Landscape-scale conservation of lions in the Kavango-Zambezi Transfrontier Conservation Area

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Summary

The conservation of wide-ranging species in an increasingly human-dominated environment reaches beyond the borders of national parks, and requires an alternative to traditional fortress conservation. Persistence of wide-ranging species requires a landscape-scale management approach, which allows for the movement of animals across international boundaries and through networks of protected areas, ensuring genetic diversity and viable populations.

This dissertation highlights the importance of the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) in southern Africa as one of the last strongholds of the African lion (*Panthera leo*) in the 21st century. It is home to what is possibly the geographically largest intact population of lions left in the wild, stretching from Hwange National Park in Zimbabwe throughout north-eastern Botswana to the Okavango Delta. The connectivity of protected areas within the TFCA is one of the major requirements to ensure the viability and genetic health of its lion population.

I use cutting edge modelling to identify nine key dispersal areas, 27 linkage corridors and 27 potential human-lion conflict hotspots throughout the KAZA TFCA and its surrounding landscape. In particular, the results highlight the importance of conserving the lands surrounding and connecting Hwange National Park in Zimbabwe and Chobe National Park, the Nxai Pan/Makgadikgadi Pans complex and the Okavango Delta in Botswana as the key dispersal area for lions throughout the region in its entirety.

The results further demonstrate that by maintaining four strategically placed corridors between this key dispersal area and the Central Kalahari Game Reserve to the south, the Chizarira National Park to the east, the Greater Kafue Ecosystem to the north and the Khaudum National Park to the west, the five most important lion core areas in the region can be linked to maintain genetic connectivity.

While habitat loss and fragmentation are major drivers of lion declines, human-lion conflict is of similar importance and must be considered in connectivity planning.

Based on changes in expected dispersal rates I modelled and mapped the zones of highest conflict potential, with the Chobe Enclave in northern Botswana, the Tsholotsho area to the south-east of Hwange National Park and the communal farming area to the north-east of Hwange National Park having the highest relative conflict risk value throughout the greater KAZA landscape.

Using resource selection functions, I identified habitat suitability criteria for four demographic categories of lions in the most important dispersal area, connecting Chobe National Park, the Okavango Delta, and the Nxai Pan/Makgadikgadi Pans complex in Botswana, and the Hwange National Park in Zimbabwe. In this semi-arid landscape, surface water and precipitation which in turn regulate prey abundance proved to be some of the most important drivers of habitat use for lions.

Predicted habitat use was highest in close proximity to water irrespective of age and sex, while it varied for precipitation depending on the demographic category. While adult lions and subadult females preferred habitat with higher than average rainfall, the opposite was the case for subadult males. The four demographic categories of lions were generally positively associated with higher levels of all prey species with the exception of gemsbok which adult females, subadult males, and subadult females avoided. The widespread predicted distributions for all four demographic categories across multiple different land-use types highlight the need to include multi-use landscapes and support large-scale transboundary conservation initiatives.

To quantify the complex interactions underlying home range selection, I used two-tier hierarchical variance partitioning as well as multivariate generalized mixed models to determine how biophysical, ecological, and anthropogenic factors influence variation in home range size across sex and season. Male and female home range size were primarily driven by the availability of water both in the dry and wet season. Anthropogenic variables had little effect on home range size of either sex in any season, except for female’s response to cattle in the dry season. Home ranges of both sexes in both seasons were generally smaller in areas with higher soil nutrients and in areas with lower extent of woodlands and higher extent of grasslands. However, the effects of these factors seemed to vary seasonally for males, such that wet season home ranges were larger and more influenced by extent of woodlands, and less influenced by soil productivity.

While there is limited time to prioritize conservation efforts in the face of rapid human population growth, this dissertation aims to contribute to regional land-use planning and serves as a conservation tool for lawmakers to plan appropriate management actions, while being applicable in the wider field of conservation management.

Zusammenfassung

Der Schutz weit umherziehender Arten in einer vom Menschen dominierten Umwelt erfordert Alternativen zu traditionellen Naturschutzkonzepten, welche über die Grenzen von Nationalparks hinausreichen. Um den Erhalt lebensfähiger Populationen und deren genetische Vielfalt zu gewährleisten, ist ein Managementansatz auf regionaler Ebene erforderlich, welcher die Wanderbewegung von Tieren durch den Einsatz geschützter Netzwerke über internationale Grenzen hinweg ermöglicht.

Als Heimat der vermutlich größten intakten Löwenpopulation, welche sich vom Hwange-Nationalpark in Simbabwe über den Nordosten Botswanas bis zum Okavango-Delta erstreckt, ist das grenzüberschreitende Naturschutzgebiet Kavango-Zambezi (KAZA TFCA) im südlichen Afrika eine der letzten Hochburgen des afrikanischen Löwen (*Panthera leo*) im 21. Jahrhundert. Die geografische und funktionelle Verbindung der Schutzgebiete innerhalb des Schutzgebietes, ist eine der groβen Herausforderungen um die Lebensfähigkeit und genetische Gesundheit der Löwenpopulation sicherzustellen.

In dieser Dissertation nutze ich modernste ökologische Habitatkonnektivitätsanalysen um die neun wichtigsten Ausbreitungsgebiete, 27 Verbindungskorridore und 27 Gebiete mit dem höchsten Konfliktpotential zwischen Menschen und Löwen in der KAZA TFCA und der umliegenden Landschaft zu identifizieren.

Die Ergebnisse unterstreichen insbesondere, dass die Erhaltung der Gebiete rund um den Hwange-Nationalpark in Simbabwe und den Chobe-Nationalpark, den Nxai Pan/Makgadikgadi Pans-Komplex und das Okavango-Delta in Botswana in ihrer Gesamtheit, als zentrales Verbreitungsgebiet für Löwen in der Region von enormer Bedeutung ist. Darüber hinaus zeigen sie, dass durch die Erhaltung von vier strategisch platzierten Korridoren zwischen diesem zentralen Verbreitungsgebiet und dem Central Kalahari Game Reserve im Süden, dem Chizarira Nationalpark im Osten, dem Greater Kafue Ökosystem im Norden und dem Khaudum

Nationalpark im Westen die fünf wichtigsten Löwenverbreitungsgebiete der Region genetisch verbunden sind.

Während der Verlust und Zerfall von Lebensräumen die Hauptursachen für den Rückgang der Löwenpopulationen sind, ist der Konflikt zwischen Mensch und Löwe von ähnlicher Bedeutung und muss bei der Landschaftsplanung ebenfalls berücksichtigt werden. Basierend auf den lokalen Differenzen der modellierten Ausbreitungsraten erweisen sich die Chobe Enclave im Norden Botswanas, die Tsholotsho Gemeinde südöstlich des Hwange Nationalparks und die Landwitschaftskommune nordöstlich von Hwange Nationalpark als die drei Gebiete mit dem höchsten Konfliktrisiko in der KAZA-Landschaft.

Mithilfe von Habitatsmodellen identifiziere ich die Habitatpräferenzen von männlichen und weiblichen adulten und subadulten Löwen im zentralen Verbreitungsgebiet welches den Chobe-Nationalpark, das Okavango-Delta und den Komplex Nxai Pan / Makgadikgadi Pans in Botswana sowie den Hwange-Nationalpark in Simbabwe beinhaltet. In diesem semi-ariden Habitat erwiesen sich Oberflächenwasser und Niederschlag (welche die Beutefülle regulieren) als wichtigste Einflüsse auf die Lebensraumnutzung des Löwen. Die prognostizierte Lebensraumnutzung war unabhängig von Alter und Geschlecht in unmittelbarer Nähe zum Wasser am höchsten, während der Einfluss von Niederschlag je nach demografischer Kategorie unterschiedlich ausfiel.

Adulte Löwen und subadulte Weibchen bevorzugten generell Lebensräume mit überdurchschnittlich hohen Niederschlägen, während subadulte Männchen diese vermieden.

Mit Ausnahme der Oryxantilope, welche von adulten Weibchen und subadulten Löwen gemieden wurde, waren alle vier demografischen Kategorien im Allgemeinen positiv mit erhöhten Tierdichten aller getesteter Beutetierarten assoziiert.

Die weiträumige Verbreitung aller vier demografischer Kategorien über verschiedene Landnutzungstypen hinweg unterstreicht die Notwendigkeit grenzüberschreitende Naturschutzinitiativen zu unterstützen welche Mehrzwecklandschaften beinhalten.

Um die komplexen Wechselwirkungen zwischen biophysikalischen, ökologischen und anthropogenen Faktoren, welche Löwenstreifgebiete je nach Jahreszeit unterschiedlich beeinflussen darzustellen, nutzte ich hierarchische Varianzpartitionierung sowie verallgemeinerte lineare gemischte Modelle.

Sowohl in der Trocken- als auch in der Regenzeit wurde die Größe der männlichen und weiblichen Streifgebiete hauptsächlich durch die Verfügbarkeit von Wasser bestimmt. Mit Ausnahme von Rinderdichte welche sich negativ auf die weibliche Streifgebietsgröβe in der Trockenzeit auswirkte, spielten anthropogene Variablen nur eine sehr geringe Rolle. Die durchschnittliche Streifgebietsgröβe beider Geschlechter war in Gebieten mit höheren Bodennährstoffen und höherem Graslandanteil generell kleiner und in Gebieten mit höherem Waldanteil gröβer. Der Einfluss dieser Faktoren schien jedoch bei männlichen Löwen saisonal zu variieren, so dass die Streifgebietsgröβe in der Regenzeit verstärkt vom Waldanteil eines Gebietes und weniger von der Bodenproduktivität beeinflusst waren.

Während angesichts des raschen Bevölkerungswachstums nur begrenzt Zeit zur Prioriätensetzung von Naturschutzinitiativen zur Verfügung steht, ist das Ziel dieser Dissertation als Leitfaden für Gesetzgeber weltweit einen Beitrag zur regionalen Naturschutzplanung zu leisten.

Introduction

While the Earth's human population continues to increase at a worrying pace, more than half of the anticipated growth between the present day and 2050 is expected to occur on the African continent (United Nations, 2017). Population growth rates are often significantly higher near protected areas due to an influx of international investment in conservation programmes (Wittemyer et al., 2008), and with a rapidly increasing population comes an increased demand for natural resources. Encroachment of wild lands through expansion of agriculture and human settlements leads to habitat destruction and deforestation - a particularly damaging process in sub-Saharan Africa, home to the greatest diversity of extant megafauna (Ripple et al., 2016).

Habitat fragmentation, the process during which a large expanse on habitat is split into smaller, isolated patches and reduced resource availability are especially damaging for large mammals as they tend to occur in lower densities and are often characterized by slow reproductive rates (Cardillo et al., 2008). At the top of the food chain, large predators have an intrinsic value to natural systems and play an important role in regulating the environment by limiting herbivores through predation (del Rio et al., 2001) and mesocarnivores through intraguild competition (Ritchie and Johnson, 2009). Due to their large area requirements and overlapping ecological needs with other wide-ranging species, conservation efforts focused on the protection of lion habitat may indirectly benefit many other smaller ranging species. This umbrella species concept is a useful tool to manage landscape scale conservation and enable comprehensive habitat protection, benefitting both ecosystems and human livelihoods (Dalerum et al., 2008).

As Africa's top predator, lions are economically valuable and attract significant revenue to host countries through tourism, which is frequently the largest and most viable local revenue generator in rural areas (Dickman et al., 2011). Despite their iconic status, they have lost over 80 % of their historic distribution range over the last century (Ray et al., 2005; Trinkel and

Angelici, 2016). The latest IUCN assessment suggests a continent wide population of 23,000 – 39,000 animals, having undergone a reduction of 43% over the last three lion generations (21 years) (Bauer et al., 2015b). Lions are therefore considered vulnerable across the African continent and listed as Endangered or Critically Endangered in parts of their historic range (Henschel et al., 2014).

In many African countries, livestock farming is one of the main income sources in rural communities (Powell and Williams, 1995), with cattle and other livestock often freely roaming along the edges of protected areas. As a wide-ranging species (Winterbach et al., 2014), lions often leave the safety of protected areas to prey on livestock (Hemson, 2004) and are therefore particularly vulnerable to anthropogenic mortality due to retaliation (Ripple et al., 2014).

In addition to human-wildlife conflict, depletion of prey and habitat loss and fragmentation are recognised as further primary drivers of their population decline (Nowell and Jackson, 1996; Bauer et al., 2015b; Lindsey et al., 2017; Gebresenbet et al., 2018).

In Africa, viable populations of lions (*Panthera leo*) are dependent upon a minimum of 50 – 100 prides with no limits to dispersal to maintain long-term genetic diversity and prevent inbreeding (Björklund, 2003). However, many protected areas are too small to support such a large number of prides, and consequently their populations face an uncertain future (Woodroffe and Ginsberg, 1998; Henschel et al., 2014). Today only five strongholds are estimated to hold more than 2,000 lions, of which three are located in East Africa (Ruaha-Rungwa Ecosystem, Serengeti-Mara Ecosystem and Selous Game Reserve), and two in southern Africa (Great Limpopo Transfrontier Park and Kavango Zambezi Transfrontier Conservation Area).

The Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) encompasses almost 520,000 km², spanning across five southern-African countries including Angola, Botswana, Namibia, Zambia, and Zimbabwe. It is one of the most spatially extensive, intact ecosystems in Africa, and is shaped by a mosaic of different land uses, ranging from protected and wildlife management areas to farmland and human settlements. At heart of KAZA's core lie the Chobe National Park, the Okavango Delta, and the Nxai Pan/Makgadikgadi Pans complex in Botswana, and the Hwange National Park in Zimbabwe, which are connected through a network of Wildlife Management Areas (WMA's) (Figure 0. 1).

However, even within this expansive ecosystem, protected areas are under threat of becoming isolated, jeopardizing genetic flow between animal populations and increasing the risk of inbreeding (Trinkel et al., 2008). The degree to which lion populations are functionally isolated and the factors that facilitate gene flow between them through dispersal are largely unknown.

Identifying the environmental and anthropological drivers that influence the distribution and dispersal of lions across this landscape is important for their management and the stability of the wildlife communities that are influenced by them.

The aim of this dissertation is to contribute to a growing body of knowledge on the landscape-scale conservation of wide-ranging species in the Anthropocene.

Using a comprehensive telemetry data set of the African lion I modelled population connectivity across the KAZA landscape, investigated how environmental and anthropogenic landscape variables influence space use in a multiuse landscape, and quantified the influence of intrinsic and extrinsic factors on the variation in home range size across sex and season. In particular, I looked at the three following topics:

1. Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa

With the human population growing at an alarming rate in sub-Saharan Africa, habitat loss and fragmentation through the expansion of agriculture and human settlement are amongst the main drivers of population decline in wild animal species (Cushman et al., 2016). The increasing demands for land puts decision makers in a challenging position of balancing the need for economic development in rural areas with the conservation of natural ecosystems. Without an evidence-based, regional land-use framework to guide policy decisions, human development will increasingly interrupt animal movement routes, preventing genetic flow between populations and resulting in human-wildlife conflict and population decline (Ripple et al., 2014).

In lions, natal dispersal - the process of a sub-adult male leaving its birthplace to establish a breeding site (Packer and Pusey, 1987; Funston, 2011) - is a key mechanism for genetic exchange between populations. Dispersal movement is often extensive and leads through human-dominated landscapes, where dispersing lions potentially come into contact with people and their livestock.

Connectivity models are modern tools to analyse habitat fragmentation scenarios in a rapidly changing landscape and develop appropriate management responses. Using cutting-edge connectivity models, I modelled patterns of population connectivity for lions across the KAZA landscape. In particular, I used a resistance surface for dispersing male lions (Elliot et al., 2014b) to calculate resistant kernel connectivity and factorial least cost paths in order to:

1. Assess the importance and vulnerability of key dispersal areas
2. Highlight and rank major linkages between key dispersal areas
3. Identify areas of high human-lion conflict risk across the KAZA landscape

2. Sex and age predict habitat selection in the world's most geographically extensive lion population

Whilst the upscaling of conservation efforts and the management of ecosystems on a landscape scale is of utmost importance, there is still a need to answer fundamental ecological questions including the quantification of the processes that govern species distribution (Sutherland et al., 2004). In the first chapter I identified key dispersal areas and linkages for lions throughout

KAZA TFCA, while the second chapter focuses on the ecological and anthropogenic drivers that govern the distribution of lions in its central core area (Figure 0. 1).

Despite their geographical importance (Cushman et al., 2018), the WMA's linking up Hwange National Park in Zimbabwe and Chobe National Park, Makgadikgadi/ Nxai Pans National Parks, and the Okavango Delta in Botswana remain relatively understudied. In contrast to the considerable research on lions that has been conducted in the surrounding national parks and game reserves (Cooper, 1991; Cozzi et al., 2013; Kesch et al., 2014; Kesch et al., 2015; Loveridge et al., 2016), information on lion distribution and resource needs in the habitat linking these protected areas is mostly anecdotal.

Using a mixed-effects resource selection framework on a large telemetry dataset I analysed how environmental and anthropogenic landscape variables, as well as prey abundance, influence space-use of four demographic categories of lions across this key dispersal area. Resource selection functions are a popular tool to identify critical resources for animal populations by comparing habitat characteristics at locations animals use to those that are theoretically available, or unused, by the animal (Boyce and McDonald, 1999; Manly et al., 2007; Millspaugh et al., 2014). They are commonly employed to identify habitat suitability criteria for large carnivores and to inform relevant conservation actions (Kunkel et al., 2013). Using multivariate generalized mixed models, I identified key ecological and anthropogenic drivers as well as important prey species for the residential stage of all adult males, adult females, subadult males and subadult females in order to:

1. Highlight the influence of water availability, habitat productivity, and prey abundance on lion occurrence

2. Investigate the negative influence of anthropogenic factors on habitat selection

3. Evaluate how the direction and magnitude of these relationships differ between the four demographic categories

I evaluated the different nature of these relationships to predict the relative probability of space use for each demographic category across the study area. I furthermore make a case for the protection of this often overlooked but geographically critical habitat and highlight its importance for ecological functionality of the KAZA TFCA.

