts A/B/C*, 31, 944–951.

McCarthy, J., Gumbricht, T., & McCarthy, T. S. (2005). Ecoregion classification in the Okavango Delta, Botswana from multitemporal remote sensing. *International Journal of Remote Sensing*, 26, 4339–4357.

McCarthy, T. S., Cooper, G. R. J., Tyson, P. D., & Ellery, W. N. (2000). Seasonal flooding in the Okavango Delta, Botswana - recent history and future prospects. *South African Journal of Science*, 96, 25–33.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, 172, 101-108.

Milzow, C., Burg, V., & Kinzelbach, W. (2010). Estimating future ecoregion distributions within the Okavango Delta Wetlands based on hydrological simulations and future climate and development scenarios. *Journal of Hydrology*, 381, 89–100.

Moqanaki, E. M., & Cushman, S. A. (2017). All roads lead to Iran: Predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. *Animal Conservation*, 20, 29–41.

Mosser, A., Fryxell, J. M., Eberly, L., & Packer, C. (2009). Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, 12, 1050–1060.

Murray-Hudson, M., Wolski, P., Cassidy, L., Brown, M. T., Thito, K., Kashe, K., & Mosimanyana, E. (2015). Remote Sensing-derived hydroperiod as a predictor of floodplain vegetation composition. *Wetlands Ecology and Management*, 23, 603–616.

Murray-Hudson, M., Wolski, P., Murray-Hudson, F., Brown, M. T., & Kashe, K. (2014). Disaggregating Hydroperiod: Components of the Seasonal Flood Pulse as Drivers of Plant Species Distribution in Floodplains of a Tropical Wetland. *Wetlands*, 34, 927–942.

Murray-Hudson, M., Wolski, P., & Ringrose, S. (2006). Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. *Journal of Hydrology*, 331, 73–84.

Northrup, J. M., Hooten, M. B., Anderson, C. R., & Wittemyer, G. (2013). Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, 94, 1456–1463.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. *Animal Conservation*, 22, 35–48.

Pitman, R. T., Fattebert, J., Williams, S. T., Williams, K. S., Hill, R. A., Hunter, L. T. B., Robinson, H., Power, J., Swanepoel, L., Slotow, R., & Balme, G. A. (2017). Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management. *Journal of Applied Ecology*, 54, 1687–1698.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143, 939–945.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., van As, J., & VanderPost, C. (2006). Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences*, 68, 310–337.

R Core Team (2019). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84, 2092–2107.

Reding, D. M., Cushman, S. A., Gosselink, T. E., & Clark, W. R. (2013a). Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (*Lynx rufus*). *Landscape Ecology*, 28, 471–486.

Richard, Y., & Armstrong, D. P. (2010). Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. *Journal of Applied Ecology*, 47, 603–610.

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

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

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances,* 1, e1400103.

Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2010). Grizzly bear movements relative to roads: Application of step selection functions. *Ecography*, 33, 1113–1122.

Rogan, M. S., Lindsey, P. A., Tambling, C. J., Golabek, K. A., Chase, M. J., Collins, K., & McNutt, J. W. (2017). Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, 210, 233–242.

Rudnick, D., Beier, P., Cushman, S., Dieffenbach, F., Epps, C.W., Gerber, L., Hartter, J., Jenness, J., Kintsch, J., Merenlender, A.M., Perkle, R.M., Preziosi, D.V., Ryan, S.J., and S. C. Trombulak. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in ecology. *Report No. 16. Ecological Society of America. Washington, DC.*

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113.

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.

Statistics Botswana. (2014). *Population and housing census 2011 analytical report*. Statistics Botswana.

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos,* 571-573.

Thito, K., Wolski, P., & Murray-Hudson, M. (2016). Mapping inundation extent, frequency and duration in the Okavango Delta from 2001 to 2012. *African Journal of Aquatic Science*, 41, 267–277.

Tomas, W. M., de Oliveira Roque, F., Morato, R. G., Medici, P. E., Chiaravalloti, R. M., Tortato, F. R., Penha, J. M. F., Izzo, T. J., Garcia, L. C., Lourival, R. F. F., Girard, P., Albuquerque, N. R., Almeida-Gomes, M., Andrade, M. H. da S., Araujo, F. A. S., Araujo, A. C., Arruda, E. C. de, Assunção, V. A., Battirola, L. D., … Junk, W. J. (2019). Sustainability agenda for the Pantanal Wetland: perspectives on a collaborative interface for science, policy, and decision-making. *Tropical Conservation Science,* 12, 1940082919872634.

Tyson, P. D., Cooper, G. R. J., & McCarthy, T. S. (2002). Millennial to multi-decadal variability in the climate of southern Africa. *International Journal of Climatology*, 22, 1105–1117.

Uroy, L., Alignier, A., Mony, C., Foltête, J. C., & Ernoult, A. (2021). How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review. *Landscape Ecology*, 36, 2487–2504.

Valeix, M., Loveridge, A., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D.W. (2010a). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337–351.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010b). How key habitat features influence large terrestrial carnivore movements:

Waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337–351.

van der Weyde, L. K., Tobler, M. W., Gielen, M.C., Cozzi, G., Weise, F. J., Adams, T., Bauer, D., Bennitt, E., Bowles, M., Brassine, A., Broekhuis, F., Chase, M., Collins, K., Finerty, G.E., Golabek, K., Hartley, R., Henley, S., Isden, J., Keeping, D., … & Flyman, M. V. (2021). Collaboration for conservation: Assessing countrywide carnivore occupancy dynamics from sparse data. *Diversity and Distributions*, 00, 1–13.

Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., Chifunte, C., Midlane, N. & Simukonda, C. (2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications*, 31, e02298.

Wasserman, T. N., Cushman, S. A., Schwartz, M. K., & Wallin, D. O. (2010). Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology,* 25, 1601-1612.

Whitesell, C. A. (2019). *Movements of lions and other carnivores in relation to domestic and wild prey in northwestern Botswana*. PhD Thesis. University of California Davis.

Wolski, P., & Murray-Hudson, M. (2006). Recent changes in flooding in the Xudum distributary of the Okavango Delta and Lake Ngami, Botswana. *South African Journal of Science*, 102, 173–176.

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

Zeller, K. A., McGarigal, K., Beier, P., Cushman, S. A., Vickers, T. W., & Boyce, W. M. (2014). Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: Pumas as a case study. *Landscape Ecology*, 29, 541–557.

Zeller, K. A., McGarigal, K., Cushman, S. A., Beier, P., Vickers, T. W., & Boyce, W. M. (2016). Using step and path selection functions for estimating resistance to movement: Pumas as a case study. *Landscape Ecology*, 31, 1319–1335

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, 27, 777–797.

Zeller, K. A., Nijhawan, S., Salom-Pérez, R., Potosme, S. H., & Hines, J. E. (2011). Integrating occupancy modelling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biological Conservation*, 144, 892–901.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14.

Chapter 5

Conclusion

Study context

Since the beginning of the 20th century, wetland habitat has declined between 64 and 71% worldwide, with inland freshwater systems experiencing the highest losses (Davidson, 2014). Wetlands are important for the provision of ecosystem services such carbon sequestration, the supply of naturally-filtered fresh water and the supply of food resources through fisheries and recession agriculture (Junk et al., 2013; Keddy et al., 2009; Tomas et al., 2019). However, the functioning of these systems is increasingly threatened by excessive water abstraction and the subsequent use of land for agricultural purposes and mining (Andersson et al., 2006; Erwin, 2009; Tomas et al., 2019). The loss of wetlands impacts regional hydrological regimes, driving perturbations in the temporal and spatial nature of hyrdroperiods, and increasing frequency of extreme flood events that are outliers to established historical patterns (Erwin, 2009). Understanding how shifts in hydrology drive changes in entire food webs and biodiversity remains elementary and there is thus a pressing need for research, particularly on wetlands in arid or semi-arid systems that are less resilient to anthropogenic impacts (Davidson, 2014; Erwin, 2009; Milzow et al., 2010).

For wildlife, wetlands act as key resources for large herbivores (Illius & O'Connor, 2000; Yoganand & Owen-Smith, 2014) by providing food and water resources at the end of the dry season in otherwise rainfall driven systems (Fynn et al., 2015). As dry season resources are often the limiting factor for herbivore populations in semi-arid or arid environments, wetlands can support higher densities of herbivores (Fynn et al., 2015; Fynn & Bonyongo, 2011; Illius & O'Connor, 2000), and by extension, the large carnivores that depend on them. Wetlands around the world therefore provide refuges to some of the world's most charismatic large carnivores, many of which are currently facing population decline (Ripple et al., 2014). For example, the Pantanal wetland in Brazil has one of the highest densities of jaguars (*Panthera onca*) in the world (Devlin, 2019; Soisalo & Cavalcanti, 2006). In India, Kaziranga National Park, characterized by seasonal flooding of the Brahmaputra River, has the highest density of tigers (*Panthera tigris*) in the world (Borah et al., 2010; Jhala et al., 2019), and the mangrove swamps of the Sundarbans, shared by India and neighbouring Bangladesh, has also been identified as a critical refuge for tigers in this region (Barlow et al., 2011; Jhala et al., 2019). As large carnivores are apex predators, they are influenced by changes in lower trophic levels (Ripple & Beschta, 2006; Wallach et al., 2015; Wolf & Ripple, 2016) and can therefore act as reliable barometers of change in ecological systems. Despite been significant research being conducted on large cat species worldwide, most of these studies have been conducted in savannah systems, where access to study species is easily facilitated (Gros et al., 1996). Only now, with advances in technology (e.g., GPS tracking collars and high-resolution camera traps) that allow us to track and detect carnivores remotely, are we beginning to understand the breadth in ecology and behaviour of large predators in more difficult to access environments such as dense forests, and in this case, wetlands.

Currently the Okavango Delta acts as a refuge for the African lion (*Panthera leo*), one of the most enigmatic large carnivores in the world. Ecologically, the Okavango Delta is a key source population for the species within the Kavango-Zambezi Transfrontier Conservation Area (KAZA) and forms a part of what is believed to be the largest contiguous population of lions stretching from the Okavango Delta to Hwange National Park in Zimbabwe (Cushman et al., 2018). Economically, the lions of the Okavango Delta contribute significantly to Botswana’s tourism industry. From 2000 to 2019, the contribution of tourism to Botswana’s Gross Domestic Product grew from 6.3% to 13.1%, increasing at an average annual rate of nearly 5% per year (Chinya, 2021). Over 90% of these tourists visited Chobe National Park and Moremi Game Reserve, indicating that the wilderness experience and the presence of wildlife was one of the key drivers for visits to Botswana (Leechor, 2017). A study investigating the value of wildlife in the Okavango Delta to tourism indicated that ‘willingness-to-pay’ for the Okavango experience was highly correlated with wildlife viewing, and that in 2002, as much as $23 million was spent on travel to the Okavango alone (Mladenov et al., 2007). As viewing lions, and particularly the potential to view ‘swimming lions’, is one of the most sought-after wildlife viewing experiences in the Okavango Delta, their loss from this ecosystem has the potential to significantly diminish economic returns for the region. Given the ecological and economic importance of lions in the Okavango Delta, their effective conservation in this ecosystem is of broader concern for the viability of the species internationally as well as regionally.

Empirical findings

In Chapter 2, I showed how camera trapping and a spatially-explicit capture-recapture analysis framework can be used as a reliable method to estimate lion densities with reasonable precision. I also showed how the resulting density map could be linked to ecological and anthropogenic covariates, accounting for heterogeneity in density across the study area, and providing insight into drivers of density which can inform conservation approaches. Previously, SECR analyses from camera trap data has been focussed on carnivores with distinct pelage patterns like leopards (Chapman & Balme, 2010; Hedges et al., 2015), jaguars (Soisalo & Cavalcanti, 2006; Tobler & Powell, 2013) and tigers (Hernandez-Blanco et al., 2013; Karanth, 1995). However, the use of a white flash at night, together with high resolution images, has enabled the individual identification of lions using whisker spot patterns, body scars and mane size, colour and pattern (see Strampelli et al., 2022), where previous surveys using infrared flashes or yielding images of lower resolution made this impossible (Cusack et al., 2015, Rich et al., 2019). This survey method can therefore be added to toolkit for estimating lion densities, which is crucial for their conservation and for measuring the success of efforts to conserve the species.

Camera traps are also ideal for a heterogenous environment like the Okavango Delta, which has varying levels of accessibility due to regular floods, vast areas which have no access roads, and thick habitats such as those dominated by *Colophospermum mopane* or *Philenoptera nelsii* woodlands which are inaccessible by vehicle. The last survey of lions for the entire Okavango Delta was conducted using call-up stations in 1998 (Winterbach et al. 1998) but camera trap surveys provide a feasible alternative method for monitoring lion densities across this landscape. While scalability of surveys to the rest of the Okavango Delta is logistically challenging and financially taxing (Strampelli et al., 2022), such extensive surveys would be advantageous to produce baseline estimates for different parts of the Okavango. For future surveys, a hybrid approach that combines the use of more cost-effective citizen science approaches to monitoring for high volume tourist areas (see Rafiq et al., 2019), with camera surveys for low volume or difficult to access areas, would likely be the best approach for scaling surveys up across the landscape.

While single density estimates are temporally static, they are a summation of factors which have influenced population demographics in the recent past. Density in animal populations, particularly for territorial species, is often inversely proportional to home range size (Efford et al., 2016), a metric which encompasses movement decisions made by individuals of the species in response to temporal and spatial variation of intrinsic and extrinsic factors in their environment (Jones & Davidson, 2016). Due to the large temporal and spatial variation in resources caused by flooding, in Chapter 3 I compared the impact of changing landscape structure on lion home range size at maximum and minimum flood conditions. This chapter showed the importance of landscape indices in influencing lion movement at the home range scale, and landscape structure proved to be an important driver of home range size across flood seasons.

At maximum flood, there was no difference in home range size between males and females, and of all the variables tested, number of patches was the only landscape index that influenced home range size, with home range size increasing as fragmentation of land increased. This suggests that if lions are faced with increasing habitat fragmentation bought on by changing flooding patterns, home ranges may increase in size, reducing the carrying capacity for lions in the Okavango. In contrast, during low floods home range size of males and females differed significantly, and like in other mesic systems (Loveridge et al., 2009; Schaller, 1972) were driven by different factors. These results suggest that females follow an area minimization strategy when floods are low; home ranges were negatively correlated with prey density and habitat heterogeneity, and were also smaller where island sizes within the home range were larger and more connected. Males, however, appear to maximize access to females (Loveridge et al., 2009) by maintaining access to high quality habitat that would be more valuable for prey year-round, as home ranges were negatively correlated with habitat heterogeneity, a landscape factor favoured by females, while prey availability had little influence. Male home range size was also negatively correlated with riparian woodland, which is sought out by herbivores in the dry season, and which provides cover for hunting. Changes in landscape structure result in different drivers of home range size with different seasons, emphasizing the importance of understanding the temporal range of responses of carnivores to changes in landscape indices, and this study adds to a growing body of literature on the topic for large carnivores (Hiller et al., 2015; Mangipane et al., 2018; Snider et al., 2021).