3. Gender and season specific drivers of home range size of African lions

Home range is a common pattern of space use in animal ecology describing the spatial extent containing all the resources an animal requires to survive and reproduce (Burt, 1943). Identifying drivers of variation in home range sizes can provide critical insights into demography, population regulation (Wang and Grimm, 2007), and spatial ecology (Rhodes et al., 2005). To appropriately scale the size of conservation units to a species needs in ecosystem management, a thorough understanding of the factors that influence variation in home range size is required (Woodroffe and Ginsberg, 2000). Despite considerable work on the drivers of home range size (Mcloughlin et al., 2000; Kelt and Van Vuren, 2001; Grigione et al., 2002; Loveridge et al., 2009b; Šálek et al., 2015) questions remain regarding inter-seasonal and inter-sexual differences in home range variation.

Drivers of home range size are often studied in isolation, however to represent a comprehensive model of the complex interactions underlying the variation, it is preferable to quantify the relative contributions of each driver, and evaluate how they differ between sex and season. Furthermore, studies often solely rely on intrinsic factors when explaining home range size, despite the strong indication that anthropogenic factors can heavily influence animal demography and spatial ecology (Corey and Doody, 2010).

Using hierarchical variance partitioning (Cushman and McGarigal, 2002) and multivariate regression models I measured the independent and joint effects of a suite of environmental and anthropogenic covariates on variation in home range size and evaluated the differences between sex and season to evaluate whether:

1. In a semi-arid environment, variation in male and female lion home range size is closely associated with the availability of waterholes (and therefore prey), with the effect stronger in the dry season compared to the wet season.

1. Access to resources (in the form of water and primary production) is the key driver for variation in female home range size, but is less important for male home range size due to different reproductive strategies.

2. Anthropogenic covariates are a limiting factor to home range size for both sexes but more so for females, as they have been shown to be much more averse to human disturbance (Elliot et al., 2014b).

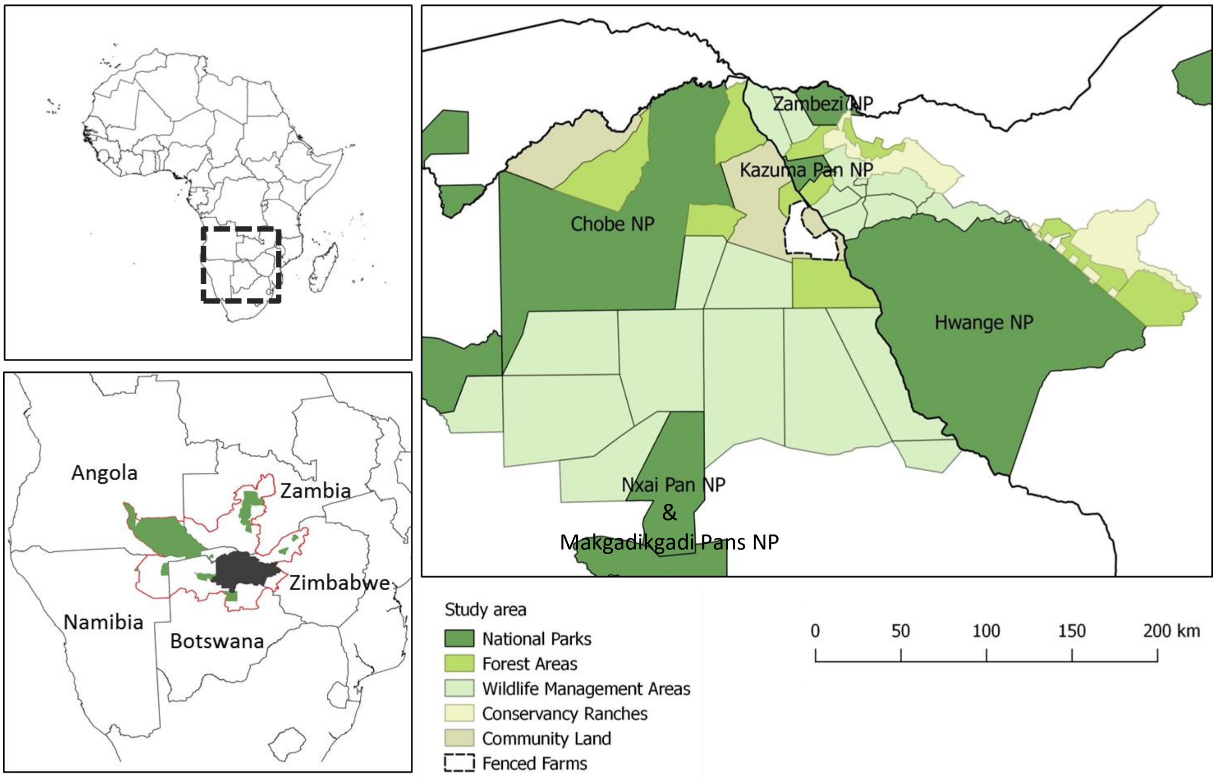

Figure 0. 1. Study area with land-uses inset, its extent (in dark grey) within the KAZA TFCA (red outline) (bottom left) and within Africa (top left).

Chapter 1: Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa

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ABSTRACT: Conservation of large carnivores, such as the African lion, requires preservation of extensive core habitat areas, linkages between them, and mitigation of human-wildlife conflict. However, there are few rigorous examples of efforts that prioritized conservation actions for all three of these critical components. We used an empirically optimized resistance surface to calculate resistant kernel and factorial least cost path predictions of population connectivity and conflict risk for lions across the Kavango-Zambezi Transfrontier Conservation Area (KAZA) and surrounding landscape. We mapped and ranked the relative importance of (1) lion dispersal areas outside National Parks, (2) corridors between the key areas, and (3) areas of highest human-lion conflict risk. Spatial prioritization of conservation actions is critical given extensive land use redesignations that are reducing the extent and increasing the fragmentation of lion populations. While our example focuses on lions in southern Africa, it provides a general approach for rigorous, empirically based comprehensive conservation planning based on spatial prioritization.

Key Words: Landscape connectivity, dispersal, linkages, lion *Panthera leo*, human-lion conflict hotspots

Introduction

Africa’s human population is expected to increase threefold by the end of this century (Gerland et al., 2014), with highest population growth near protected areas (Wittemyer et al., 2008). Rising human and livestock populations increase demand for resources, driving conversion of land currently protected for wildlife to uses, such as agriculture or mining, that are perceived to be more economically profitable or politically expedient (Macdonald, 2017; Mbaiwa, 2018). Accelerating declines of carnivores as a result of human-carnivore conflict and habitat loss are likely (Woodroffe, 2000).

In the case of the African Lion (Panthera leo), human-wildlife conflict and habitat loss are the primary drivers of recent declines, with lion populations within protected areas becoming increasingly isolated (Bauer et al., 2015b). Bjorklund (Björklund, 2003) found that a minimum of 50–100 prides, linked by dispersal, is required to maintain long-term genetic diversity. Very few remaining populations contain this number of prides (Bauer et al., 2015b) and some populations already have reduced genetic diversity, which has been shown to decrease reproductive performance (Packer et al., 1991) and increase susceptibility to disease (Trinkel et al., 2017). Many existing protected areas are too small to support large populations and are therefore unlikely to be viable in the long term. Dispersal between remnant populations is therefore critical in maintaining long-term genetic health and providing demographic rescue of regional lion populations (Lande, 1993) and inbreeding depression (Packer et al., 1991; Trinkel et al., 2017). In response to growing conservation concern, similar to those introduced above for lions, the creation or protection of dispersal corridors has emerged as a popular strategy to improve population connectivity and enhance viability (Sawyer et al., 2011; Zeller et al., 2012; Cushman et al., 2013c).

The Kavango-Zambezi Transfrontier Conservation Area, KAZA (~520,000 km2), in southern Africa is of immense conservation importance for lions as it contains 13 ‘Lion Conservation Units’ (IUCN, 2006), including the Okavango-Hwange population, one of

Africa’s 10 remaining lion ‘strongholds’ (Riggio et al., 2013). In this paper, we present a comprehensive approach to prioritizing lion conservation actions based on spatial optimization with empirical connectivity models. We assess the importance and vulnerability of the key dispersal areas (defined as areas outside national parks and game reserves with high dispersal value for lions and therefore the overall integrity of lion range) and movement corridors between them, and identify areas of high human-lion conflict risk across the KAZA landscape.

Materials and Methods

The project involved the use of data on lion movements obtained from GPS collars. All lion handling, collaring and research was approved under stringent protocols and approvals granted by the University of Oxford, and all lion handling was done by a professional and certified wildlife veterinarian.

Resistance surface

We used a resistance surface that was empirically optimized for the study extent using Global Positioning System data collected from male natal dispersers (Figure 1. 1; for a full description of the study extent and resistance surface modelling, see (Elliot et al., 2014b). Briefly, Elliot et al. (Elliot et al., 2014b) used a multi-scale, path-selection function to predict landscape resistance based on movement data for adult female, adult male and dispersing juvenile male lions. Given that juvenile dispersal is disproportionately important in population connectivity we use the resistance surface produced by (Elliot et al., 2014b) for dispersing juvenile males in this analysis. This surface was produced with a 500m pixel size, and predicted that juvenile males selected movement paths preferentially in protected areas and avoided communal lands, proximity to towns, areas with high human population density, and large roads.

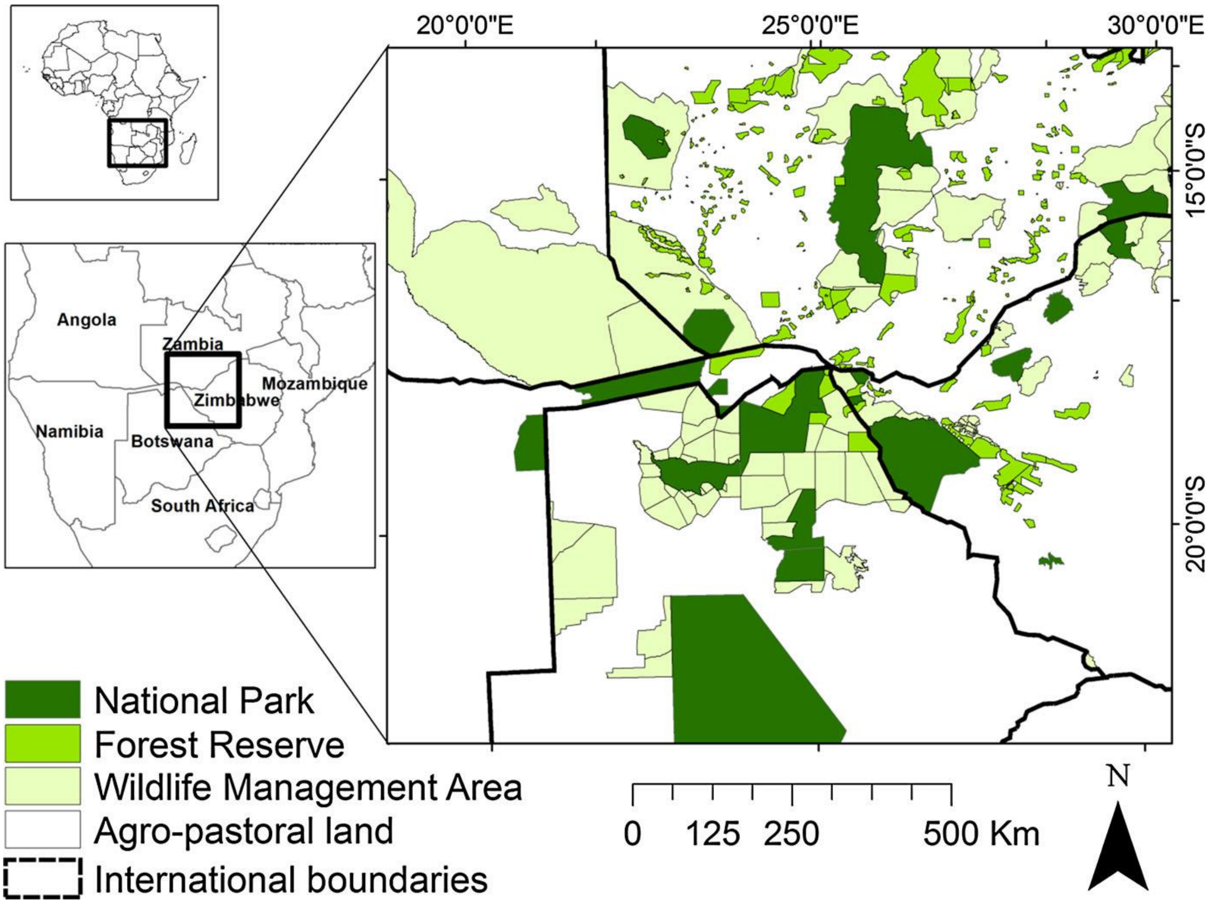

Figure 1. 1. Study area orientation map. Top left shows study area extent within the African continent; bottom left shows study area extent within southern Africa, with inset of land-uses in the study area

Source points for connectivity modelling

The connectivity modelling approaches used in this study (resistant kernel and factorial least cost path) are based on predicting movement from a set of source points that reflect the distribution and density of the underlying population. Source points were established by intersecting the protected area extent with a map of estimated site carrying capacity for lions based on climatic correlates of prey biomass (Loveridge et al., 2009a). Specifically, we down sampled the predicted density based on carrying capacity to reflect the low densities of lions outside of protected areas and also adjusted in areas where we had first-hand knowledge that the lion population differed from the prediction (Loveridge et al., 2009a) (e.g., Angola). We converted these densities to source points for connectivity modelling following a three-step process. First, we rescaled the density layer such that it reflected the probability of a lion occurring in each 500m pixel. Second, we took the product of the rescaled density layer and a raster layer of uniform random values between 0 and 1. Third, we selected all values of the product that were positive as source points, producing a selection of source points that matches the density predicted by the density surface.

Resistant kernel and factorial least cost path modelling

The resistance map provides resistance values for all locations in the study extent, in the form of the cost of crossing each pixel relative to the least-cost condition (Elliot et al., 2014b). We used UNICOR (Landguth et al., 2012) to calculate cumulative resistant kernel and factorial least cost path maps. We specified a dispersal threshold of 1,000,000 cost units for the resistant kernel analysis (Cushman et al., 2013a). We calculated the factorial least cost path network without a dispersal threshold [as in (Cushman et al., 2013a; Moqanaki and Cushman, 2017)] to provide a broad scale assessment of the regional pattern of potential linkage.

The factorial least cost path analysis calculates the least cost paths among all combinations of source points and sums them to create a path density map reflecting the relative strength of linkage across the network. The resistant kernel model calculates the expected movement of dispersing lions in each pixel, given the dispersal ability of the species and the resistance of the landscape (Compton et al., 2007; Cushman et al., 2010). The cumulative resistant kernel density can be interpreted as the probability of a dispersing lion traversing that pixel, given the location of the source points and the resistance of the landscape.

Identifying key lion dispersal areas and linkage corridors

We defined key dispersal areas as contiguous patches of cumulative resistant kernel values greater than the 25th percentile of the cumulative kernel surface. These reflect areas of moderate to high predicted movement rates. Our goal was to evaluate the importance of key lion areas ('dispersal areas') that were outside National Parks and Game Reserves, so we selected the cumulative kernel surface values outside of these strictly protected areas for analysis of the number and relative importance of these dispersal areas. Likewise, we selected linkage corridors that were greater than the 25th percentile of the distribution of values in the factorial least cost path surface, and outside the network of National Parks/Game Reserves and dispersal areas, as identified above.

Mapping relative conflict risk

We reasoned that areas with rapid change in cumulative kernel value (i.e. rapid changes from high to low expected dispersal rates) are potential hotspots where high lion movement intersects high conflict risk. We predicted conflict risk zones by calculating the standard deviation of the cumulative kernel surface within a 10km focal radius for all areas outside of National Parks/Game Reserves, and selected values above the 25th percentile for further analysis. Essentially, this index calculates the spatial variation in local cumulative kernel value, identifying areas with high change that we would expect to represent areas with high relative conflict risk.

Evaluating the relative importance of predicted key lion dispersal areas, linkage corridors and conflict hotspots

We used several criteria to evaluate the importance of predicted dispersal areas, linkage corridors, and conflict hotspots. For dispersal areas, we identified three main characteristics that contribute to their importance to regional lion populations: (1) The size of the area, since lion populations require large areas; (2) The summed kernel value, reflecting the total predicted movement of dispersing lions in that region of the landscape; (3) The degree to which a key dispersal area was connected to other areas, because dispersal areas that are nodes connecting the regional populations are likely more important than peripheral populations (Figure 1. 2). We therefore produced a measure of dispersal area importance based on number of National Parks/Game Reserves it connected. We produced a composite score by averaging the ranks produced by these three measures.

We used two measures to evaluate the importance of predicted linkage corridors (Figure 1. 2). (1) We extracted the maximum value of the factorial least cost path surface for each linkage corridor segment. This reflects corridor strength [*sensu* (Cushman et al., 2013b)] in terms of the number of pairwise linkages between source points predicted to traverse that corridor segment. (2) We weighted linkage corridor strength as a function of corridor redundancy. Specifically, a corridor between two dispersal areas that have no other linkage between them is more important than a corridor linking another two dispersal areas that are also linked by other corridors. We calculated corridor redundancy for each corridor by calculating the proportion of total connectivity (as measured by the sum of maximum corridor strength measures across all linkages between the two dispersal areas joined by the focal corridor) that is provided by the focal corridor. We produced a composite linkage that is the product of these two measures of corridor importance. Linkage corridors that are individually strong and have low redundancy are weighted highest, while those that have low strength and multiple alternative corridor routes are weighted lowest in importance.