Following on from the theme of Chapter 3, which showed the importance of taking temporal variation in population parameters into account in dynamic ecosystems, Chapter 4 similarly focuses on the temporal variation in resource selection and the resulting changes in the size of population cores and connectivity between different parts of the Okavango Delta and surrounding habitats in response to different flooding regimes. While many studies of connectivity pathways using resource selection functions take the influence of spatial scale into account, many ignore the possibility of temporal variation in selection of resources and resulting movements, which may lead to erroneous interpretation of connectivity pathway outcomes (Cushman, 2006; Kaszta et al., 2021; Osipova et al., 2019). As the Okavango experiences both inter- and intra-annual changes in flood regime (Murray-Hudson et al., 2014; Ramberg et al., 2006), this system provided an ideal scenario for testing temporal differences in connectivity as the Delta fluctuates between high and low flood conditions.

The results showed that during high flood phases, there were significant decreases in connectivity between different parts of the Okavango Delta, and a notable decrease in the size of population cores, and concomitant increase in isolation, of the central, western and southern regions, with the western core and connectivity to the western core disappearing almost completely in high flood conditions. During extended periods of high flood, lions in the western Okavango Delta specifically are pushed towards the buffalo fence, an area vulnerable to anthropogenic threats, including bushmeat harvesting and retributive killings for actual and perceived impacts on livestock (Rogan et al., 2017; Whitesell, 2019). Interestingly, the limited connectivity during high flood phases between northern Chief's Island and the western Delta, mirrors patterns of genetic diversity for the Okavango Delta (Dures et al., 2020), where lions in these two areas had more unique genetic markers compared to more connected areas in the south and east. The restrictions of movement outwards from the Okavango, particularly to the west and south, do not match predictions of other broader connectivity models for the region (see Cushman et al., 2018). However, this may be due to the lack of dispersal data available for this study, as dispersers are typically less risk averse (Elliot et al., 2014a, 2014b). Alternatively, the observed difference may be due to the differences in scale between the two studies, or indicative that local adaptations to the Okavango Delta and relative resource richness to surrounding dryland areas may discourage dispersal outwards (see Dures et al., 2020).

Spatially, habitat and resource selection are hierarchical processes (Johnson, 1980), and this thesis examines how both environmental and anthropogenic factors influence lion space use in the Okavango Delta at multiple selection scales, while also accounting for potential temporal variability at these scales. Interestingly, across all scales, proxies of habitat quality such as normalized difference vegetation index for density (Chapter 2) at the landscape scale, and at the scale of home range and movements within the home range, habitat type and habitat heterogeneity (Chapter 3 and 4), were stronger predictors of lion density, seasonal home range size and seasonal habitat selection than prey availability. Despite the established relationship between prey density and lion density (Ogutu & Dublin, 2002; Schaller, 1972; van Orsdol et al., 1985), prey density was only predictive of female home range size during the minimum flood season, which was expected due to the close relationship between prey availability and cub survival in this landscape (Kotze et al., 2021). We suggest that this observed pattern is likely to the temporal and spatial variation in prey availability, which may be typical of wetlands influenced by variations in flood patterns (Bartlam-Brooks., et al., 2013b; Bennitt et al., 2014; Burger, 2020). While large herbivores may follow seasonal patterns of vegetation productivity across the landscape, which is influenced by a mixture of rainfall as well as flooding patterns and have species-specific population responses to flooding patterns (Bartlam-Brooks., et al., 2013a; Bennitt et al., 2014, 2019; Burger, 2020) it would be energetically costly for lions to continually adapt to this variation (Macdonald & Carr, 1989). It is therefore likely that areas of long-term habitat quality are more influential in determining density and home ranges, and that lions respond to prey distribution within their home ranges seasonally. This is corroborated by Midlane et al. (2014), who also found that habitat type, rather than prey biomass, was more predictive of lion distribution across Kafue National Park, another landscape influenced by seasonal flooding. As there are several studies on herbivores in this system that have linked the same habitat proxies observed to impact lions in this study to herbivore habitat selection and distribution (Bonyongo, 2004; Bonyongo & Harris, 2007; Burger, 2020; Kotze et al., 2021), these proxies can be linked to lion ecology in the absence of prey density data. When prey density data is collected and linked to aspects of lion ecology such as home range use and abundance, this data may need to be averaged between seasons on annual timescales to account for seasonal movements of prey in response to changing resource availability to be most accurate.

With regards to the influence of anthropogenic factors, proximity to the southern buffalo fence or resident villages, had a negative influence on the distribution of lion density throughout the study area (Chapter 2), and when investigating seasonal movements, human settlements were avoided during both maximum and minimum flood seasons (Chapter 4). Retaliatory killing of carnivores on the Okavango's periphery (LeFlore et al., 2019; Weise et al., 2019a) may be introducing edge effects, which are well known to affect carnivore populations in other protected areas (Balme et al., 2010; Loveridge et al., 2010; Woodroffe & Ginsberg, 1998), and the avoidance of people appears to be operating at multiple scales. In addition, the potential for bushmeat harvesting depleting prey availability along the peripheries may lead to lower densities of prey and lions in these areas and could possibly result in larger home ranges to compensate for increased prey dispersion (Goodheart et al., 2021; Vinks et al., 2021). The influence of human settlements on lion movement was refuted by Dures et al. (2020) as a factor which explained low genetic connectivity between the Okavango Delta and surrounding habitats. However, our connectivity models, which are based on local lion movements, indicate that there is less movement of lions to the west and south of the Okavango Delta regardless of season. The combination of flooding and larger densities of human populations to the west and south have led to increased isolation of the western Delta in particular, while movement to the east, and to an extent, north, towards the Linyanti system is less impeded by people. This once again points to the differences in results from studying the same system at different scales to provide a more holistic understanding of intrinsic and extrinsic factors governing different population processes.

Lastly, as a wetland area, water was influential in determining the amount of available dry land, but unlike in drier savannah systems environments like the Serengeti or Kruger National Park (Smuts, 1978; Valeix et al., 2010), water was not a limiting resource for lions across this system. Lion density was not influenced by water, likely due to its ubiquity (Chapter 2). However, during maximum and minimum flood season, lions did select for areas closer to water (Chapter 4), seemingly in response to the seasonal dispersion of prey (Bennitt et al., 2014; Burger, 2020). Water was most influential in the spatial and temporal changes induced by the annual flood pulse across the landscape, which affected lion home range size (Chapter 3) as well as potential connectivity between different lion groups in the Okavango Delta. In Kafue National Park, flood patterns resulted in similar expansion of home ranges for lions, and in some cases home range shifts (Midlane, 2013). Similarly, floods in the Pantanal affect jaguar home range use, although they have the opposite effect on home range size (Crawshaw & Quigley, 1991). The influence of flooding on connectivity, however, provides unique insight into how wetlands can influence landscape connectivity under different flood regimes. When conducting conservation planning for wetland areas, both maximum and minimum flood conditions should be considered to account for extreme temporal variability and associated changes in density and movements to ensure the long-term viability of predator populations.

Shortfalls

Studying lions in a dynamic environment, where flooding constantly dictates access to study areas and study animals is extremely challenging. This study took place as a continuation of a long-term initiative started in 1997, during which time one of the lowest flood levels was recorded in history for the Okavango Delta. Following assumed tectonic movements, the flow of water down the Xudum distributary changed drastically and with that the flood regime for the region, with larger floods and lower access to the study area (Wolski & Murray-Hudson, 2006). As most of this study was conducted from a vehicle with no base camp, this presented considerable difficulties in collecting more data on the lions themselves and their prey. As some of the study lions occupied areas which were impossible to access year-round, it was not possible to collect robust information on pride sizes and compositions, which also affect elements of space use such as home range size (Loveridge et al., 2009; Mbizah et al., 2019; Spong, 2002).

The second issue regarding all analyses were constraints imposed by sample size. Particularly for Chapter 3, where we investigated the relationship between home range size and various ecological factors, a reduced sample size prevented me from conducting more detailed analyses such as mixed effects modelling with multiple covariates, or hierarchical partitioning to determine the relative contribution of landscape and habitat features to determining home range size. As with zebra in the Okavango Delta (Bartlam-Brooks et al., 2013b), there are likely nuances in home range size and factors influencing them between lions that live in the Delta's interior and those that live towards the Delta's periphery. Furthermore, home range and movement behaviour of lions on the periphery are likely influenced by cattle densities (Weise et al., 2019a), potential prey depletion due to bushmeat harvesting (Goodheart et al., 2021, Rogan et al., 2017, Vinks et al., 2021) and comparisons between interior lions and those on the periphery may have provided interesting insight into human-wildlife conflict (see Whitesell, 2019). Similarly, for Chapter 4, resource selection functions were limited to a few animals, all of which were resident. Inclusion of data from dispersers would have likely improved conclusions drawn about movements around the Okavango Delta, particularly if data could be added from movement of lions in areas surrounding the Okavango Delta.

Conservation Challenges and Recommendations

In Africa, the Okavango Delta is one of the world's least impacted inland Delta's, and to date has largely been unaffected by development (Gumbricht et al., 2000). However, as the flood waters originate in the highlands of Angola, there is rising concern of the potential impacts of upstream activities such as water extraction for agriculture in Angola and Namibia, on the downstream hydrology of the Okavango Delta itself (Gule et al., 2021; Murray-Hudson et al., 2006). In addition to development concerns, projected climate change in this region poses a long-term threat to the hydrological functioning of the Okavango: with a predicted 10% decrease in rainfall for the region by 2050, and a projected decline of 30 to 40% by 2099 (Batisani & Yarnal, 2010). Reduced rainfall will be accompanied by increased temperatures which would increase rates of evapotranspiration and surface drainage could be reduced by up to 50% (Batisani & Yarnal, 2010; de Wit & Stankiewicz, 2011). As the number of floral and faunal species in wetlands is often tied directly to its surface area (Findlay & Houlahan, 1997), the decrease in water supply to the Okavango will have a negative cascading effect on biodiversity including large carnivores. Together with the increasing demand for freshwater resources by a rapidly growing human population, there will be a need to effectively manage the Delta for the preservation of wildlife as well as for the benefit of people.

As most climate change scenarios predict a reduction in flood extent, the likely changes that will come with that must be considered in the context of conserving lions for this region. Seasonally flooded areas are rich in nutrients, maintain a higher diversity of species and support numerous grazing species such as buffalo (*Syncerus caffer*), zebra (*Equus* quagga), tsessebe (*Damaliscus lunatus*), wildebeest (*Connochaetes taurinus*) and red lechwe (*Kobus leche*), all large to medium-sized prey species which are important for lion (Burger, 2020; Kotze et al., 2018, 2021). While this study shows that lions fare better during drier years, and that reduced flooding increases connectivity and movement throughout the Okavango, overall lower flood extent will result in a smaller surface area of the Okavango and extended dry periods can result in the conversion of floodplains to dry wooded areas (Milzow et al., 2010; Murray-Hudson et al., 2006). This may ultimately decrease the carrying capacity for lion in the long-term. Scenarios such as increased deforestation and the frequency and extent of fires associated with a rising human population may reduce upstream vegetation biomass and increase runoff (Murray-Hudson et al., 2006). If the latter is combined with more stochastic rainfall and fewer but more severe rainfall events, then this can lead to increased amplitude of flood peaks. These higher flood levels could have negative consequences for lions, by decreasing connectivity between different areas of the Okavango (Chapter 4), decreasing available dry land (Chapter 3) and pushing both lions and prey toward the Delta's periphery, increasing their vulnerability to the effects of bushmeat harvesting as well as negative interactions with people (Chapter 4).

While extreme wet and extreme dry scenarios both have potential negative consequences for the Okavango Delta and the resident lion population, the maintenance of natural flood rhythms, as far as possible, is necessary to preserve the ecological functioning of this wetland. Under historical natural flood regimes, large herbivores and carnivores follow natural population oscillations which appear to be sustainable at the Okavango's current extent. While climate change is inevitable, understanding the effects of natural oscillations can assist in future management plans by incorporating expected variation, and mitigating other threats which may exacerbate changes in flood regime (Erwin, 2009). One of these threats is upstream water extraction. For example, in the Kafue flats, the offtake of water through the construction of the Kafue Gorge dam has had disastrous consequences for Kafue lechwe by altering natural flood regimes that produce dry season grazing for the species (Chansa & Kampamba, 2010; Rees, 1978). Upstream management of the Okavango Delta's source in Angola, as well as the management of human activities along the Okavango River will be important in minimizing the impact of people on the system and maintaining the natural functioning of this wetland as far as possible. Sustainable management strategies that incorporate political, ecological and economic factors across international boundaries of Angola, Botswana and Namibia will need to be established to achieve this outcome (Erwin, 2009; Keddy et al., 2009; Tomas et al., 2019).

In the meantime, other extenuating factors in the Okavango Delta need to be addressed. Of particular concern is the increase in cattle numbers, and their dependence on the Okavango for grazing and water during the dry season. Since the eradication of the tsetse fly and associated *Trypanasomiasis* in the Okavango Delta in the early 1960s and 1970s (Bolaane, 2007), cattle numbers have grown in Ngamiland, and cattle is one of the largest agricultural sectors in the country and makes up a significant portion of the rural economy (Winterbach et al., 2014). Consequently, there is increasing conflict with large carnivores, particularly lions, on the peripheries of the Okavango Delta where lions predate on cattle (LeFlore et al., 2019; Whitesell, 2019). Cattle on the edges of the Delta are attracted to fresh grazing and water in the floodplains at the end of the dry season, increasing their vulnerability to predation by lions that reside in the wildlife management areas (Weise et al., 2019a). The conflict is further exacerbated during drought years, when limited grazing outside the boundaries of the Okavango causes pastoralists to cut the buffalo fence and push their cattle into the Okavango for access to fresh grazing and water to ensure their survival (Kotze pers. observation). This conflict may have significant edge effects on lion populations, and conflict records suggest that a significant number of lions are killed in retaliation for loss of livestock each year (LeFlore et al., 2019; Weise et al., 2019b; Whitesell, 2019).