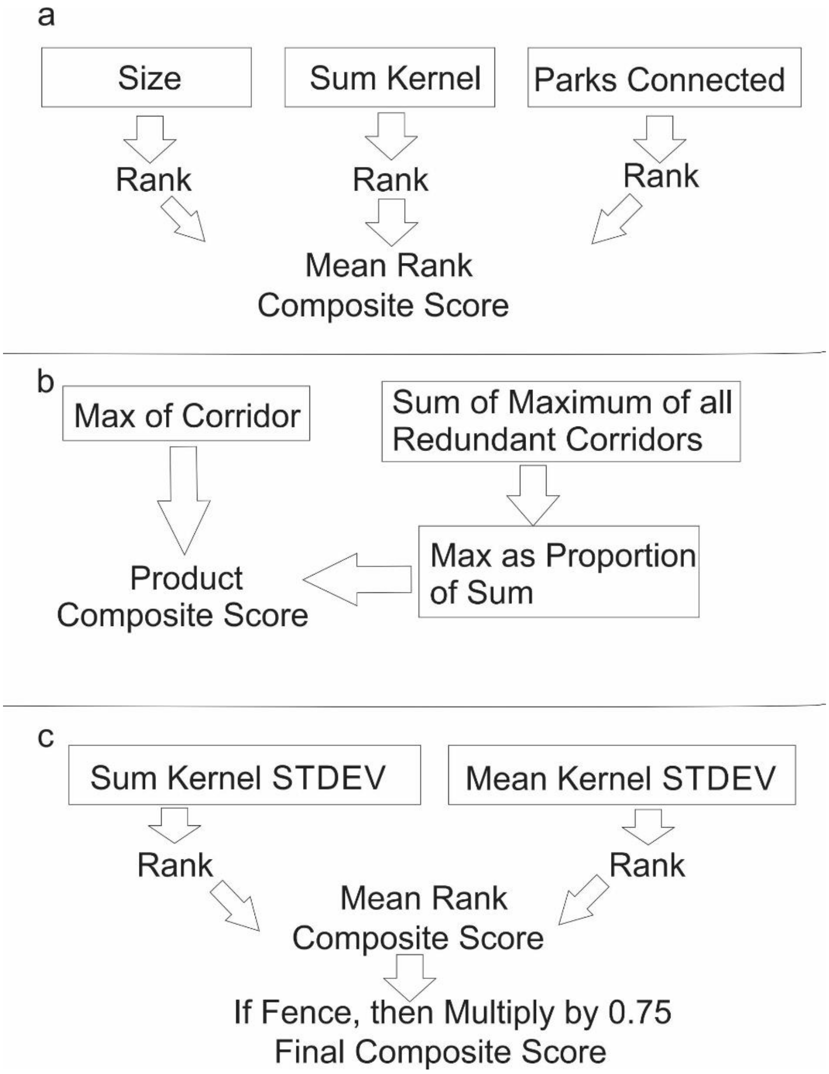

Figure 1. 2. Schematic of ranking. Steps to produce composite ranks for (a) core areas, (b) corridors, and (c) conflict hotspots

Finally, we produced two measures of the importance of predicted conflict hotspots (Figure 1. 2): (1) We measured conflict hotspot strength based on the sum of the kernel standard deviation surface within each identified patch of predicted high conflict risk. This measure weights areas based on total conflict risk and is highly dependent on the area of the predicted conflict hotspot; (2) We calculated the mean value of the kernel standard deviation surface within each predicted conflict hotspot patch. This measure identifies areas of highest potential conflict risk, regardless of size. For management purposes, both of these measures are informative, and we combined them with equal weight; (3) We multiplied the conflict hotspot combined value by 0.75 if it was traversed by a fence since conflict hotspot patches that coincide with the location of a wildlife fence likely have reduced conflict risk since the fence partly separates people and cattle from lions, and also because the fence itself, as a resistant feature in the resistance model, contributes to the high values of the kernel standard deviation surface.

Results

Location and importance of key dispersal areas

We identified nine key dispersal areas, which differed dramatically in predicted strength (Figure 1. 3 and Figure 1. 4). Based on the scree-plot of relative importance ranking (Figure 1. 3) we selected four key dispersal areas to emphasize. Dispersal area 1, ranked as by far the most important, surrounds and connects Chobe, Nxai Pan, Moremi, Hwange, and Makgadikgadi Pans protected areas. The second most important dispersal area connected the protected areas of Chete, Chizarira, Chirisa, Charara, Mana Pools, Chewore, Doma in Zimbabwe and Lower Zambezi in Zambia. This dispersal area had a composite importance score of 50.6% of the highest ranked dispersal area. The third ranked dispersal area surrounded Kafue National Park in Zambia. The composite importance measure for this predicted dispersal area was 23.7% of the highest ranked dispersal area. The fourth ranked dispersal area surrounded the Central Kalahari Game Reserve, particularly concentrated on the western boundary, with a composite score of 21.6% of the highest ranked dispersal area.

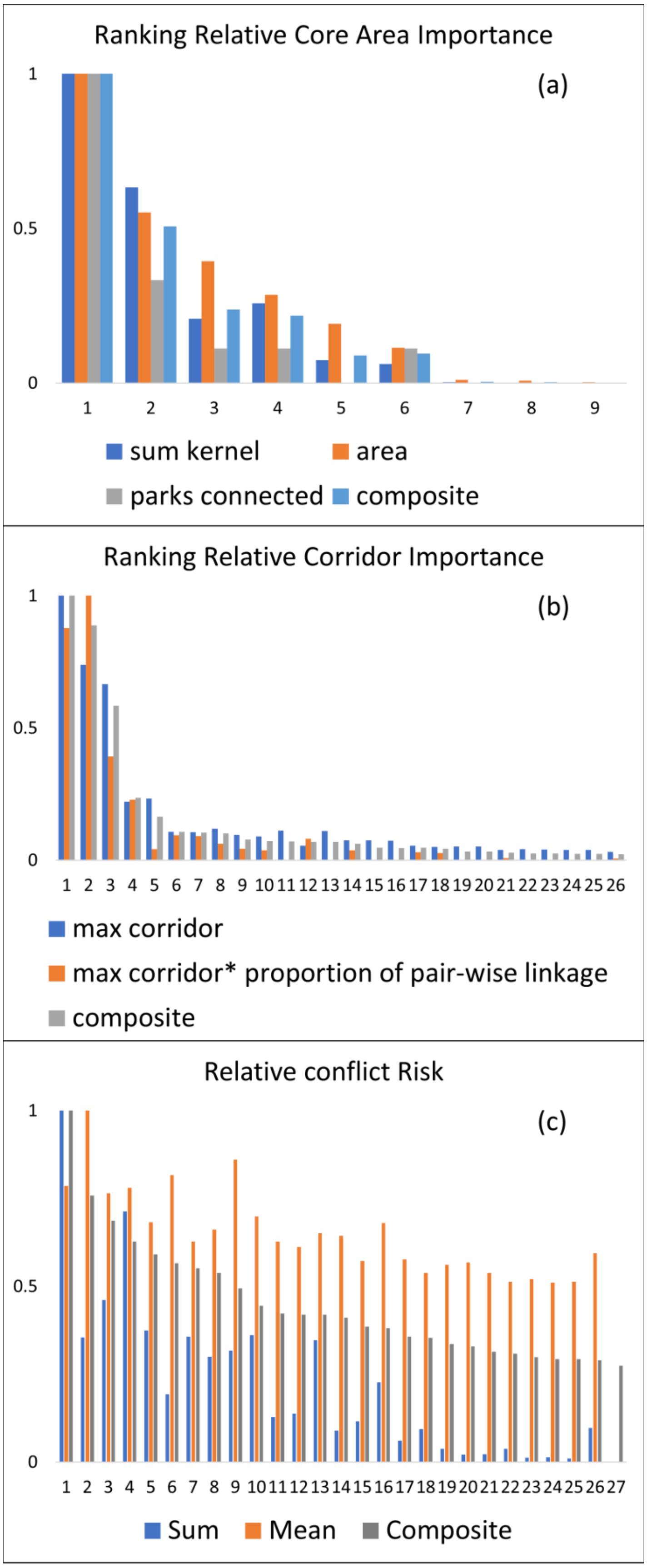

Figure 1. 3. Relative importance rankings. (a) key lion dispersal areas, (b) lion linkage corridors, (c) human-lion conflict risk in the Kavango-Zambezi Transfrontier Conservation Area and surrounding landscape. Numbers refer to labels in Figures 1. 4, 1. 5 and 1. 6

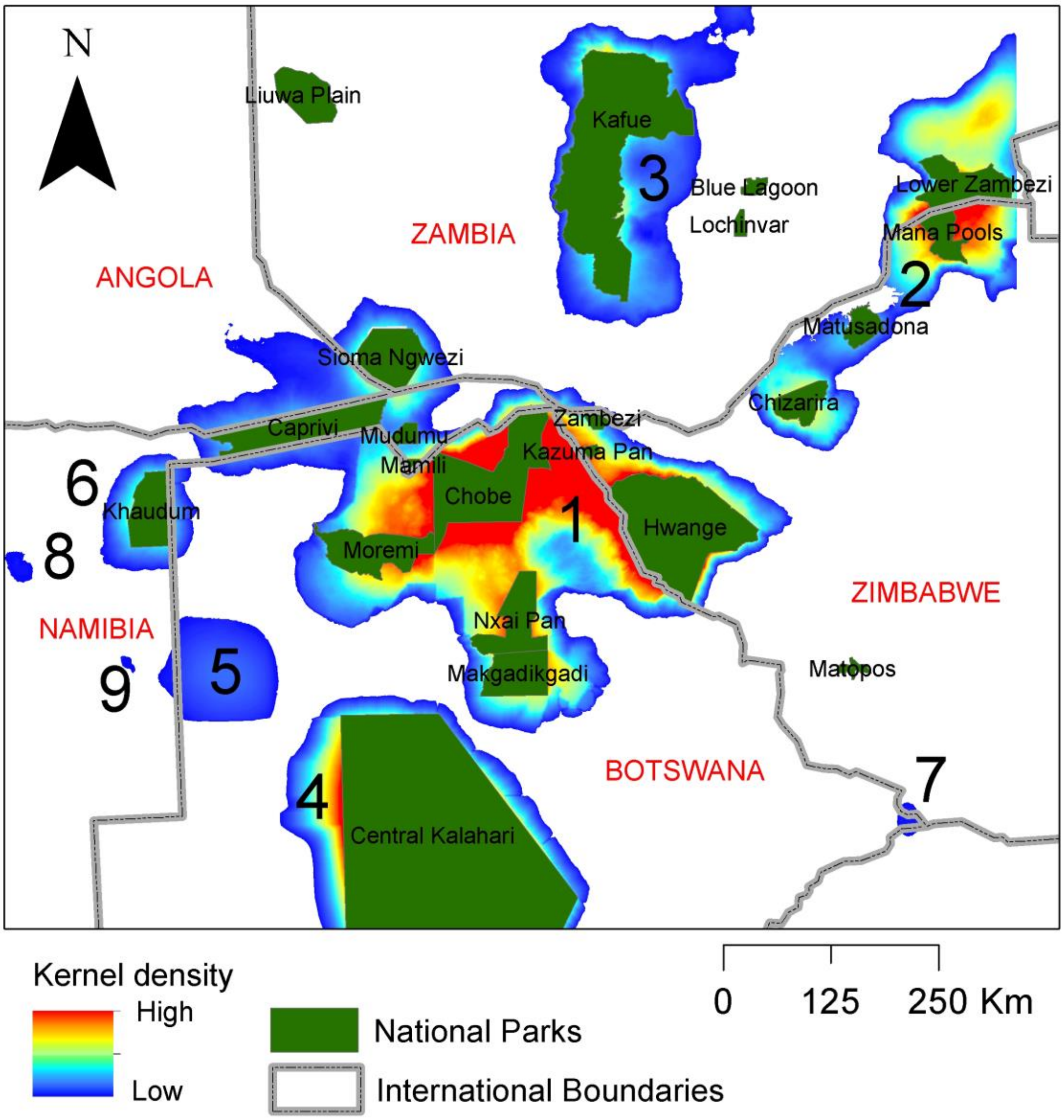

Figure 1. 4. Dispersal areas. Ranked values of composite lion dispersal area importance within the Kavango-Zambezi Transfrontier Conservation Area and surrounding landscape

Location and importance of predicted linkage corridors

We predicted 27 linkage corridors between the nine key dispersal areas (Figure 1. 5), which differed greatly in strength and relative importance. Based on the scree plot of composite ranking (Figure 1. 3) we selected three linkage corridors to emphasize. The highest ranked corridor was located between the southwestern corner of the central (highest ranking) dispersal area and the dispersal area surrounding the Central Kalahari Game Reserve, proximally linking Makgadikgadi Pans National Park and Central Kalahari Game Reserve. The second highest ranked corridor was located between the northeastern corner of the central dispersal area and the southwestern corner of the second highest ranked dispersal area, proximally linking Hwange and Chizarira National Parks. This corridor had a relative composite value of 88.8% of the highest ranked corridor. The third highest ranked corridor was near and parallel to the first, between the Makgadikgadi Pans and Central Kalahari protected areas, and had a composite value of 58.4% of the highest ranked corridor.

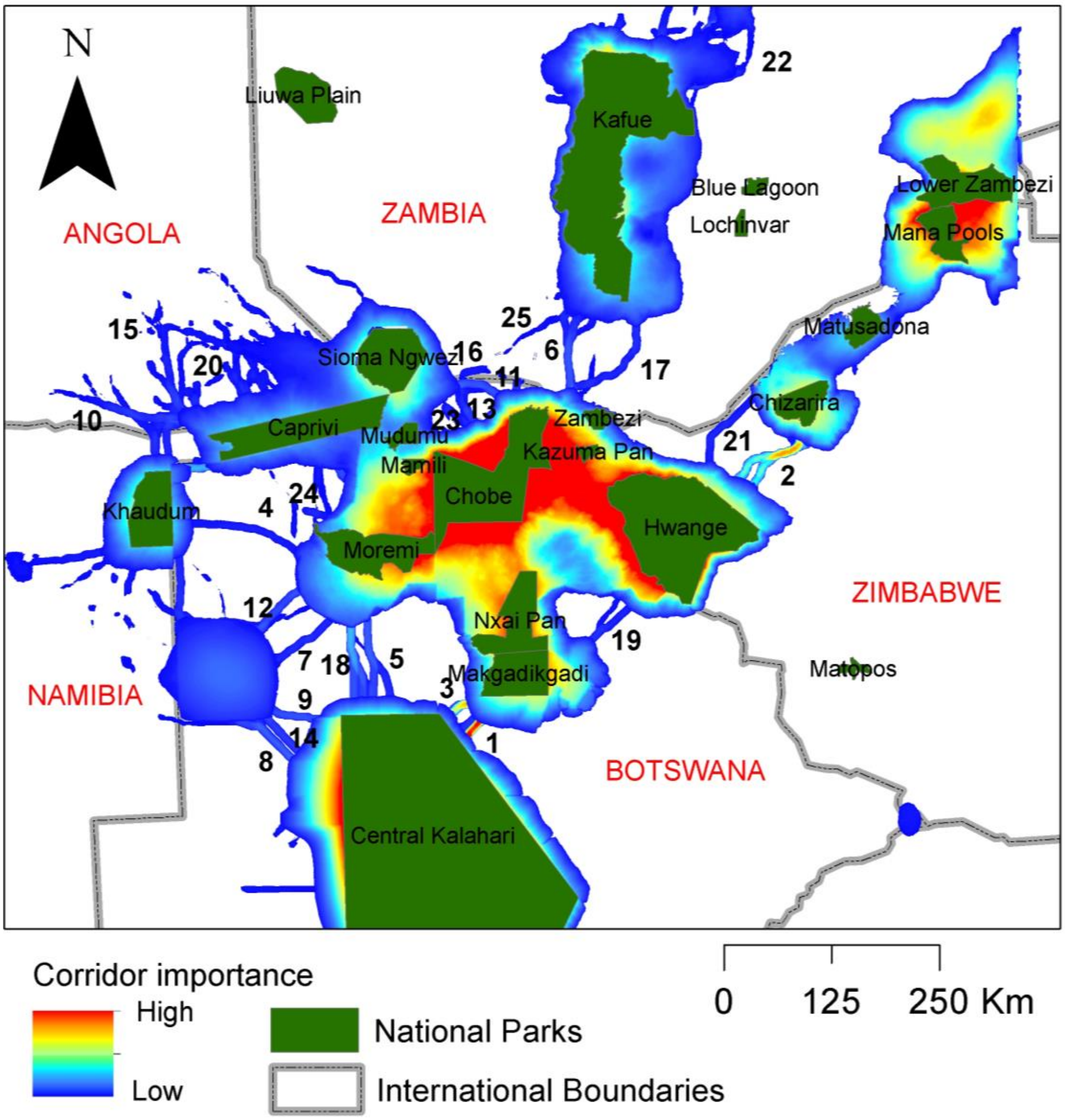

Figure 1. 5. Corridors. Ranking of relative lion linkage corridor importance within the Kavango-Zambezi Transfrontier Conservation Area and surrounding landscape

Location and importance of predicted conflict hotspots

The highest ranked predicted conflict hotspot area runs along the northern edge of the central dispersal area from Mudumu National Park in the west to Zambezi National Park in the east, with an area of particularly intense predicted conflict within the Chobe Enclave north of Chobe National Park (Figure 1. 6 and Figure 1. 3). The second highest ranked conflict risk zone is along the eastern edge of the central dispersal area, running along the eastern boundary of Hwange National Park. This conflict hotspot had a composite score of 75.8% of the highest ranked conflict hotspot. The third highest ranked conflict hotspot was also adjacent to Hwange National Park in the central dispersal area, running along the northern boundary of the park, with a relative conflict risk value of 68.7% of the highest ranked conflict risk hotspot.