As the Okavango Delta is already isolated as a wetland in the middle of an arid Kalahari system (Bartlam-Brooks et al., 2013b), the increasing competition for water, grazing and space will need to be addressed, particularly if both wildlife and communities are to adapt to pending climate change. Rangeland management and livestock husbandry, which includes kraaling of cattle at night, herding during the day and management of disease (Basupi et al., 2019; Weise et al., 2018; Weise et al., 2019a, 2019b) is important for limiting livestock loss caused by lions. Furthermore, reform of the beef industry which allows better access to markets and makes rural cattle ownership more economically viable, needs to be addressed at much larger scales across the Ngamiland landscape to benefit pastoralists and improve incentives for cattle management (see van Rooyen, 2016). Given the current challenges, emphasis should also be placed on alternative livelihoods to diversify rural economies (Basupi et al., 2019). As a RAMSAR wetland and recognized World Heritage Site, the Okavango and its wildlife are valuable resources for the region. In addition to conflict, bushmeat hunting on the periphery of the Okavango Delta is becoming a lucrative commercial industry and is primarily undertaken to provide an additional income to rural communities (Rogan et al., 2017). The offtake of preferred prey can considerably reduce the carrying capacity for lions (Goodheart et al., 2021, Rogan et al., 2017), and this study already indicates that densities of lions are lower close to the buffalo fence in the southern Delta (Chapter 2). Local tourism enterprises which take advantage of the access to wildlife on the borders of the wetland should be encouraged and developed, to ensure that local communities benefit from wildlife (Blackburn et al., 2016; Osano et al., 2013). For example, in the seasonal wetlands in the Pantanal, Brazil, ranchers are adopting eco-tourism ventures to offset cattle losses to jaguars, which promotes the conservation of jaguars and boosts local economies (Tortato et al., 2017).

Lion populations along the southern and western borders of the Okavango Delta are particularly vulnerable to edge effects caused by human bushmeat harvesting and conflict. Particularly during phases of high floods, lions in the western and southern Okavango Delta may be pushed closer to the buffalo fence (Chapter 4), be isolated by water from the rest of the Okavango Delta (Chapter 4) and may expand home ranges to compensate for loss of land (Chapter 3). During phases of extended high flood in the Okavango's multi-decadal cycles, and with the hard boundary created by the buffalo fence and surrounding human population, these lions are more vulnerable to human-induced population decline and stochastic events (Winterbach et al., 2013), during a phase in which the population will decline naturally from high flood levels (Kotze et al., 2018, 2021). While one could argue that these populations would simply be restored once connectivity resumes with the rest of the Okavango Delta, the decline would nevertheless result in loss of genetic diversity and possibly the unique behavioural adaptations to this wetland environment (Dures et al., 2020; Moore et al., 2016). As genetic diversity in the KAZA region has already been substantially depleted over the last century, the unique alleles present in the Okavango Delta lion population need to be preserved to maintain genetic diversity in the southern African populations as a whole (Curry et al., 2021; Dures et al., 2019).

Future studies

Future studies in the Okavango should focus primarily on the interface between lions and people on the periphery of the Okavango Delta. The temporal and spatial aspects of negative interactions between people and lions, and how this is influenced by varying flood levels needs to be further assessed. Studies should also focus on the socio-economic impacts of negative interactions between lions and people on the boundaries and use this to inform education programmes and long-term mitigation solutions. These data, combined with population viability analyses of lion populations in the Okavango Delta under different climate change scenarios, could provide useful insight into the future of the Okavango's lion population. To this extent, ecological and socio-economic studies of the surrounding landscape, particularly in the corridor areas with high density of people to the south, west and to some extent along the panhandle, could provide insight into how best to establish or preserve corridors in these areas.

Lastly, from an ecological perspective, dispersal behaviour of lions in the Okavango is still relatively understudied. Given the differences in connectivity between the various parts of the Okavango Delta and the link between flood levels and population fluctuations, the relationship between current density, dispersal and flooding would shed further light on population dynamics of the system. During the earlier years of the study, I observed a relatively low turnover of adult males. One of the collared males and his coalition partner in the southern part of the study area held tenure for about 4 years, while a subgroup of females in the north of the concession were without pride males for more than two years while raising a cohort of eight cubs to dispersal age. However, during the camera trap surveys of 2017, I observed an influx of mature and sub-adult males, likely because of successful recruitment following a few years of low flood maxim, coupled with greater connectivity across the south-western delta associated with lower floods (Chapter 4).

Conclusion

This study contributes to our growing knowledge on the dynamics of the ecology of big cats in wetlands, which are keystone habitats for big cats around the world (Barlow et al., 2011; Figel et al., 2019; Kotze et al., 2021). Providing density estimates for lions using camera traps for photographic capture-recapture, is proving to be a reliable way of estimating large carnivores for wetlands, and overcomes some of the challenges associated with carnivores, and seasonally flooded areas, such as limited road access, wide distribution of target animals or spatial and temporal avoidance of human presence (Henschel et al., 2016, 2020). This method has proven successful in the Okavango Delta for lions (Chapter 1; Rich et al., 2019) and in the Brazilian Pantanal for jaguars (Devlin, 2019; Soisalo & Cavalcanti, 2006), and provides an improved alternative to spoor surveys and call-up stations previously conducted in the Okavango Delta (Cozzi et al., 2013) and Busanga Floodplains of Kafue National Park (Midlane et al., 2015). While camera trapping may be more costly than abundance indices, once the equipment is available, surveys are repeatable, and will provide reliable estimates. Due to their social structure, lion population change is not linear, and changes in populations occur in two-year leaps (the time it takes from birth to recruitment; Mosser & Packer, 2009; Packer et al., 1988, 2005). Repeated surveys could therefore take place at larger scales across the Okavango at four- to five-year intervals, with more intense monitoring through citizen science or long-term projects in areas of concern at shorter time scales.

The influence of flooding on home range size is largely in agreement with studies of lions in other flooded areas, in which home ranges expand in response to seasonal flooding, as resources become more dispersed, or in avoidance of flood waters (Midlane, 2013; Tumenta et al., 2013), but is contrary to studies on jaguars in which home ranges decreased in size during the flood season (Crawshaw & Quigley, 1991). Both patterns, however, are linked to the resulting dispersion of prey caused by seasonal flooding, with prey being more clustered in the Pantanal and leading to smaller home ranges (Crawshaw & Quigley, 1991). The dispersion of prey in seasonal wetlands is therefore something that should be further investigated. This study did, however, build on our knowledge of the mechanisms by which floods change the landscape by incorporating specific landscape indices relating to fragmentation and island configuration of dry land in response to flooding. This builds on a growing body of research on how landscape indices should not be overlooked when investigating ecological or anthropogenic induced land changes on at the home range sizes for large carnivores (Hiller et al., 2015; Kauhala & Holmala, 2011; Mangipane et al., 2018; Snider et al., 2021). Investigating ecological processes at the home range scale and understanding the spatial and temporal scales at which they occur, is important for making informed conservation management decisions (Tumenta et al., 2013).