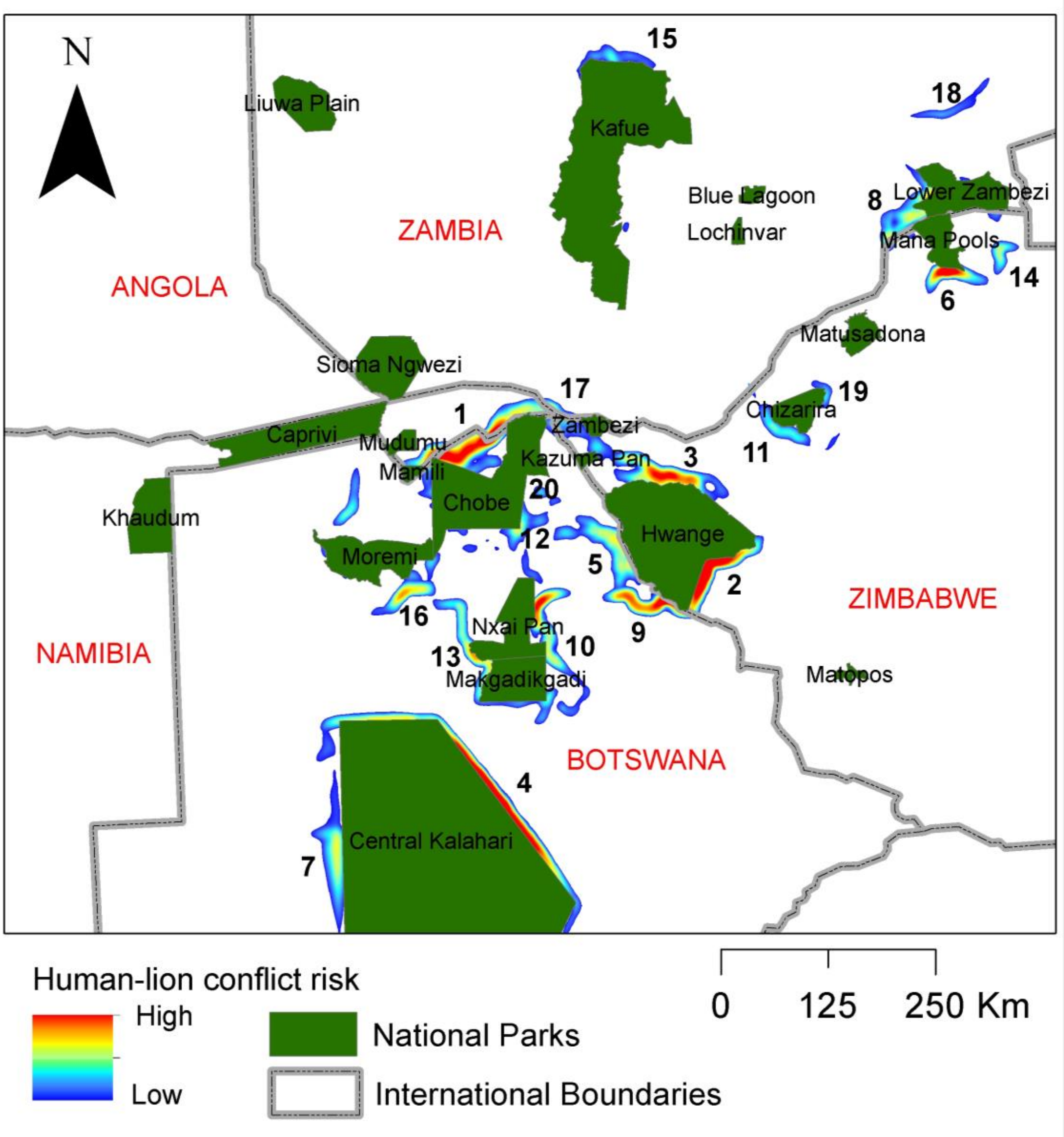

Figure 1. 6. Conflict hot-spots. Ranking of relative human-lion conflict hotspot importance within the Kavango-Zambezi Transfrontier Conservation Area and surrounding landscape

Discussion

Habitat loss and fragmentation, coupled with severe human-wildlife conflict, have reduced lion populations to less than 10% of their historic range. It is widely recognized that conservation of lions, and other large carnivores, requires a combined strategy incorporating the preservation of extensive core habitat areas, linkages between them, and mitigation of human-wildlife conflict. However, there have been few rigorous examples of efforts that have spatially prioritized conservation actions for all three of these critical components. As human populations continue to grow (Gerland et al., 2014), so too does demand for land, which is likely to exacerbate the two most pertinent threats facing lions, habitat loss and human-lion conflict (Bauer et al., 2015a). It is therefore imperative that policy makers prioritize conservation actions based on the available scientific evidence. Our paper presents a comprehensive strategy for lion conservation across the Kavango-Zambezi Transfrontier Conservation Area in southern Africa, which combines a validated empirical connectivity model with spatial prioritization of core areas, corridors and conflict risk hotspots, to motivate directed and immediate conservation for this region. This is particularly critical at the present moment given rapidly increasing human populations leading to extensive land use redesignations that are reducing the extent and increasing the fragmentation of the lion population.

We identified nine key dispersal areas, 27 linkage corridors and 27 potential human-lion conflict hotspots outside National Parks in the KAZA Transfrontier Conservation Area and its surrounding landscape. Our results suggest that it is critical to ensure that Dispersal Areas 1, 2 and 3 continue to be managed for wildlife in their entirety. With four strategically placed corridors (Corridors 1, 2, 4 and 6; Figure 1. 4 and Figure 1. 5), the five most important Dispersal Areas can be linked, and we urge that these be designated and enhanced, perhaps by establishing funneling fences to direct dispersers into them (Cushman et al., 2016). Finally, the four areas most at risk of human-lion conflict (Figure 1. 6) require conservation action, either in the form of strategically placed fences, or mitigation measures, or both. In summary, our results suggest that the most effective means of maintaining the long-term viability of lions in this region is to maintain the current Protected Area network, protect the most important Dispersal Areas, protect and enhance Corridors 1, 2, 4, 5 and 6, and implement conflict mitigation measures in the areas most at risk.

While habitat loss and fragmentation are major drivers of lion declines, so too is human-lion conflict (Bauer et al., 2015a), and therefore human-lion conflict must be addressed in connectivity planning. Our analysis highlighted the area within the Chobe Enclave as being most at risk of conflict, while the Tsholotsho area, to the south-east of Hwange National Park was ranked second. The third area most at risk of conflict is located to the north-east of Hwange National Park, while the fourth is east of the Central Kalahari Game Reserve. All these areas are known conflict hotspots (Loveridge et al., 2017a), and according to our least cost path analysis, offer little or no connectivity to other areas. We therefore suggest one of two courses of action to minimize human-lion conflicts in these hot spots. First, strategically placed fences could be erected to limit movement of lions into these specific areas, a measure which is unlikely to reduce connectivity in these particular locations (Cushman et al., 2016). A strong caveat to this solution is that fences must be predator proof and adequately maintained. The second alternative would be to implement community-based mitigation initiatives aimed at either reducing the levels of conflict or maximizing the incentives to protect wildlife. It is likely that the area east of the Central Kalahari Game Reserve experiences less conflict due to the fence in that area and we advocate that the fence is maintained and reinforced to minimize conflicts.

The analyses presented here focus on identifying the most important core areas, the strongest potential corridors that connect them, and the locations of the highest potential conflict risk. Our recommendation is to (1) protect the most important core areas, (2) establish movement across the most important corridors, and protect them from development and conflict risk, and (3) implement conflict mitigation measures and strategic fencing to reduce mortality risk to lions in the identified conflict hot spots. In some cases, it may no longer be possible to functionally restore some of the movement corridors identified in our analyses. In such cases, a potential alternative would be to mimic the outcomes that would result if the corridors were functional, such as translocations of individual lions reciprocally across the gap (Miller et al., 2013). Translocations between fenced protected areas has been a successful strategy for maintaining lion genetic diversity, but where possible we advocate for establishing and protecting functional corridors, since functional corridors would provide connectivity for a large number of species, in addition to lions.

It is important for conservation proposals to include consideration of risks, hidden risks, opportunity costs and cost implementation. The prioritization presented here is based exclusively on ranking locations for conservation based on biological criteria only, and does not include discussion of societal, political, or economic considerations. As such, it should not be considered to be a recommendation for specific action, but rather a step in the process of decision-making. We believe these results will be useful to managers and decision-makers in their efforts to identify solutions that meet conservation and social objectives simultaneously in a cost-effective manner. Future research, combining sociology, economics and ecology, should work on formalizing that process of balancing the conservation and social objectives surrounding lion conservation in southern Africa.

This example, while for lions in southern Africa, provides a general approach for rigorous, empirically based comprehensive conservation planning based on spatial prioritization. We propose a method to quantitatively develop a comprehensive strategy for population-level carnivore conservation based on combining validated empirical connectivity models with spatial prioritization of core areas, corridors and conflict risk hotspots. By spatially mapping and ranking the relative importance of these areas our approach allows managers to identify the highest priority areas for directed and immediate conservation.

Author Contribution:

I hereby confirm that Dominik Bauer conceived and conceptualized the experiment and wrote the paper.

Hamburg,

Jörg Ganzhorn

Prof. Dr. Jörg Ganzhorn

Chapter 2: Sex and age predict habitat selection in the world's most geographically extensive lion population

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ABSTRACT: Conservation of large carnivore populations requires effective management strategies that promote landscape scale protection and genetic connectivity. Pivotal to the success of these strategies is sufficient evidence, including the quantification of the processes that govern species distribution. We used telemetry data from 63 lions from the Kavango Zambezi Transfrontier Conservation Area in southern Africa to analyse inter-demographic differences in habitat relationships using a mixed-effects resource selection analysis approach. In this semi-arid landscape, surface water and precipitation which in turn regulate prey abundance are some of the most important drivers of habitat use for lions. Predicted habitat use was highest in close proximity to water irrespective of age and sex while it varied for precipitation depending on the demographic category. While adult lions and subadult females selected habitat with higher than average rainfall, the opposite was the case for subadult males. The predicted probability of habitat use was generally positively associated with higher levels of prey abundance for all four demographic categories with the exception of gemsbok which was negatively correlated with adult female, subadult male and subadult female habitat use. The predicted distributions for all four demographic categories were widespread across multiple different land-use types highlighting the need to extend the traditional concept of formally protected areas to include multi-use landscapes and support large-scale transboundary conservation initiatives.

Key Words: Lion *Panthera leo*, habitat use, resource selection, landscape conservation, demographic differences, Kavango Zambezi Transfrontier Conservation Area

Introduction

In the face of rapidly increasing human populations, habitat loss and fragmentation driven by the expansion of agriculture and human settlements are amongst the main drivers of wildlife decline (Pereira et al., 2010). Wide-ranging species such as large carnivores are particularly affected, and are forced to compete with humans for suitable habitat (Valenzuela-Galván et al., 2008), resulting in human-wildlife conflict and population decline (Ripple et al., 2014). With the threat of habitat loss unabated (Laurance, 2010), it is essential to understand and predict how animals respond and adapt to changes in their environment to mitigate global biodiversity loss. Persistence of large carnivore populations requires effective management and protection strategies that promote landscape scale protection and genetic connectivity. Pivotal to the success of these strategies is sufficient evidence, including the quantification of the processes that govern species distribution (Sutherland et al., 2004).

Habitat selection in large carnivores has been shown to be influenced by a number of bottom-up and top-down factors. Carnivore densities generally reflect prey abundance in natural ecosystems (Carbone and Gittleman, 2002; Karanth et al., 2004; Hayward et al., 2007; Hatton et al., 2015), which in turn is regulated by primary productivity (East, 1984; Chase, 2003; Hopcraft et al., 2010) and water distribution and availability (Valeix et al., 2010). Additionally, carnivore densities are strongly negatively affected by anthropogenic pressures. These can include retaliatory killings in response to human-wildlife conflict (Treves et al., 2004; Kissui, 2008), overexploitation through trophy-hunting (Loveridge et al., 2007), as well as unsustainable bushmeat harvesting that depletes natural prey populations (Henschel et al., 2011; Everatt et al., 2014).

Resource selection functions (RSFs) are a popular tool to identify critical resources for animal populations by comparing habitat characteristics at locations animals use to those that are theoretically available, or unused, by the animal (Boyce and McDonald, 1999; Manly et al., 2007; Millspaugh et al., 2014). They are commonly used to identify habitat suitability criteria for large carnivores and to determine relevant conservation actions (Kunkel et al., 2013). However, these models often neglect demographic differences, pooling locational data irrespective of sex or age class (Güthlin et al., 2011; Klaassen and Broekhuis, 2018). This potentially obscures important species-habitat relationships (Roever et al., 2014) in species such as large carnivores that might have different ecological needs according to their demographics (Elliot et al., 2014b; Zeller et al., 2018).

The objective of our study was to assess how a suite of environmental and anthropogenic landscape variables, as well as prey abundance, influence space use of four demographics categories of lions (adult male, adult female, subadult male, and subadult female) in this multiuse landscape.

We hypothesize that in this semi-arid landscape, lion occurrence would be positively influenced by the availability of water, habitat productivity and prey abundance. We expect habitat productivity to be less influential for subadult males as they are not strong enough to challenge for a pride, therefore being forced to rely on marginal habitat instead. In addition, we hypothesize that lion occurrence is negatively influenced by anthropogenic factors. With the different demographics showing varying levels of tolerance towards human disturbance (Elliot et al., 2014b) we expect adult females to be most influenced by anthropogenic factors and subadult males the least.

We used the results to predict the relative probability of space use for each demographic category across the study area. We discuss the implications of our findings for the management and protection of this geographically critical habitat and highlight its importance to the ecological functionality of the KAZA TFCA.

Materials and Methods

Study area

We situated our study in a ~70.000 km^2 section of the KAZA TFCA at the border of Botswana and Zimbabwe (between 17°47’ – 20°15’S and 23°32’ – 27°44’E; Figure 2. 1). There are five national parks, ten forest reserves, 19 wildlife management areas (WMAs), as well as several conservancy ranches, communal areas, and high intensity farming blocks in our study area. The area experiences two distinct seasons; a dry season from April to October, and a rainy season from November to March. Annual mean precipitation ranges from 680 mm in the northeast to around 400 mm in the southwest (Batisani and Yarnal, 2010; Mazvimavi, 2010). In this semiarid landscape, there is no natural surface water during the dry season other than the perennial Chobe and Zambezi Rivers to the north and the Okavango Delta to the west of the study area. However, water is available at over 250 artificial waterholes, of which more than 80% are located in Zimbabwe. Tree and shrub savannah vegetation is dominated by *Baikiaea plurijuga* in the north, *Combretum* spp., *Acacia* spp., and *Terminalia sericea* in the south, and *Colophospermum mopane* in the southwest.

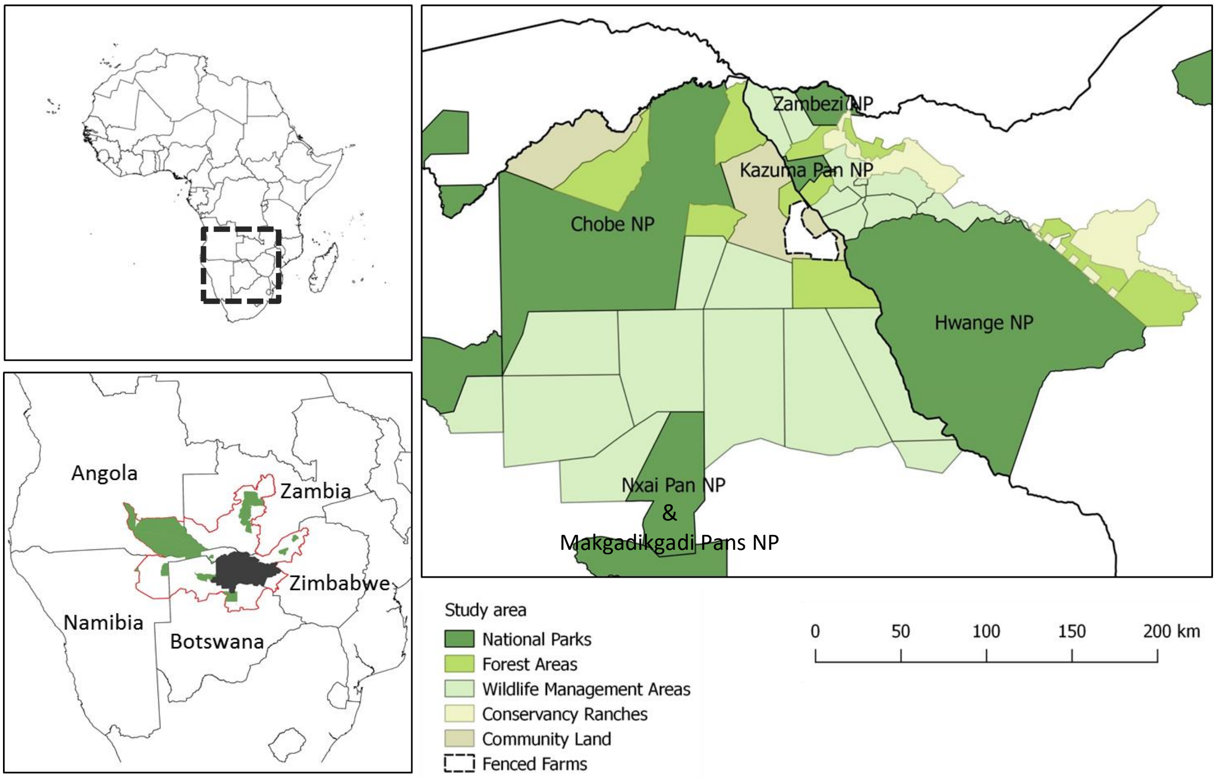


Figure 2. 1. Study area with land-uses inset, its extent (in dark grey) within the KAZA TFCA (red outline) (bottom left) and within Africa (top left)

Covariates

Environmental and anthropogenic

Based on *a priori* rationale, we considered seven site-specific covariates to affect lion distribution across the study area (Table 2. 1). Specifically, we considered covariates associated with primary productivity such as mean annual precipitation *(Precipitation)*, percent canopy cover *(VCF)* and Normalized Difference Vegetation Index *(NDVI)*. We accounted for water availability by calculating distance to the nearest waterhole or perennial river *(Distance to Water)*, and human disturbance by calculating distance to the nearest settlement *(Settlement Distance)* and settlement density *(Settlement Density)*. We developed a database of these different geospatial layers representing each covariate as a raster using QGIS v.2.14 (QGIS Development Team, 2016) and online available (i.e. MODIS, VCF, NDVI), field collected (i.e. waterholes, roads), and manually digitized data (settlements).

Table 2. 1. Covariates hypothesized to influence lion habitat use across the study area

Covariate	Description	Resolution	Source
ENVIRONMENTAL			
Precipitation	Mean annual precipitation (mm)	1000m	http://worldclim.org
VCF	Vegetation Continuous Fields Percent canopy cover	250m	MODIS MOD44B http://glcf.umd.edu/data/vcf
NDVI	Normalized Difference Vegetation Index	250m	MODIS MOD13Q1 https://modis.gsfc.nasa.gov
Distance to Water	Distance to nearest available dry season surface water	100m	this study - euclidean distance to the nearest waterhole (rivers treated as series of waterholes spaced 100m apart)
Water Density	Relative density of surface water per 100m^2	100m	this study - kernel density estimation algorithm with 10 km radius and a quartic (biweight) kernel
ANTHROPOGENIC			
Distance to Settlement	Distance to nearest human settlement as a proxy of anthropogenic impact	100m	this study - euclidean distance to the nearest point vector of house
Settlement Density	Relative density of houses per 100m^2	100m	this study - kernel density estimation algorithm with 10 km radius and a quartic (biweight) kernel

Prey abundance

To determine prey abundance across the study area we employed vehicle-based spoor counts. Spoor counts were conducted in the early morning hours to avoid potential disturbance by other vehicles. A four-wheel drive vehicle was driven at an average speed of 15 km/h, with a tracker sitting on a seat fixed to the bull-bar scanning the road ahead. All trackers participating in the study had several years of tracking experience and were thoroughly trained for this particular type of data collection. We recorded spoor of nine primary prey species of lions across the study area to be analysed in an occupancy modelling framework (Henschel et al., 2016). These species included African buffalo (*Syncerus caffer*), common *eland (Taurotragus oryx)*, gemsbok *(Oryx gazella)*, giraffe *(Giraffa camelopardalis)*, impala (*Aepyceros melampus*), *greater kudu (Tragelaphus strepsiceros)*, warthog (*Phacochoerus africanus*), wildebeest (*Connochaetes taurinus*), and Burchell's zebra (*Equus burchelli*).

We divided *a posteriori* the surveyed road network in 201 road segments (mean length 22.8±0.87 km) using an 8*8 km grid across the entire landscape. To create the detection histories for occupancy modelling, we split the road sections within each grid cell into 2 km segments and treated each of them as a spatial replicate where the presence or absence of the respective species was recorded. We addressed concerns about spatial dependence of detections in consecutive road segments by stepwise increasing the segment length by 2 km until the single-season occupancy model without Markovian dependence (MacKenzie et al., 2002) outperformed the occupancy model with Markovian dependence (Hines et al., 2010) by at least two Akaike Information Criterion (AIC) values (Anderson and Burnham, 2004). Since there was considerable difference in spoor encounter rate across sampling units we assumed that the detection probability was also influenced by variation in animal abundance. We therefore evaluated for each species the performance of an abundance induced heterogeneous detection probability model (Royle and Nichols, 2003) against that of MacKenzie (MacKenzie et al., 2002) using Akaike Information Criterion (AIC) to rank models.

Again based on *a priori* rationale, we considered nine site-specific covariates that could affect animal occupancy – or in the case of Royle-Nichols models, prey abundance – across the study area (Table S. 1, Supporting Information). Using the package "unmarked" (Fiske and Chandler, 2011) in R (R Core Team, 2018) we fitted single-season, single-species occupancy models to our detection histories. Candidate models were built by testing each site-specific covariate using univariate analysis. We tested for correlation between the remaining covariates and eliminated the one with higher AICc when collinearity was observed (|r| > 0.70). We then ran the global model with all possible combinations and assessed the goodness of fit using Pearson's chi square statistic with 1000 parametric bootstraps in the R package "AICcmodavg"

(Mazerolle, 2019). Models with ΔAICc ≤ 2 received equal support and we used the “MuMIn” package in R (Barton, 2015) for conditional model averaging.

We used the top models’ covariate coefficients to estimate the relative probability of prey intensity of habitat use across the study area. For species that Royle-Nichols models performed better than MacKenzie models, we rescaled the predicted map values to 0-100 range so as to facilitate comparison across species. An account of the modelling process is provided by Henschel et al. (Henschel et al., 2016).

Resident lion data

GPS collar data

Between 2012 and 2016 we fitted GPS telemetry collars to a total of 63 individual lions (14 adult males, 20 adult females, 22 sub-adult males and seven sub-adult females) from 48 groups. In our post-processing of the telemetry data, we filtered for impossible movements (such as spikes in speed >50 km/h) and retained only fixes with a low Positional Dilution of Position (PDOP<10) (Lewis et al., 2007; Frair et al., 2010). We randomly selected one fix per day per collared lion so as to improve independence of detections and to standardize across collars featuring different position recording rate of collars. This temporal resolution of locations is considered sufficient for examining large scale processes such as residency or transience (Weston et al., 2013).

Selecting resident data

Telemetry data extended in some cases over multiple years, during which the tracked individuals could progress through demographic stages and disperse. To exclude non-residential movement, we used a biologically informed threshold based on the expected movement distances and maximum excursion duration of ten breeding and therefore resident females in the study area (Weston et al., 2013). We identified their focal home range centres which we measured as the centroids of the 95% minimum convex polygons (MCPs). We calculated their maximum ranging distance from the centroid as 21.76 km and defined the usual ranging distance (15.85 km) as the value for which 98% of their movement distances fell below.

Using the package "adehabitatLT" (Calenge, 2011) in R we calculated Net Squared Displacement (NSD; (Bunnefeld et al., 2011) for each individual from their starting location. The starting location was set as the average location for the first seven days of each data set. Data was labelled as dispersal once the Net Distance (ND) of an individual exceeded the maximum ranging distance and the individual did not return within usual ranging distance (98th percentile) for a period of one month (see Figure S. 1, Supporting Information for example). All positional data past the determined dispersal date were subsequently excluded from the RSF analysis of resident lions.

Resource selection functions

For each individual lion we calculated utilization distributions (UDs) using kernel density estimators to create a spatial extent for third order resource selection analysis. When using kernel analysis to delineate UDs, the choice of a suitable bandwidth estimator is critical considering the large sample sizes of modern GPS telemetry datasets (Walter et al., 2011). Whereas the least square cross validation (LSCV) method regularly outperforms reference bandwidth methods (Rodgers and Kie, 2010), it is susceptible to large sample sizes and often tends to under-smooth when calculating UDs (Hemson et al., 2005; Kie et al., 2010). Evidence suggests that second generation bandwidth estimators, such as solve-the-equation plug-in, are the most reliable in terms of overall performance (Gitzen et al., 2006; Walter et al., 2011).

We therefore used a bivariate plug-in matrix calculating separate bandwidths to generate contiguous 95% annual dry season home ranges (April-October) for each individual lion with at least two months of positional data. We then used estimates of date of birth (estimated based on physical examination of each animal during the collaring process or from project records of known age lions) to assign each seasonal home range to one of four demographic categories: adult male, adult female, subadult male (≤ 4 years), and subadult female (≤ 4 years), based on age at the start of the season.

We considered observed locations (n= 40.271) as “used” and randomly generated available locations within 95% UDs while maintaining a 1:4 ratio of “used” vs “available” (Millspaugh et al., 2014). We extracted values of the candidate explanatory variables for both “used” and “available” points using a GIS software (QGIS 2.14). The variables *Water Density* and *Settlement Density* did not show any variation at our selected points and were thus excluded on the basis that there was no discrete choice available to lions. We tested for correlation between our candidate explanatory variables using Variance Inflation Factor (VIF).

We stepwise eliminated the covariates with the highest VIF values until the remaining ones dropped below the critical threshold of three (Zuur et al., 2010).

As this study aims to describe the relative impact of individual variables rather than just the overall probability of use at each point in the landscape, we created three candidate sets of variables: *environmental* and *anthropogenic* variables only, *prey* only and both sets of variables combined. Each of these three sets were run in separate RSFs with a used-available design in a binomial *generalized linear mixed model (*GLMM) framework (from here on referred to as *environmental model, prey model* and *general model* respectively).

Model selection

All analyses were run using the “lme4” package in R (Bates et al., 2014). In the global model, all candidate variables were included as fixed effects, and their interaction with the categorical variable demographic category. Two random factors were incorporated to account for repeated sampling from individuals, and from multiple seasonal home ranges within individuals. We considered the inclusion of random intercepts, random slopes, and the correlation between these variance components. To optimize our random effects structure, we followed the procedure from (Bates et al., 2018), where a global model (in terms of random effects structure) balances the inclusion of adequate components with the fitting of over-specified random effects given the information in the data. In all cases, random intercepts for individual and home range within individual were retained, along with random slopes for each covariate.

We assessed the significance of each fixed effect term by dropping each higher-level term in turn from the global model, using likelihood ratio tests (LRT). Where an interaction term between the landscape variables and demographic category was significant, this would indicate that the data is better described by separate slopes per category.

Results

Between April 2012 and October 2016 we tracked a total of 63 lions (14 adult males, 20 adult females, 22 sub-adult males and seven sub-adult females) via GPS telemetry. On average we tracked adult males for 1.42 dry seasons (range one to four), adult females for 1.44 (range one to three), subadult males for one and subadult females for 1.66 (range one to three). After post-processing of the telemetry data we retained 3261 daily locations for adult males, 3875 for adult females, 1789 for subadult males, and 1859 for subadult females. We used these to develop 52 UD estimates from 36 individual lions.

Spoor count transects covered 474 sites with an average of 9.68 km per site, which resulted in a total transect length of 4.598 km. For each species spatial independence of detections in consecutive road segments was achieved at 6 km. Detection probability was influenced by variation in animal abundance and the abundance induced heterogeneous detection probability model (Royle and Nichols, 2003) outperformed that of MacKenzie (MacKenzie et al., 2002) for each species. None of the models indicated lack of fit (p-value > 0.05) or showed signs of overdispersion ($\hat{c} < 1.7$). Maps predicting the spatially explicit abundance using the top model beta coefficients for each species can be found in the supporting information (Figure S. 2, Supporting Information).

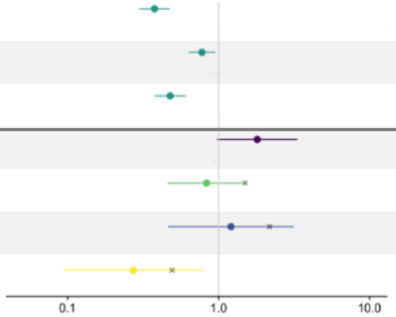
RSFs

Environmental model

All candidate explanatory variables from the global model were significant predictors for relative probability of habitat use (Table 2. 2). For *Distance to Water*, *Distance to Settlement,* and *NDVI* the data were best described by a single slope for all animals, however selection in response to *Precipitation* was described best with separate slopes for each demographic category, as shown by the significant interaction term (Table 2. 2).

Predicted relative intensity of habitat use was severely reduced with increased distance to surface water, dropping from more than 50% in close proximity to almost zero at a larger distance (Figure 2. 2). Predicted habitat use was significantly higher in open grassland (low *NDVI*) than dense forest (high *NDVI*). Furthermore, the model suggested that probability of occurrence was higher in proximity to human settlements. Whereas the model suggested that precipitation was positively related to habitat use of adult males, adult females, and subadult females, the relationship was opposite for subadult males (Figure 2. 3).

Table 2. 2. Environmental model: Fixed effects output from generalised mixed-effects model describing the predicted relative intensity of habitat use as a function of environmental and anthropogenic covariates and demographic category. Estimated effect sizes and their standard errors are presented, with significance of removal of term assessed using likelihood ratio tests. All continuous covariates have been scaled and centred, indicated by a z. prefix before covariate name. Adult females act as a reference category, and all interaction terms are presented as differences from this in intercept or slope respectively. Odds ratios of the model slopes are shown with 95% confidence intervals plotted around intercepts. For model terms where estimate is different from the reference category, the sum of it and reference category is represented by an x to show overall sign of slope.

		Wald Z-test				Likelihood ratio test		
	β	SE	Z-statistic	P_z	Odds Ratios	df	χ^2	$Pr(\chi^2)$
(Intercept)	-1.56	0.26	-5.93	<0.001				
subadult females	-0.37	0.47	-0.78	0.44				
adult males	-0.85	0.42	-2.00	0.05				
subadult males	0.35	0.46	0.75	0.45				
z.*Distance to Water*	-0.98	0.12	-8.20	<0.001		1	38.88	<0.001
z.*Distance to Settlement*	-0.25	0.10	-2.44	0.01		1	5.45	0.020
z.*NDVI*	-0.74	0.12	-6.05	<0.001		1	24.74	<0.001
z.*Precipitation*	0.59	0.31	1.88	0.06		3	9.98	0.019
z.*Precipitation*:subadult females	-0.18	0.30	-0.60	0.55				
z. *Precipitation*:adult males	0.19	0.49	0.39	0.70				
z. *Precipitation*:subadult males	-1.30	0.54	-2.39	0.02				

Model statistics: Marginal R2 0.25 Conditional R2 0.63

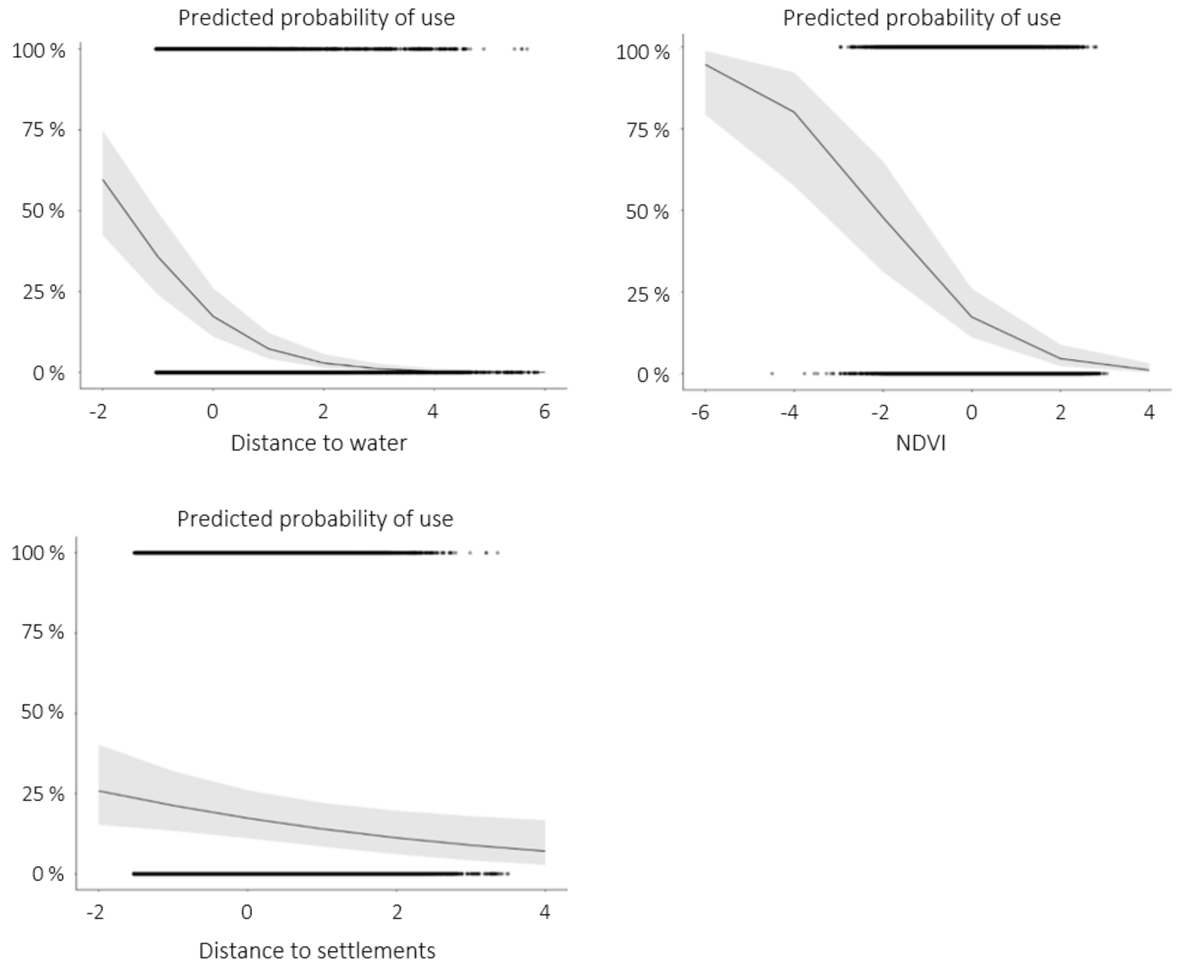


Figure 2. 2. Predicted probability of lion use (95% CI) in relation to variation in Distance to Water, NDVI and Distance to Settlements