The role of floodwater in temporally influencing connectivity is a relatively new application to wetland systems. Most research on connectivity for large carnivores has tried to shift emphasis from specific populations to range-wide connectivity analyses that focus on metapopulations across vast areas. While these studies are necessary for wider range conservation efforts, many do not accommodate the nuances in ranging behaviour specific to a particular population (see Dures et al., 2020), nor the local environmental conditions which may affect this behaviour and ultimately affect the accuracy of predicted outcomes. Furthermore, many studies ignore potential temporal changes in connectivity with season, and the effect this has on species-specific dispersal potential (Kaszta et al., 2021; Osipova et al., 2019). For example, in the Kaziranga Orang Riverine Landscape, studies have been done on the potential use of river islands for dispersal of tigers across the landscape, but this has not been extended to include how connectivity would vary with changes in flood conditions (Borah et al., 2010). In the Okavango itself, range-wide connectivity analyses have identified the Okavango Delta as part of the number-one ranked core area for lions within the Kavango-Zambezi Transfrontier Conservation Area, with the 4th and 5th most important corridors linking the Okavango to neighbouring lion populations to the west and south respectively (Cushman et al., 2018). However, this was based on movement behaviour specific to lion from Hwange National Park. Our study therefore builds on this model to increase accuracy of predictions at a local scale, while also including potential temporal variation, which can be used to inform the local conservation efforts for securing corridors linked to this model. This study shows limited current connectivity along these two corridors, largely due to high densities of people (Chapter 4), but also as a result of high levels of reported conflict (Whitesell, 2019, DWNP pers. comment). Land use planning and mitigation of negative interactions between people and lions will need to be employed in management plans if these corridors are to be functional.

This work contributes to baseline information on the complex relationships between flooding and higher trophic levels (Milzow et al., 2010; Murray-Hudson et al., 2006), which are important for the long-term management plans for the system, and the lions that inhabit it. Additionally, the varying flood conditions, particularly conditions under high flood, mimic the fragmentation and loss of habitat that many large carnivores face today because of anthropogenic pressures, giving us an ideal system to test the response of different population parameters of large carnivores to these conditions (see also Kotze et al., 2018, 2021). While some medium-sized carnivores, or generalist carnivores, such as bobcats (*Felis rufus*), coyotes (*Canis latrans*) and leopards (*Panthera pardus*), have been shown to adapt to intermediate levels of fragmentation (Crooks, 2002; Snider et al., 2021), most large carnivores adapt poorly to habitat loss and fragmentation, and the associated depletion of prey (Crooks, 2002). Polar bears (*Ursus maritimus)* are perhaps the large carnivores which are most immediately threatened by loss and fragmentation of available sea ice (Peacock et al., 2010), which impacts their movements locally as well as over longer distances, and imposes energetic costs associated with more swimming and large travel distances to find sufficient prey (Peacock et al., 2010). While the conditions experienced by polar bears are likely irreversible, for the lions in the Okavango Delta, and other wetland cats that rely on the sustained ebb and flow of flood conditions, this study provides insight into impacts by alternative scenarios which will aid in future conservation management plans.

References

Andersson, L., Wilk, J., Todd, M. C., Hughes, D. A., Earle, A., Kniveton, D., Layberry, R., & Savenije, H. H. G. (2006). Impact of climate change and development scenarios on flow patterns in the Okavango River. *Journal of Hydrology*, 331, 43–57.

Balme, G. A., Slotow, R., & Hunter, L. T. B. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, 13, 315–323.

Barlow, A. C. D., Smith, J. L. D., Ahmad, I. U., Hossain, A. N. M., Rahman M, & Howlader A. (2011). Female tiger *Panthera tigris* home range size in the Bangladesh Sundarbans: the value of this mangrove system for the species' conservation. *Oryx*, 45, 125–128.

Bartlam-Brooks, H. L. A., Beck, P. S. A., Bohrer, G., & Harris, S. (2013a). In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, 118, 1427–1437.

Bartlam-Brooks, H. L. A., Bonyongo, M. C., & Harris, S. (2013b). How landscape scale changes affect ecological processes in conservation areas: External factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta. *Ecology and Evolution*, 3, 2795–2805.

Basupi, LV, Quinn, CH, Dougill, & Dougill, A, J. (2019). Adaptation strategies to environmental and policy change in semi-arid pastoral landscapes: evidence from Ngamiland, Botswana. *Journal of Arid Environments*, *166*, 17-27.

Batisani, N., & Yarnal, B. (2010). Rainfall variability and trends in semi-arid Botswana: Implications for climate change adaptation policy. *Applied Geography*, 30, 483–489.

Bennitt, E., Bonyongo, M. C., & Harris, S. (2014). Habitat selection by African buffalo (*Syncerus caffer*) in response to landscape-level fluctuations in water availability on two temporal scales. *PloS ONE*, 9, 1–14.

Bennitt, E., Hubel, T. Y., Bartlam-Brooks, H. L. A., & Wilson, A. M. (2019). Possible causes of divergent population trends in sympatric African herbivores. *PloS ONE*, 14, e0213720.

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

Bolaane, M. M. (2007). Tsetse and trypanosomiasis control in the Okavango Delta, c. 1930s-1970s: feature: livestock diseases and veterinary science. *South African Historical Journal*, 58, 91–116.

Bonyongo, C. (2004). *The ecology of large herbivores in the Okavango Delta, Botswana*. PhD Thesis. University of Bristol.

Bonyongo, M. C., & Harris, S. (2007). Grazers species-packing in the Okavango Delta, Botswana. *African Journal of Ecology,* 45, 527–534.

Borah, J., Firoz Ahmed, M., & Kumar Sarma, P. (2010). Brahmaputra River islands as potential corridors for dispersing tigers: A case study from Assam, India. *International Journal of Biodiversity and Conservation*, 2, 350–358.

Burger, K. (2020). *The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta*. PhD Thesis. University of the Witwatersrand.

Chansa, W., & Kampamba, G. (2010). The population status of the Kafue Lechwe in the Kafue Flats, Zambia. *African Journal of Ecology*, 48, 837–840.

Chapman, S., & Balme, G. (2010). An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *African Journal of Wildlife Research*, 40, 114–120.

Chinya, C. (2021). *The Tourism Industry in Botswana - 2021*. Botswana.

Cozzi, G., Broekhuis, F., McNutt, J. W., & Schmid, B. (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.

Crawshaw, P. G., & Quigley, H. B. (1991). Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology*, 223, 357–370.

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16, 488–502.

Curry, C. J., Davis, B. W., Bertola, L. D., White, P. A., Murphy, W. J., & Derr, J. N. (2021). Spatiotemporal Genetic Diversity of Lions Reveals the Influence of Habitat Fragmentation across Africa. *Molecular Biology and Evolution*, 38, 48–57.

Cusack, J. J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A. J., Kosmala, M., Lintott, C. & Rowcliffe, J. M. (2015). Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. *The Journal of Wildlife Management*, 79, 1014-1021.

Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, 128, 231–240.

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., & Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS ONE*, 13, e0196213.

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, 65, 934–941.

de Wit, M., & Stankiewicz, J. (2011). Changes in Surface Water Supply. *Science*, 311, 1917–1921.

Devlin, A. L. (2019). *Drivers of jaguar (*Panthera onca*) distribution, density, and movement in the Brazilian Pantanal.* SUNY College of Environmental Science and Forestry.

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion-conservation stronghold. *Diversity and Distributions*, 25, 870–879.

Dures, S. G., Carbone, C., Savolainen, V., Maude, G., & Gottelli, D. (2020). Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation,* 23, 502-515.

Efford, M. G., Dawson, D. K., Jhala, Y. V., & Qureshi, Q. (2016). Density-dependent home-range size revealed by spatially explicit capture-recapture. *Ecography*, 39, 676–688.

Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014a). The devil is in the dispersers: Predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51, 1169–1178.