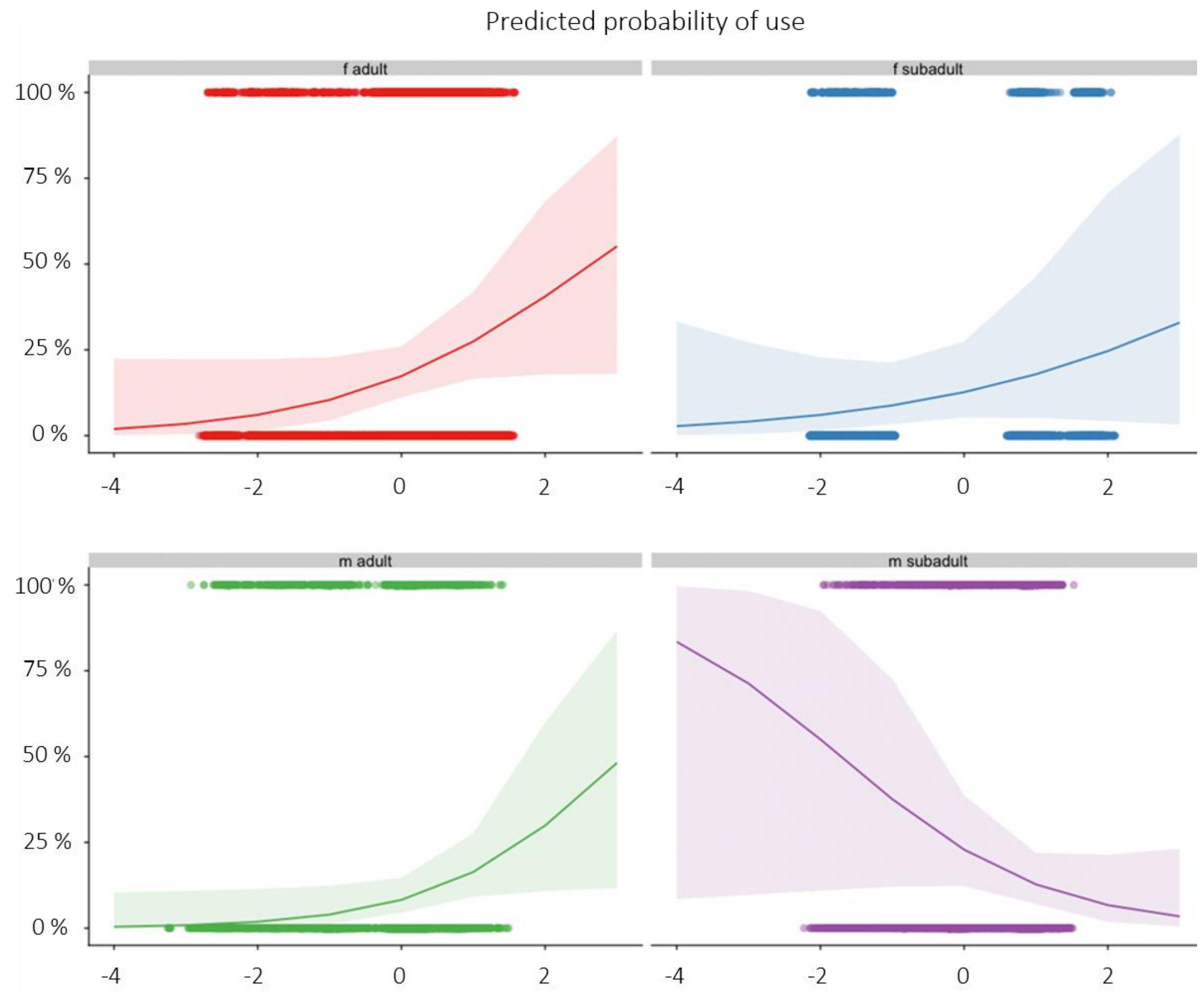


Figure 2. 3. Predicted probability of use (95% CI) for four demographics in relation to variation in mean annual precipitation

Prey model

All covariates in the final prey model had a significant effect on the predicted relative probability of habitat use by all four demographic categories (Table 2. 3). The top model included *eland* and *gemsbok* with a group-level interaction with separate slopes for each demographic category, and *buffalo*, *warthog* and *wildebees*t without a random effect (Table 2. 3). The model revealed that predicted relative intensity of habitat selection correlated positively with an increasing abundance of *buffalo*, *warthog*, and *wildebeest* (Figure 2. 4) with relatively narrow confidence intervals. *Eland* abundance seemed to have a relatively weak effect on habitat selection despite some variation between demographic categories (Figure 2. 5). The overall effect of *gemsbok* abundance on the predicted habitat use of lions was strong but varied considerably between demographic categories, with adult males seeming to prefer habitat with high *gemsbok* numbers (Figure 2. 6).

Table 2. 3. Prey model: Fixed effects output from generalised mixed-effects model describing the predicted relative intensity of habitat use as a function of prey covariates and demographic category. Output is displayed as in Table 2.2

	Wald Z-test					Likelihood ratio test		
	β	SE	Z-statistic	P_z	Odds Ratios	df	χ^2	Pr (χ^2)
(Intercept)	-1.99	0.18	-10.83	0.00				
subadult females	0.63	0.29	2.16	0.03				
adult males	-0.30	0.29	-1.02	0.31				
subadult males	-0.03	0.32	-0.10	0.92				
z.*buffalo*	0.42	0.09	4.55	0.00		1	14.38	<0.001
z.*eland*	0.05	0.10	0.51	0.61		3	10.28	0.016
z.*eland*:subadult females	-0.29	0.12	-2.30	0.02				
z.*eland*:adult males	-0.40	0.16	-2.47	0.01				
z.*eland*:subadult males	-0.03	0.18	-0.15	0.88				
z.*gemsbok*	-0.57	0.28	-2.03	0.04		3	8.90	0.031
z.*gemsbok*:subadult females	-0.26	0.15	-1.72	0.09				
z.*gemsbok*:adult males	0.80	0.38	2.12	0.03				
z.*gemsbok*:subadult males	-0.02	0.40	-0.04	0.97				
z.*warthog*	0.73	0.09	8.03	0.00		1	34.40	<0.001
z.*wildebeest*	0.16	0.05	3.31	0.00		1	7.65	0.006

Model statistics: Marginal R2 0.17 Conditional R2 0.51

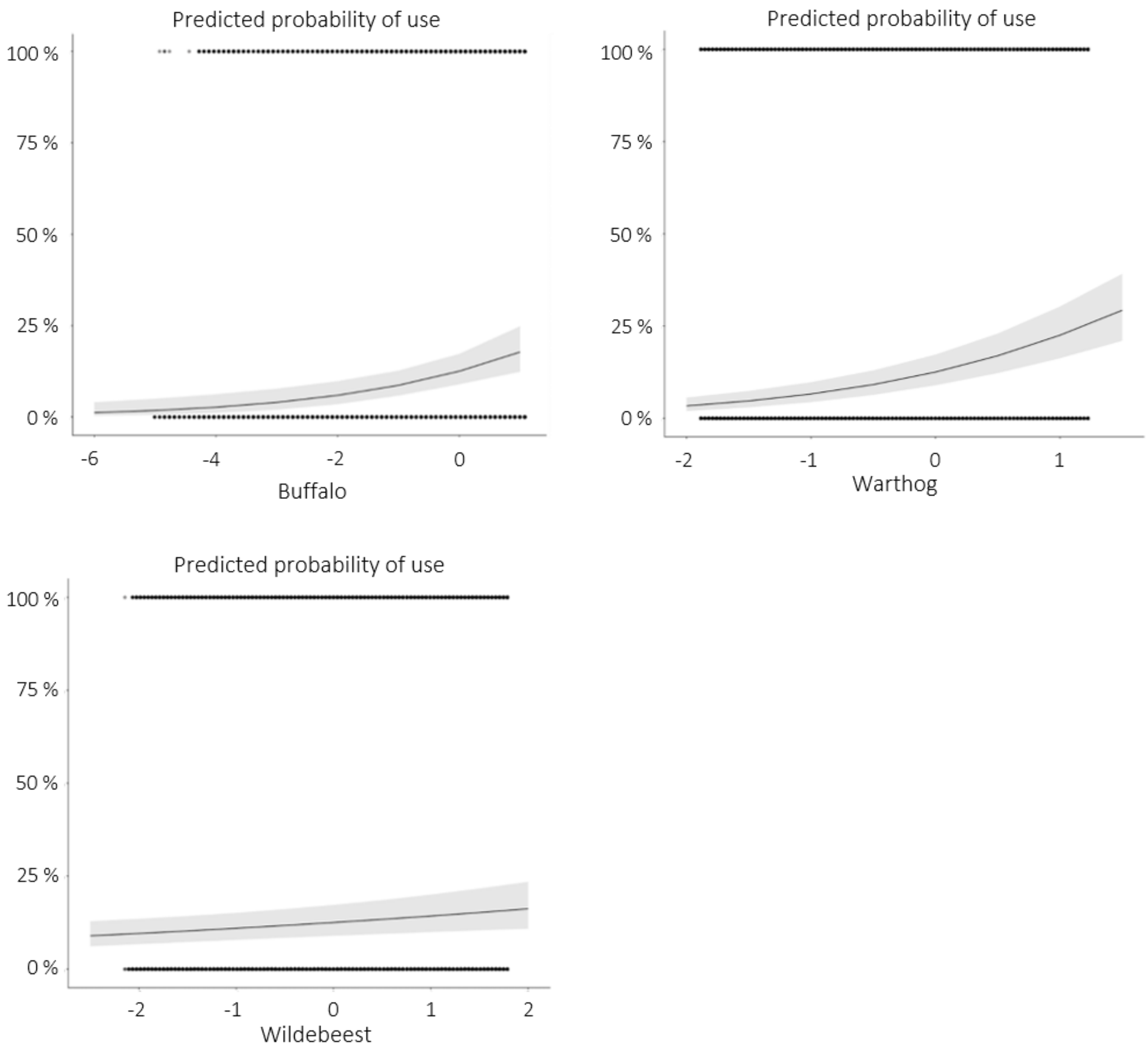


Figure 2. 4. Predicted probability of lion use (95% CI) in relation to variation in Buffalo, Warthog and Wildebeest densities

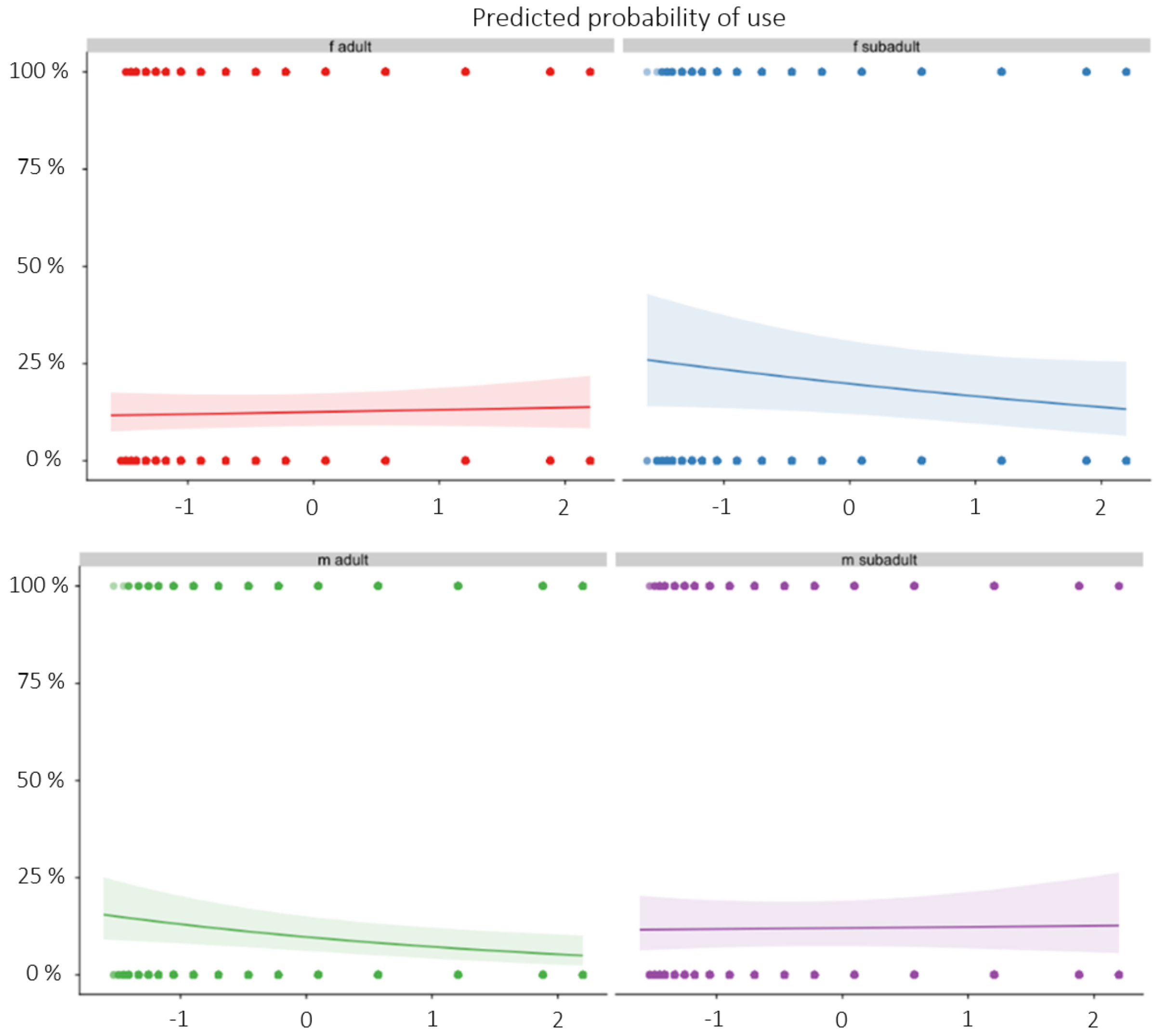


Figure 2. 5. Predicted probability of use (95% CI) for four demographics in relation to variation in eland densities

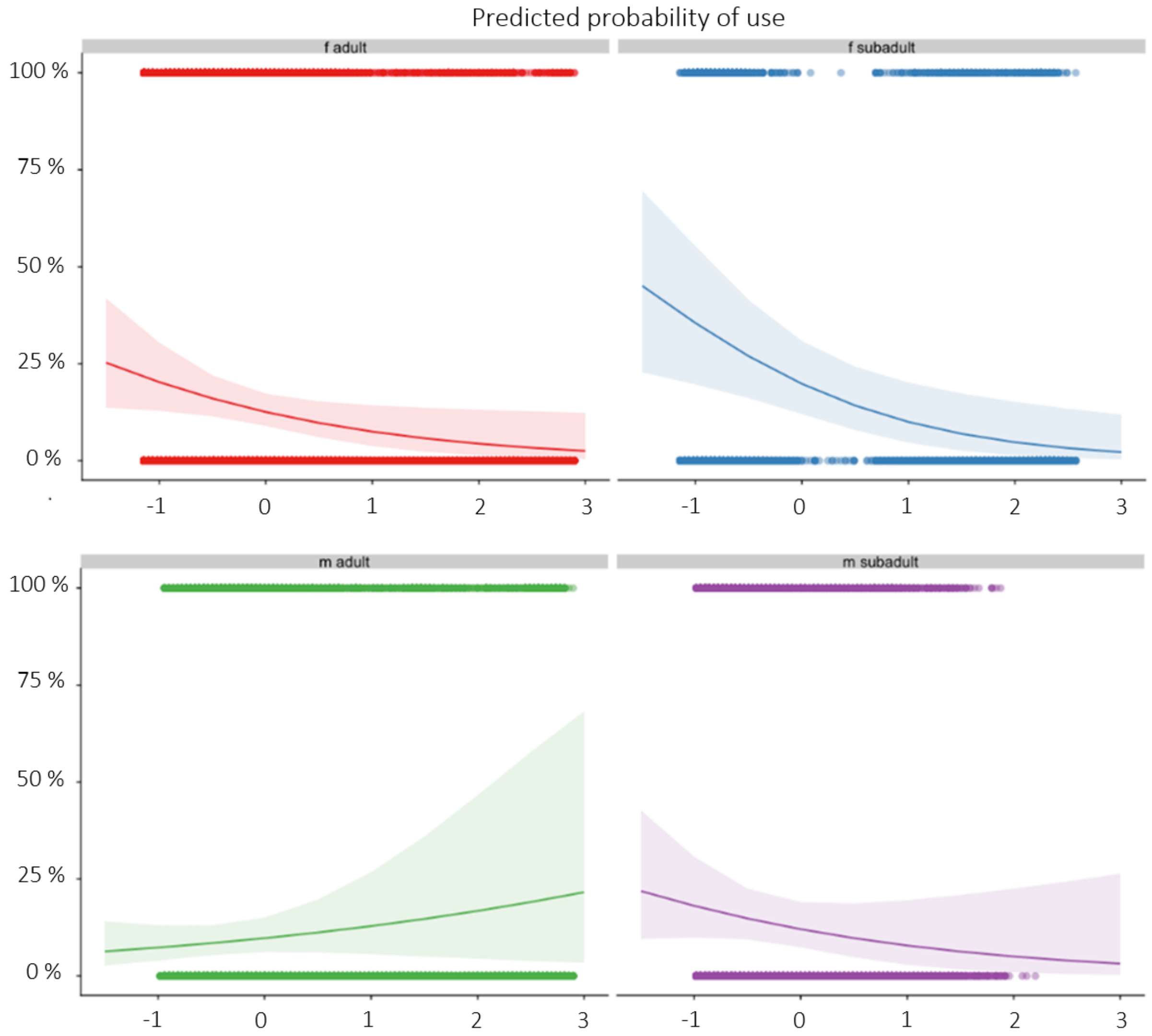


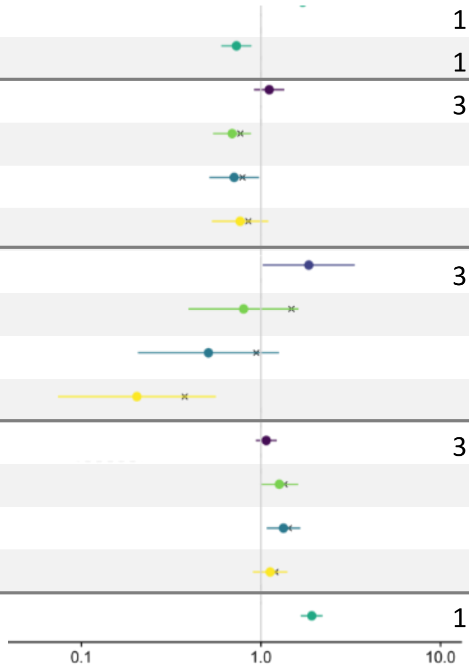
Figure 2. 6. Predicted probability of use (95% CI) for four demographics in relation to variation in gemsbok densities

General model

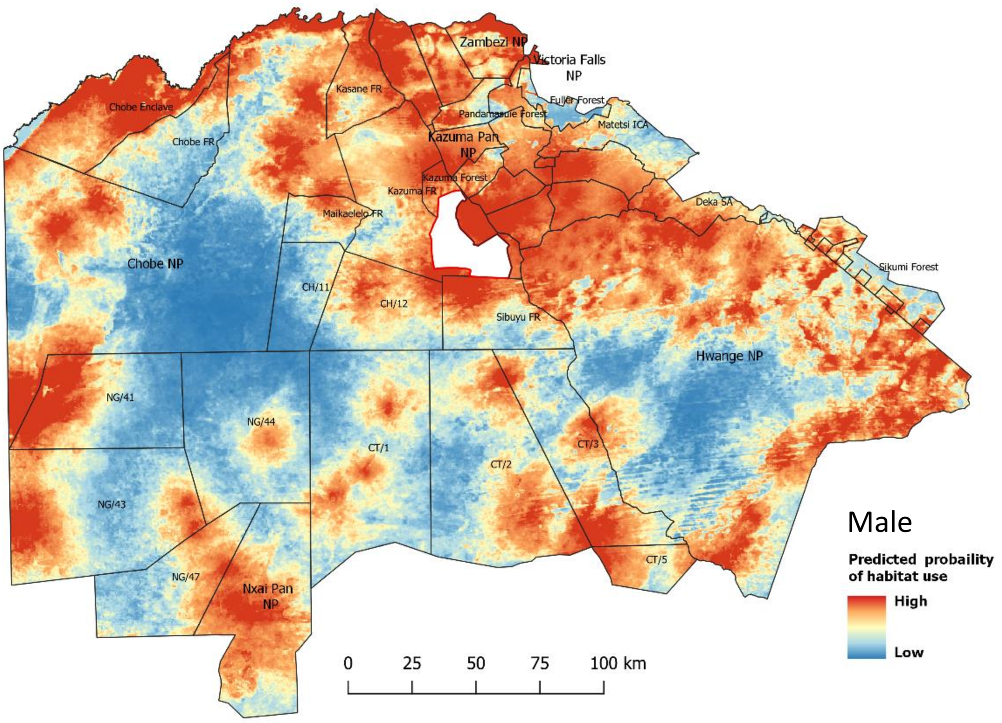
We developed maps depicting the predicted relative intensity of habitat use for each demographic category (Figure 2. 7) using the model-averaged coefficients in Table 2. 4. The predicted intensity of habitat use was broadly distributed throughout the whole study area for all four demographics. However, *Precipitation* correlated positively with adult and subadult females' probability of occurrence, while it showed the opposite effect in subadult males.