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014b). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, 95, 2860–2869.

Erwin, K. L. (2009). Wetlands and global climate change: The role of wetland restoration in a changing world. *Wetlands Ecology and Management*, 17, 71–84.

Figel, J. J., Botero-Cañola, S., Forero-Medina, G., Sánchez-Londoño, J. D., Valenzuela, L., & Noss, R. F. (2019). Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot. *PloS ONE*, 14, 1–16.

Findlay, C. S., & Houlahan, J. (1997). Anthropogenic Correlates of Species Richness in Southeastern Ontario Wetlands: Correlativos Antropogénicos de la Riqueza de Especies en Humedales del Sureste de Ontario. *Conservation Biology*, 11, 1000-1009.

Fynn, R. W. S., & Bonyongo, M. C. (2011). Functional conservation areas and the future of Africa’s wildlife. *African Journal of Ecology*, 49, 175–188.

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, 23, 559–581.

Goodheart, B., Creel, S., Becker, M. S., Vinks, M., Schuette, P., Banda, K., Sanguinetti, C., Rosenblatt, E., Dart, C., Kusler, A., Young-Overton, K., Stevens, X., Mwanza, A. & Simukonda, C. (2021). Low apex carnivore density does not release a subordinate competitor when driven by prey depletion. *Biological Conservation*, 261, 109273.

Gros, P. M., Kelly, M. J., Caro Gros P M, T. M., J, K. M., Gros, P. M., Kelly, M. J., & Caro, T. M. (1996). Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. *Oikos*, 197-206.

Gule, T. T., Tsheboeng, G., Dlamini, W. M., Mabaso, S. D., & Cassidy, L. (2021). Change detection of riparian woodland vegetation in the Okavango Delta, Botswana. *Remote Sensing Applications: Society and Environment*, 22, 100497.

Gumbricht, T., McCarthy, J., & McCarthy, T. (2000). Portraying the geophysiology of the Okavango Delta, Botswana. In *Proceedings of the 28th International Symposium on Remote Sensing of the Environment*, *Cape Town, South Africa, ICRSE* (Vol. 4, pp. 10-13).

Hedges, L., Lam, W. Y., Campos-Arceiz, A., Rayan, D. M., Laurance, W. F., Latham, C. J., Saaban, S., & Clements, G. R. (2015). Melanistic leopards reveal their spots: Infrared camera traps provide a population density estimate of leopards in Malaysia. *Journal of Wildlife Management*, 79, 846–853.

Henschel, P., Petracca, L. S., Ferreira, S. M., Ekwanga, S., Ryan S D, & Frank, L. G. (2020). Census and distribution of large carnivores in the Tsavo national parks, a critical east African wildlife corridor. *African Journal of Ecology*, 58, 383–398.

Henschel, P., Petracca, L. S., Hunter, L. T. B., Kiki, M., Sewadé, C., Tehou, A., & Robinson, H. S. (2016). Determinants of distribution patterns and management needs in a Critically Endangered lion *Panthera leo* population. *Frontiers in Ecology and Evolution*, 4, 110.

Hernandez-Blanco, J. A., Rozhnov, V. v., Lukarevskiy, V. S., Naidenko, S. v., Chistopolova, M. D., Sorokin, P. A., Litvinov, M. N., & Kotlyar, A. K. (2013). Spatially explicit capture-recapture method (SECR, SPACECAP): A new approach to determination of the Amur tiger (*Panthera tigris altaica*) population density by means of camera-traps. *Doklady Biological Sciences*, 453, 365–368.

Hiller, T. L., Belant, J. L., & Beringer, J. (2015). Sexual size dimorphism mediates effects of spatial resource variability on American black bear space use. *Journal of Zoology*, 296, 200–207.

Illius, A. W., & O'Connor, T. G. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, 89, 283–294.

Jhala, Y., Qureshi, Q., & Nayak A. K. (2019). Status of tigers, co-predators and prey in India in 2018. *National Tiger Conservation Authority, Government of India, New Dehli and Wildlife Institute of India, Dehradun*.

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, 61, 65–71.

Jones, M. E., & Davidson, N. (2016). Applying an animal-centric approach to improve ecological restoration. *Restoration Ecology*, 24, 836–842.

Junk, W. J., An, S., Finlayson, C. M., Gopal, B., Květ, J., Mitchell, S. A., Mitsch, W. J., & Robarts, R. D. (2013). Current state of knowledge regarding the world's wetlands and their future under global climate change: A synthesis. *Aquatic Sciences*, 75, 151–167.

Karanth, K. U. (1995). Estimating tiger (*Panthera tigris*) populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333-338.

Kaszta, Ż., Cushman, S. A., & Slotow, R. (2021). Temporal non-stationarity of path-selection movement models and connectivity: an example of African elephants in Kruger National Park. *Frontiers in Ecology and Evolution*, 9, 553263.

Kauhala, K., & Holmala, K. (2011). landscape features, home-range size and density of northern badgers *(Meles meles*). *Annales Zoologici Fennici*, 48, 221–232.

Keddy, P. A., Fraser, L. H., Solomeshch, A. I., Junk, W. J., Campbell, D. R., Arroyo, M. T. K., & Alho, C. J. R. (2009). Wet and wonderful: the world's largest wetlands are conservation priorities. *BioScience*, 59, 39–51.

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E. K., & Marshal, J. P. (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.

Kotze, R., Marshal, J. P., Winterbach, C. W., Winterbach, H. E. K., & Keith, M. (2021). Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment. *African Journal of Ecology*, 59, 63–73.

Leechor, C. (2017). Developing tourism in Botswana: progress and challenges. *Botswana Documents*. https://library.wur.nl/ojs/index.php/Botswana_documents/article/view/16029

LeFlore, E. G., Fuller, T. K., Tomeletso, M., & Stein, A. B. (2019). Livestock depredation by large carnivores in northern Botswana. *Global Ecology and Conservation*, 18, e00592.

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). African lions on the edge: reserve boundaries as "attractive sinks": In D. W. Macdonald & A. J. Loveridge (Eds.), *Biology and Conservation of Wild Felids* (p. 183). Oxford University Press.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W. (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., & Carr, G. M. (1989). Food security and the rewards of tolerance. In *Comparative socioecology: the behavioural ecology of humans and animals* (pp. 75–99). Blackwell Scientific Oxford.

Mangipane, L. S., Belant, J. L., Hiller, T. L., Colvin, M. E., Gustine, D. D., Mangipane, B. A., & Hilderbrand, G. v. (2018). Influences of landscape heterogeneity on home-range sizes of brown bears. *Mammalian Biology*, 88, 1–7.

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (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.

Midlane, N. (2013). *The conservation status and dynamics of a protected African lion* Panthera leo *population in Kafue National Park, Zambia.* PhD Thesis. University of Cape Town.

Midlane, N., Justin O'Riain, M., Balme, G. A., & Hunter, L. T. B. (2015). To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, 24, 1311–1327.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, 172, 101–108.

Milzow, C., Burg, V., & Kinzelbach, W. (2010). Estimating future ecoregion distributions within the Okavango Delta Wetlands based on hydrological simulations and future climate and development scenarios. *Journal of Hydrology*, 381, 89–100.

Mladenov, N., Gardner, J. R., Flores, N. E., Mbaiwa, J. E., Mmopelwa, G., & Strzepek, K. M. (2007). The value of wildlife-viewing tourism as an incentive for conservation of biodiversity in the Okavango Delta, Botswana. *Development Southern Africa*, *24*(3), 409–423.