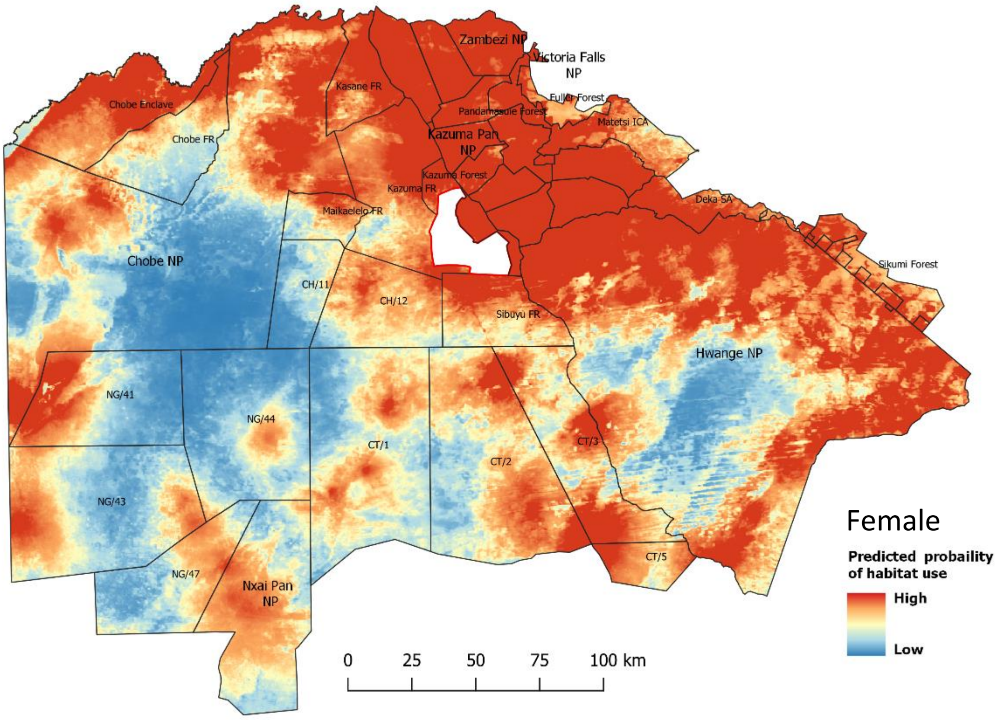
Table 2. 4. General model: Fixed effects output from generalised mixed-effects model describing the predicted relative intensity of habitat use as a function of environmental, anthropogenic, prey covariates and demographic category. Output is displayed as in Table 2.2 & Table 2.3

	Wald Z-test					Likelihood ratio test		
	β	SE	Z-statistic	P_z	Odds Ratios	df	χ^2	Pr (χ^2)
(Intercept)	-1.68	0.29	-5.71	<0.001				
subadult females	-0.25	0.58	-0.43	0.67				
adult males	-0.43	0.45	-0.95	0.34				
subadult males	0.19	0.48	0.40	0.69				
z.*buffalo*	0.53	0.11	4.87	<0.001		1	18.86	<0.001
z.*Distance to Settlement*	-0.31	0.10	-3.18	<0.001		1	8.90	<0.001
z.*eland*	0.11	0.10	1.07	0.29		3	12.19	0.007
z.*eland*:subadult females	-0.37	0.12	-2.98	<0.001				
z.*eland*:adult males	-0.34	0.16	-2.11	0.03				
z.*eland*:subadult males	-0.27	0.19	-1.45	0.15				
z.*Precipitation*	0.61	0.30	2.04	0.04		3	10.30	0.016
z. *Precipitation*:subadult females	-0.22	0.36	-0.62	0.54				
z. *Precipitation*:adult males	-0.67	0.46	-1.46	0.15				
z. *Precipitation*:subadult males	-1.59	0.52	-3.08	<0.001				
z.*wildebeest*	0.07	0.07	0.98	0.33		3	9.66	0.022
z.*wildebeest*:subadult females	0.23	0.12	1.88	0.06				
z.*wildebeest*:adult males	0.29	0.11	2.61	0.01				
z.*wildebeest*:subadult males	0.12	0.11	1.03	0.30				
z.*zebra*	0.65	0.07	9.08	<0.001		1	40.80	<0.001



Model statistics: Marginal R2 0.18 Conditional R2 0.55


Zambezi NP
Victoria Falls NP
Kasane FR
Chobe Enclave
Fuller Forest
Pandamatenga Forest
Matetsi ICA
Chobe FR
Kazuma Pan NP
Kazuma Forest
Kazuma FR
Deka SA
Maikaelelo FR
Sikumi Forest
Chobe NP
CH/11
CH/12
Sibuyu FR
Hwange NP
NG/41
NG/44
CT/1
CT/3
CT/2
NG/43
Male
NG/47
Nxai Pan NP
CT/5
Predicted probaility of habitat use
High
Low
0
25
50
75
100 km


Zambezi NP
Victoria Falls NP
Kasane FR
Chobe Enclave
Fuller Forest
Pandamatenga Forest
Matetsi ICA
Chobe FR
Kazuma Pan NP
Kazuma Forest
Kazuma FR
Deka SA
Maikaelelo FR
Sikumi Forest
Chobe NP
CH/11
CH/12
Sibuyu FR
Hwange NP
NG/41
NG/44
CT/1
CT/3
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Nxai Pan NP
CT/5
Predicted probaility of habitat use
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0
25
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100 km

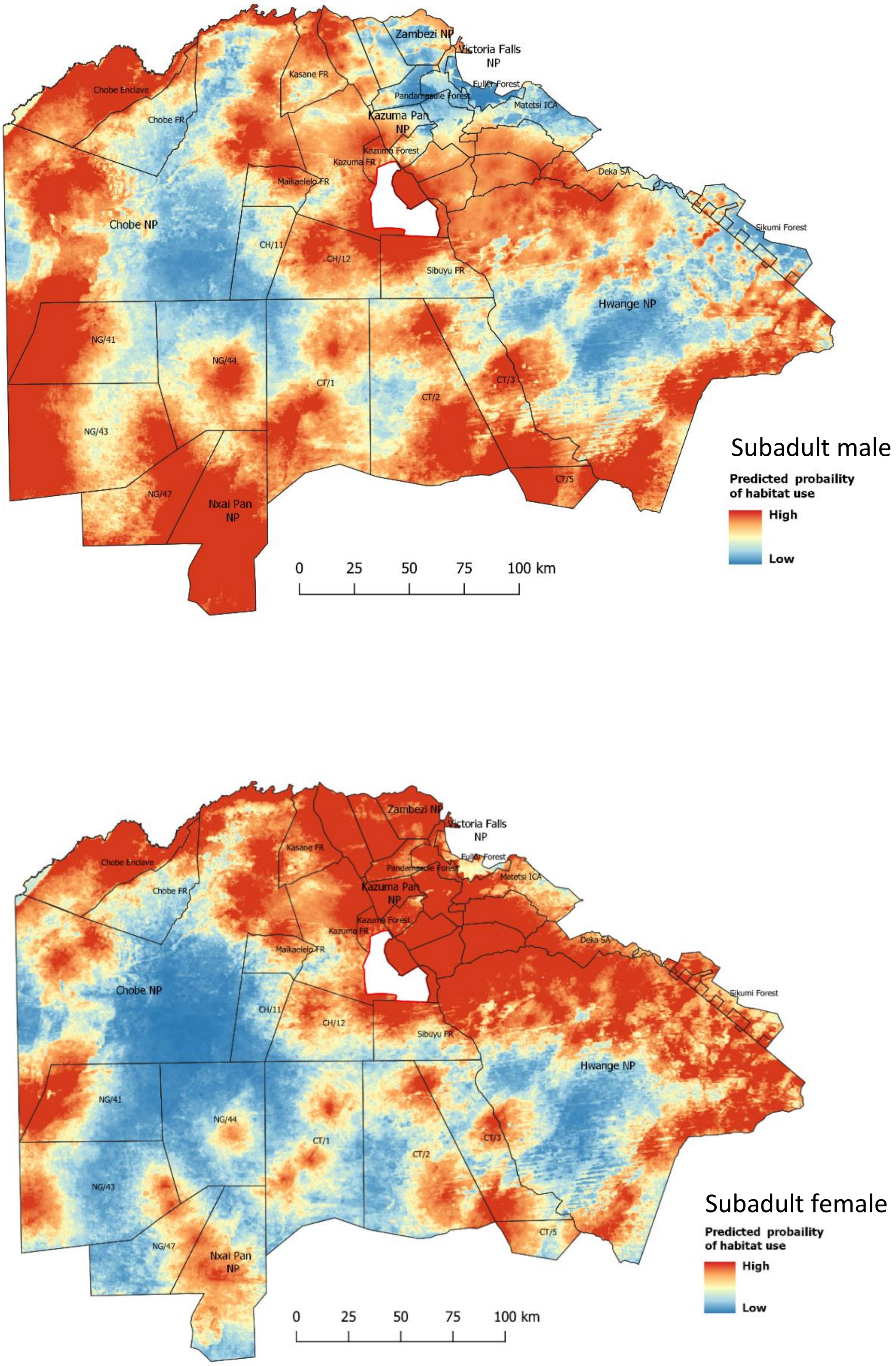


Figure 2. 7. Predicted relative intensity of habitat use for each demographic category using the model-averaged coefficients from the general model.

Discussion

With a growing human population and habitat loss threatening natural ecosystems it is essential to understand and predict how animals respond to variation in their environment. Our study shows that RSFs are a useful tool for evaluating these responses and that they provide valuable insights into the biotic and anthropogenic factors that determine the distribution of carnivores across an extensive landscape. We show that in this semi-arid landscape, surface water and precipitation which in turn regulate prey abundance are some of the most important drivers of habitat use for lions, and that the inclusion of prey availability is more informative than relying on conventional environmental proxies. We highlight the differences in response between demographics and thereby contribute to a growing body of knowledge on large carnivore species ecology which is essential for their effective conservation management.

Environmental and anthropogenic drivers

Our results show that habitat use of lions was highest in close proximity to water irrespective of age and sex (see Figure 2. 2). These findings are supported by previous studies that show that water availability strongly influences the distribution, density, and behaviour of animals in a semi-arid environment (Rozen-Rechels et al., 2015; Sirot et al., 2016). In landscapes with limited access to surface water, many herbivore species must meet their nutritional requirements within the constraints set by the location of water sources (Redfern et al., 2003), which predators use to their advantage (Rosas-Rosas et al., 2008; de Boer et al., 2010). While lions are relatively independent of water (Eloff, 1973b), studies have shown that they actively select areas in proximity to waterholes (Valeix et al., 2010) which play a key role in shaping their home ranges (Loveridge et al., 2009b).

Apart from the perennial Chobe and Zambezi Rivers to the north and the Okavango Delta to the west of the study area, all available water is provided through artificial water sources. The provision of artificial water is a common management tool and has been widely applied in Australia, the United States, and southern Africa to increase the abundance and distribution of ungulates, and mitigate the impact of man-made barriers blocking access to dry season water sources (Owen-Smith, 1996; Krausman et al., 2006; Selebatso et al., 2018). While the provision of artificial water has been shown to expand the distribution of common water-dependent species such as buffalo, zebra, and blue wildebeest (McLoughlin and Owen-Smith, 2003), the negative effects on biodiversity have been demonstrated in multiple studies (Owen-Smith, 1996; Parker and Witkowski, 1999; Grant et al., 2002). Under natural conditions, large herbivores need to move frequently between locations that offer sufficient water and forage. The provision of water encourages herbivores to become sedentary (Mills and Retief, 1984), which generates pressure on the surrounding habitat and leads to range degradation (Thrash, 1998).

The negative effects of artificial waterholes are likely lower in Botswana than in Zimbabwe, as the distances between waterholes are generally beyond the maximum foraging distance of most large herbivores, making the habitat relatively resilient to herbivore utilisation pressure (Sianga et al., 2017). However the numerous artificial water sources in Hwange National Park are in close proximity to each other, and are likely to have a long-term effect on the surrounding herbaceous vegetation and woodland (Parker and Witkowski, 1999; Chamaillé-Jammes et al., 2009; Mukwashi et al., 2012). The effects of water provision on the herbivore and plant communities have been well documented in recent years (Western, 1975; Thrash, 1998; Chamaillé-Jammes et al., 2007), however its influence on predator populations is less well understood. The increase in herbivore populations likely boost predator numbers in the short and medium term (Smuts, 1976; McLoughlin and Owen-Smith, 2003), but the impact of habitat changes and its implications for the long term sustainability of predator-prey systems is unclear.

The year-round provision of water in Hwange National Park (an area with little natural surface water) has certainly contributed to its attractiveness as a tourism destination, with the income generated supporting the long-term protection of its flora and fauna. Furthermore, the artificial waterholes in the WMAs of Botswana have allowed water-dependent prey species and therefore lions to access areas previously too dry to support them, creating a large connected population across the entire central KAZA region. Strategically placed waterholes could serve as a tool to promote landscape connectivity by strengthening (or even re-establishing) lion corridors. Maintaining a prescribed minimum distance between water sources or the rotational opening and closing of waterholes would facilitate herbivore movement while allowing the vegetation to recover, thus avoiding habitat degradation. However, care has to be taken when placing waterholes in the vicinity of human settlements or near to the boundary of protected areas, as this can aggravate human-wildlife conflict and increase anthropogenic edge effects (Woodroffe and Ginsberg, 1998).

Contrary to our hypothesis our models revealed a strong negative correlation between NDVI and habitat use for lions irrespective of age or sex (Table 2. 2). In recent years, NDVI has played a prominent role in ecological studies predicting animal distribution, movement, and life history traits (Pettorelli et al., 2011; Abade et al., 2014). NDVI correlates with photosynthetically active plant biomass and vegetation productivity (Reed et al., 1994) and is therefore commonly used as a proxy for the biomass of herbivores (Boone et al., 2006; Young et al., 2009). With the distribution and densities of dominant carnivore species clearly linked to the biomass of suitable prey (Carbone and Gittleman, 2002), their presence is commonly positively correlated with NDVI (Gavashelishvili and Lukarevskiy, 2008; Henschel et al., 2016).

In our study, the predicted probability of habitat use for all demographic categories was highest in areas with low to moderate positive NDVI values (dry shrub and grassland) and lowest in areas with NDVI values above 0.5 (woodland). The negative relationship may reflect the fact that the areas with the highest NDVI in the study area were teak forests (*Baikiaea plurijuga*), which are characterized by sandy and nutrient poor soils and low forage quality in the dry season (Gambiza et al., 2008; Chidumayo and Gumbo, 2010). Furthermore, previous studies have recommended a careful approach when using NDVI as a proxy for vegetation in semi-arid and arid environments as it can be biased by soil reflectance (Asrar et al., 1984; Huete, 1988), although others used it successfully even in sparsely vegetated areas (De La Maza et al., 2009).

The way in which lions responded to rainfall depended on an interaction with demographic category. The effect of rainfall on net primary productivity and its positive correlation with total large herbivore biomass in arid savannahs (Coe et al., 1976) has been documented previously (Owen-Smith and Ogutu, 2003; Ogutu et al., 2008). Carnivore densities correlate with the biomass of the preferred prey species or size class of prey (East, 1984; Hayward et al., 2007). A study in the Serengeti showed that rainfall positively affected short-term reproductive success of lions (Mosser et al., 2009) and that population dynamics followed the variation in rainfall patterns (Packer et al., 2005). This relationship is reflected in our results which show that adult males, adult females, and subadult females preferred habitat with higher than average rainfall. For subadult males the relationship was inverse, with the predicted probability of habitat use showing a strong negative correlation with annual precipitation. This supports our hypothesis and is most likely due to the fact that all of the subadult males collared in this study were between 28 and 48 months old – a time in which they approach or have reached sexual maturity and are pushed into marginal, less productive areas by the stronger, territorial adult males (Loveridge et al., 2017b).

In contrast to our hypothesis, our results predicted a positive correlation between habitat selection by lions and human settlements irrespective of demographic category. This is a surprising result as although some predators have been shown to adapt to a more urban environment (Bateman and Fleming, 2012; Fechter and Storch, 2014; Braczkowski et al., 2018), lions are generally considered incompatible with most current livestock production practices (Rossell, 2016) and avoid areas of communal subsistence farming, which is prevalent in the study area (Loveridge et al., 2017b). We believe this result is most likely an artefact of the large number of artificial waterholes that have been placed in key tourism areas close to the border of Hwange National Park. With multiple human settlements in close proximity on the adjoining communal farmland this would explain why lions seemingly prefer areas with high human disturbance. This further highlights the need to exercise caution when establishing artificial waterholes on the edge of wildlife areas to avoid drawing predators into the vicinity of human settlements. Developing a cross-border policy framework to harmonise the management of man-made water sources across the TFCA would help balance the needs of its wildlife and communities.