Moore, A. E., Cotterill, F. P. D., Winterbach, C. W., Winterbach, H. E. K., Antunes, A., & O'Brien, S. J. (2016). Genetic Evidence for Contrasting Wetland and Savannah Habitat Specializations in Different Populations of Lions (*Panthera leo*). *Journal of Heredity*, 107, 101–103.

Mosser, A. & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour,* 78, 359-370.

Murray-Hudson, M., Wolski, P., Murray-Hudson, F., Brown, M. T., & Kashe, K. (2014). Disaggregating hydroperiod: components of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands*, 34, 927–942.

Murray-Hudson, M., Wolski, P., & Ringrose, S. (2006). Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. *Journal of Hydrology*, 331, 73–84.

Ogutu, J. O., & Dublin, H. T. (2002). Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology*, 40, 120–129.

Osano, P. H., Said, M. Y., de Leeuw, J., Ndiwa, N., Kaelo, D., Schomers, S., Birner, R., & Ogutu, J. O. (2013). Why keep lions instead of livestock? Assessing wildlife tourismbased payment for ecosystem services involving herders in the Maasai Mara, Kenya . *Natural Resources Forum*, 37, 242–256.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. *Animal Conservation*, 22, 35–48.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, W., Mduma, S., & Sinclair, A. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science,* 436, 927-928.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J., & Mulder, M. B. (1988). Reproductive success of lions. In *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed.) T. H. Clutton-Brock (pp. 363–383). University of Chicago Press.

Peacock, E., Derocher, A. E., Lunn, N. J., & Obbard, M. E. (2010). Polar bear ecology and management in Hudson Bay in the face of climate change. *A Little Less Arctic: Top Predators in the World's Largest Northern Inland Sea, Hudson Bay*, 93–116.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A., Meloro, C., Wich, S. A., McNutt, J. W. & Hayward, M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, 29, R681-R682.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., van As, J., & VanderPost, C. (2006). Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences*, 68, 310–337.

Rees, W. A. (1978). The Ecology of the Kafue Lechwe: Its Nutritional Status and Herbage Intake. *The Journal of Applied Ecology*, 15, 193.

Rich, L. N., Miller, D. A. W., Muñoz, D. J., Robinson, H. S., McNutt, J. W., & Kelly, M. J. (2019). Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data. *Biological Conservation, 233,* 12-20.

Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation*, 133, 397–408.

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

Rogan, M. S., Lindsey, P. A., Tambling, C. J., Golabek, K. A., Chase, M. J., Collins, K., & McNutt, J. W. (2017). Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, *210*, 233–242.

Schaller, G. (1972). *The Serengeti Lion: A study of predator-prey relations*. University of Chicago Press.

Smuts, G. L. (1978). Interrelations between predators, prey, and their environment. *BioScience*, 28, 316–320.

Snider, M. H., Athreya, V. R., Balme, G. A., Bidner, L. R., Farhadinia, M. S., Fattebert, J., Gompper, M. E., Gubbi, S., Hunter, L. T. B., Isbell, L. A., Macdonald, D. W., Odden, M., Owen, C. R., Slotow, R., Spalton, J. A., Stein, A. B., Steyn, V., Vanak, A. T., Weise, F. J., Wilmers, C. C., & Kays, R. (2021). Home range variation in leopards living across the human density gradient. *Journal of Mammalogy*, 102, 1138–1148.

Soisalo, M. K., & Cavalcanti, S. M. C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129, 487–496.

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.

Strampelli, P., Searle, C. E., Smit, J. B., Henschell, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., & Dickman, A. J. (2022). Camera trapping and spatially explicit capture-recapture for the monitoring and conservation management of lions: Insights from a globally important population in Tanzania. *Ecological Solutions and Evidence*, 3, e12129.

Tobler, M. W., & Powell, G. V. N. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*, 159, 109–118.

Tomas, W. M., de Oliveira Roque, F., Morato, R. G., Medici, P. E., Chiaravalloti, R. M., Tortato, F. R., Penha, J. M. F., Izzo, T. J., Garcia, L. C., Lourival, R. F. F., Girard, P., Albuquerque, N. R., Almeida-Gomes, M., Andrade, M. H. da S., Araujo, F. A. S., Araujo, A. C., Arruda, E. C. de, Assunção, V. A., Battirola, L. D., … Junk, W. J. (2019). Sustainability Agenda for the Pantanal Wetland: Perspectives on a Collaborative Interface for Science, Policy, and Decision-Making. *Tropical Conservation Science, 12,* 1940082919872634.

Tortato, F. R., Izzo, T. J., Hoogesteijn, R., & Peres, C. A. (2017). The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation*, 11, 106–114.

Tumenta, P. N., Van't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo De Haes, H. A., de Iongh, H. H., & Zachos, F. E. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, 78, 461–469.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: Waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337–351.

van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*, 206, 97–112.

van Rooyen, J. (2016). *Livestock production and animal health management systems in communal farming areas at the wildlife-livestock interface in southern Africa*. PhD Thesis. University of Pretoria.

Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., Chifunte, C., Midlane, N. & Simukonda, C. (2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications*, 31, e02298.

Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J., & Shanas, U. (2015). What is an apex predator? *Oikos*, 124, 1453–1461.

Weise, F. J., Fynn, R. W. S., Stein, A. B., Tomeletso, M., Somers, M. J., & Périquet, S. (2019a). Seasonal selection of key resources by cattle in a mixed savannah-wetland ecosystem increases the potential for conflict with lions. *Biological Conservation*, 237, 253–266.

Weise, F. J., Hauptmeier, H., Stratford, K. J., Hayward, M. W., Aal, K., Heuer, M., Tomeletso, M., Wulf, V., Somers, M. J., & Stein, A. B. (2019b). Lions at the gates: Trans-disciplinary design of an early warning system to improve human-lion coexistence. *Frontiers in Ecology and Evolution*, 7, 1–19.

Weise, F. J., Hayward, M. W., Casillas Aguirre, R., Tomeletso, M., Gadimang, P., Somers, M. J., & Stein, A. B. (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.

Whitesell, C. A. (2019). *Movements of lions and other carnivores in relation to domestic and wild prey in northwestern Botswana*. PhD Thesis. University of California Davis.

Winterbach, C. W., Winterbach, H., Rutina, L., & Kat, P. W. (1998). Results of the coordinated dry season lion survey for the Okavango Delta, 1998. *Tau Constultants, Unpublished report. Maun, Botswana.*

Winterbach, H. E. K., Winterbach, C. W., & Somers, M. J. (2014). Landscape suitability in Botswana for the conservation of its six large African carnivores. *PloS ONE*, 9, 1–12.

Winterbach, H. E. K., Winterbach, C. W., Somers, M. J., & Hayward, M. W. (2013). Key factors and related principles in conservation of large African carnivores. *Mammal Review,* 43*,* 89-100.

Wolf, C., & Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*, 3, 160252.

Wolski, P., & Murray-Hudson, M. (2006). Recent changes in flooding in the Xudum distributary of the Okavango Delta and Lake Ngami, Botswana. *South African Journal of Science*, 102, 173–176.

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280, 2126–2128.

Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: Key resources concept expanded. *Ecography*, 37, 969–982.

List of Tables

Chapter 2

Chapter 3

Chapter 4

List of Figures

Chapter 2

Chapter 3

Chapter 4