Our results suggest that adult and subadult males are less likely to occur in hunting areas (Figure S. 3, Supporting Information) than adult and subadult females (Figure 2. 7). We were unable to include trophy hunting as a predictor in our analysis as it was restricted to a small part of our study area and therefore had no influence on the majority of the dataset. However, as these areas contain virtually the same intact habitat as fully protected areas, trophy hunting is likely to exert a top-down effect.

High levels of trophy hunting have been shown to impact predator populations, sex ratio, and spatial behaviour (Packer et al., 2009; Creel et al., 2016; Loveridge et al., 2016). A previous study in the Hwange area identified trophy hunting as the primary cause of mortality in male lions, with trophy hunting concessions representing mortality hotspots in the landscape (Loveridge et al., 2017b). While it is primarily adult males that are targeted by hunters, due to the lack of suitable trophy males in the hunting concessions (Hunt, personal communication, August 28, 2019) subadult individuals (≤4 years) are frequently harvested (Loveridge et al., 2007). This would explain the lower predicted occurrence in hunting areas for both demographics when compared to adult and subadult females.

Prey

Our results confirm our hypothesis that the predicted probability of habitat use was generally positively associated with higher levels of relative prey abundance for all four demographic groups. This corroborates previous findings that show that the distribution of dominant carnivore species is governed by the availability and biomass of suitable prey (Orsdol et al., 1985; Carbone and Gittleman, 2002; Hayward et al., 2007). Our findings are congruent with those of Davidson *et al.* (Davidson et al., 2013) that showed that buffalo and medium-sized bovidae such as wildebeest were the most frequently utilised prey for male and female lions in the dry season. While warthog did not contribute such a significant proportion to their diet (Davidson et al., 2013), the positive correlation between habitat selection of lions and warthog abundance is most likely an artefact of warthogs dependence on water (D'Huart and Grubb, 2001), which lions actively seek out for hunting grounds (Valeix et al., 2010; Davidson et al., 2013).

Our results suggest the relative abundance of eland is a significant predictor for the intensity of lion habitat use, however compared to other predictors the effect was relatively small (Table 2. 3). The number of eland spoor encountered was low and therefore the final Royle-Nichols model did not show high variation. We believe that with a larger dataset the relationship between relative abundance of eland and predicted probability of lion use might differ.

As a water-independent species (Western, 1975), gemsbok distribution was restricted to the southernmost part of the study area (see Figure S. 2, Supporting Information). While the relationship of relative gemsbok abundance and the predicted probability of habitat use by lions was negative for adult females, subadult females, and subadult males, it was slightly positive for adult male lions. This result might be explained by the fact that adult gemsbok are a dangerous prey species to hunt (Eloff, 1973a), with only the much larger and powerful males attempting to do so.

Conclusion

The predicted distributions for all four demographic categories show the need to extend the traditional concept of formally protected areas to include multi-use landscapes and support initiatives such as TFCAs. Given that populations span across borders and boundaries, conservation area networks with sound land-use planning, emphasizing the needs of people and wildlife alike, are a promising movement to shape conservation in a human-dominated landscape.

Our results suggest that there are significant demographic differences in response to precipitation and a number of prey species while the availability of water and prey generally positively influenced habitat selection, which is congruent with studies from other areas. Considering the influence of prey on the distribution of lions, it is crucial to maintain sufficient prey populations and efforts should be made to combat bushmeat harvesting across the whole conservation network. While we were unable to include trophy hunting as a predictor in our analysis our results suggest that trophy hunting does have a negative effect on lion occurrence. The use of robust population estimates when allocating hunting quota is critical to ensure sustainable off-takes and avoid the creation of detrimental population sinks.

Our study area forms the core of the KAZA lion population (Cushman et al., 2018), and is part of what is arguably the geographically largest contiguous lion population left in the world, spanning across several hundred kilometres from Hwange National Park in Zimbabwe to the western parts of the Okavango Delta in Botswana (Bauer et al., 2015a). The insights we have provided on the biotic and anthropogenic factors that drive their distribution on a landscape-level are essential for the development of a comprehensive strategy for lion conservation across the KAZA TFCA which plays a key role in the survival of the species. With unrelenting habitat loss across the globe, the persistence of many wide-ranging species will depend on methods such as these to predict their response to environmental change and inform effective and successful large-scale landscape conservation strategies.

Supporting Information

Table S. 1. Spatially explicit covariates included in the occupancy modelling process for nine prey species

Covariate	Description	Resolution	Source
ENVIRONMENTAL			
Precipitation	Mean annual precipitation (mm)	1000m	http://worldclim.org
VCF	Vegetation Continuous Fields (percent canopy cover)	250m	MODIS MOD44B http://glcf.umd.edu/data/vcf
NDVI	Normalized Difference Vegetation Index	250m	MODIS MOD13Q1 https://modis.gsfc.nasa.gov
Carbon	Organic Carbon (g per kg at 5 cm depth)	250m	Hengl et al., 2017
Nitrogen	Total Nitrogen by wet oxidation (ppm)	250m	Hengl et al., 2017
Distance to Water	Distance to nearest available dry season surface water	100m	this study – euclidean distance to the nearest waterhole (rivers treated as series of waterholes spaced 100m apart)
Water Density	Relative density of surface water per 100m^2		this study - kernel density estimation algorithm with 10.000m radius and a quartic (biweight) kernel
ANTHROPOGENIC			
Distance to Settlement	Distance to nearest human settlement as a proxy of anthropogenic impact	100m	this study – euclidean distance to the nearest point vector of house
Settlement Density	Relative density of houses per 100m^2	100m	this study - kernel density estimation algorithm with 10.000m radius and a quartic (biweight) kernel

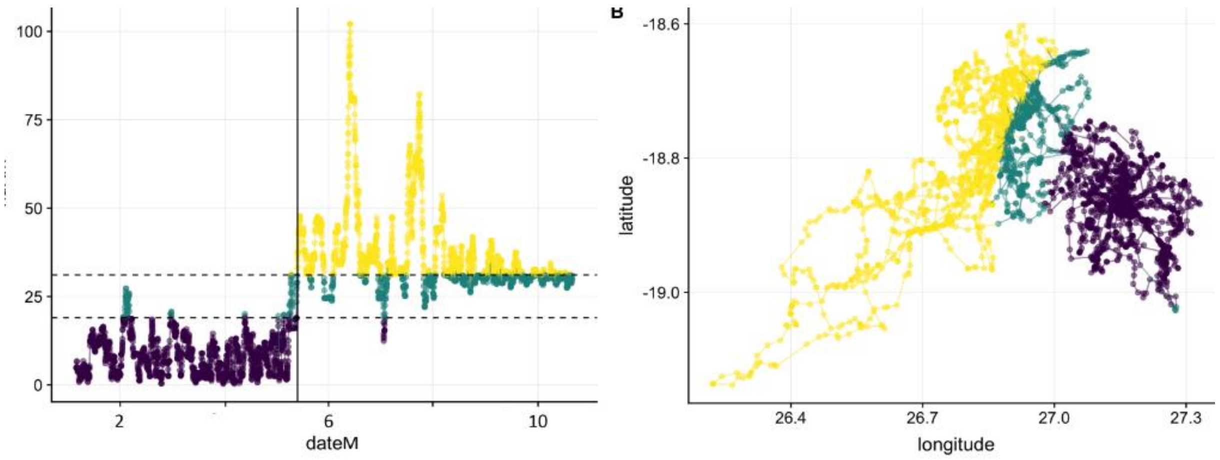
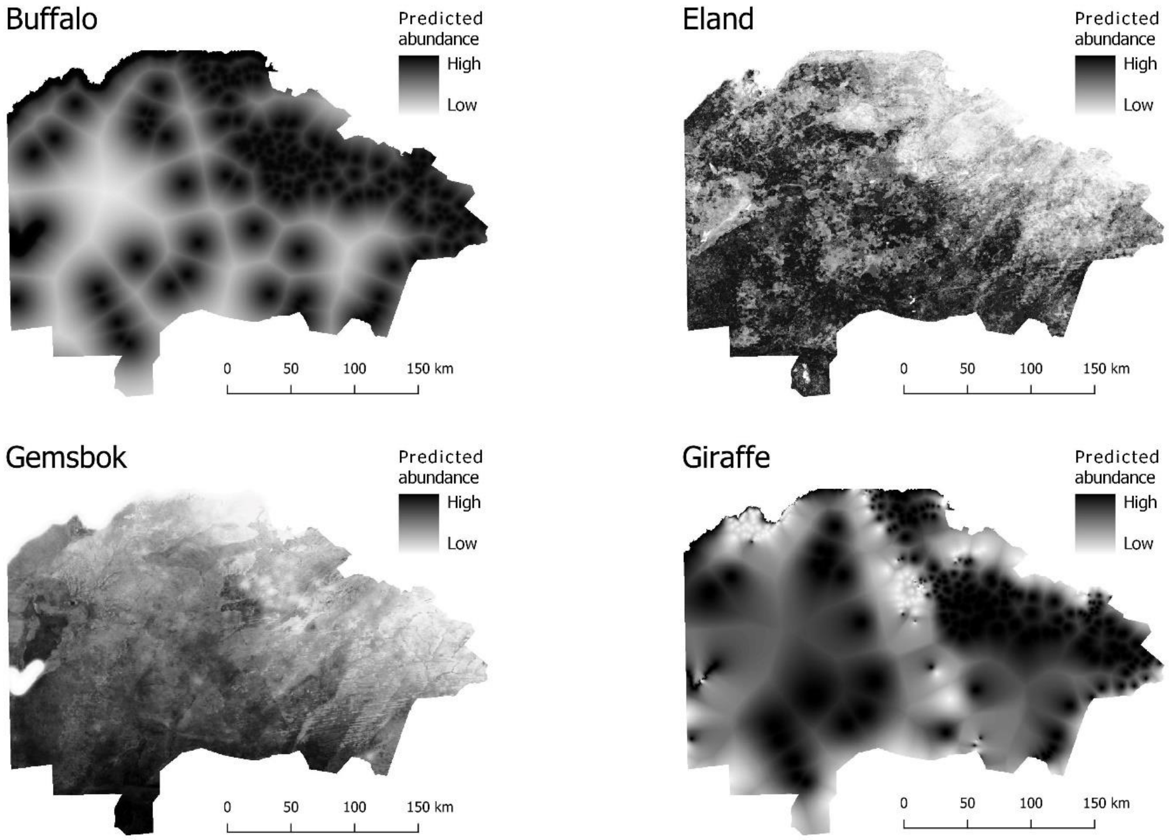


Figure S. 1. Net Distance of a sub-adult male pre- and post dispersal
Example of natal dispersal of a sub-adult male. The two dashed lines represent usual and maximum ranging distance (bottom and top) from the centroid of the animals 95% MCP. The vertical line represents date of dispersal (in months since the beginning of the study). Purple dots showcase data < 98th percentile values, green dots values between 98th percentile and maximum, and yellow dots represent data > maximum ranging distance for residents (roughly corresponding to resident, exploratory and dispersal movement respectively)



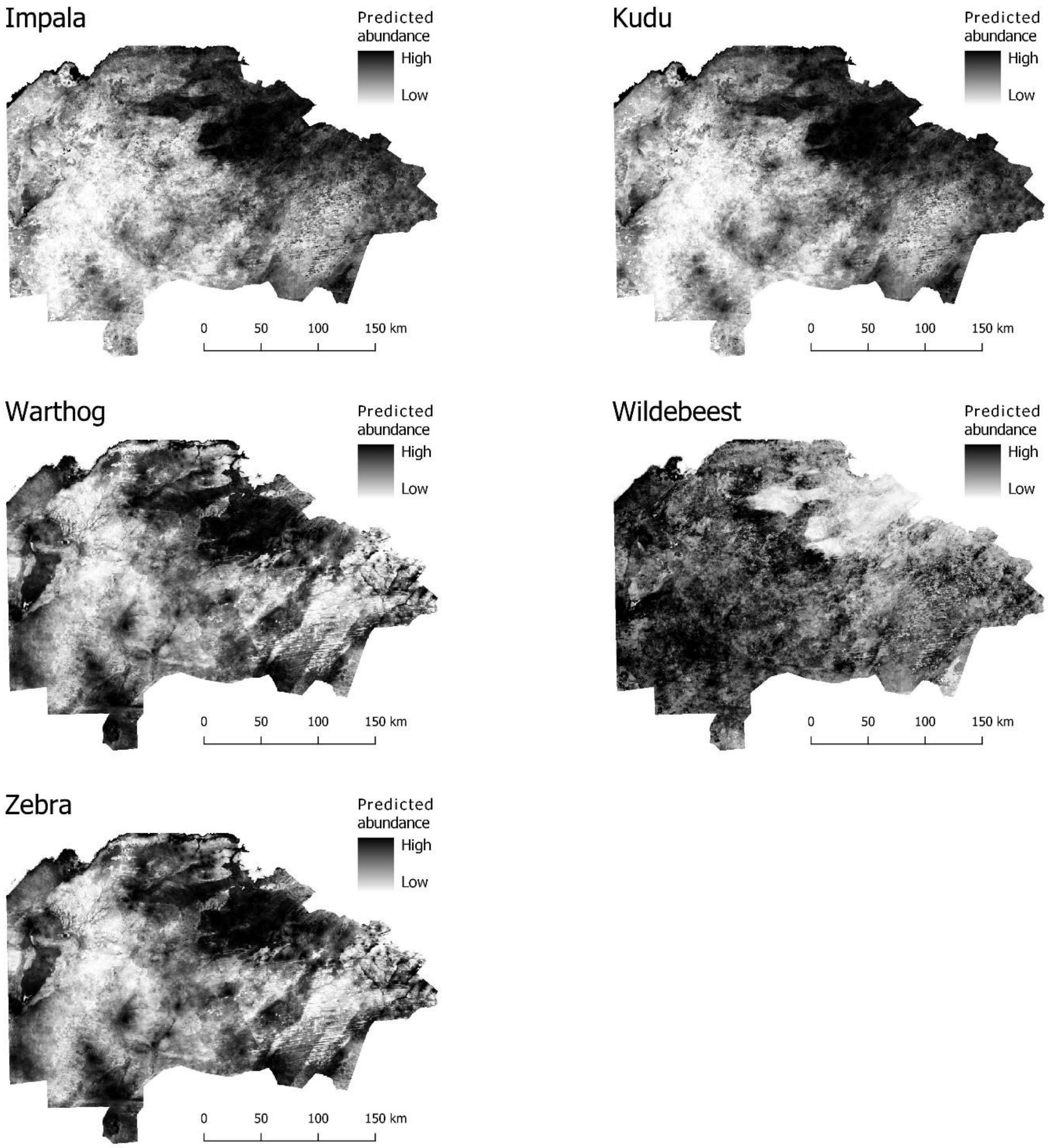


Figure S. 2. Predicted abundances for nine primary prey species of lions

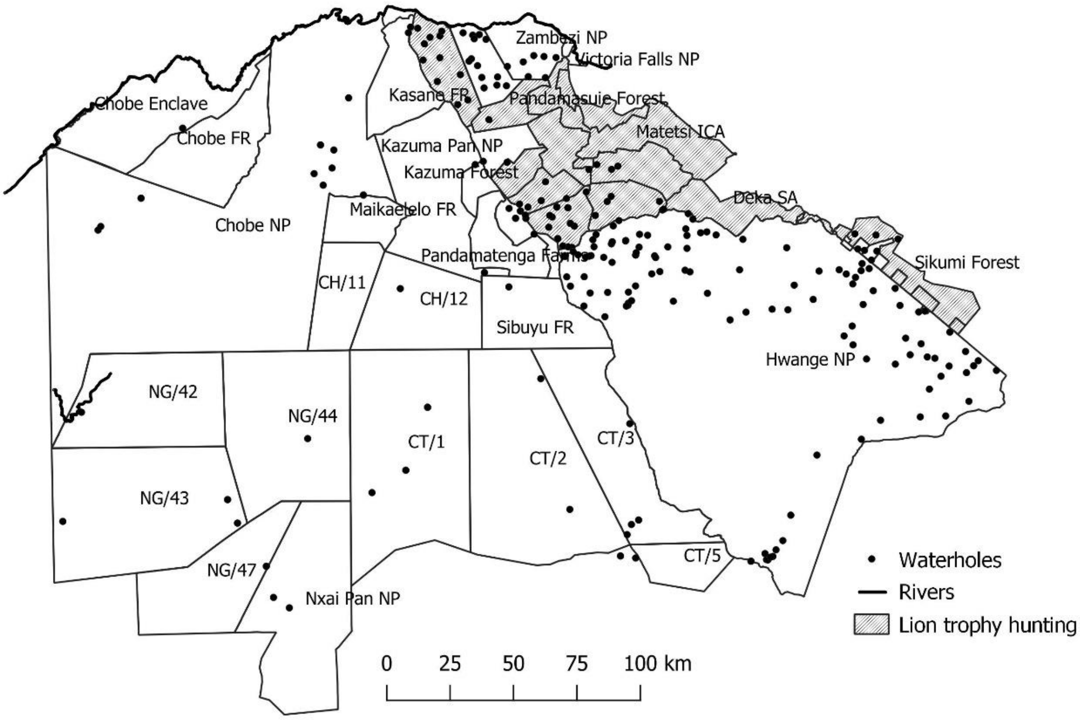


Figure S. 3. Artificial waterholes, rivers and lion hunting areas

Author Contribution:

I hereby confirm that Dominik Bauer conceived and conceptualized the experiment, analysed the data and wrote the paper.

Hamburg,

Jörg Ganzhorn

Prof. Dr. Jörg Ganzhorn

Chapter 3: Gender and season specific drivers of home range size of African lions

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ABSTRACT: Identifying drivers of variation in home range sizes can provide critical insights into demography, population regulation and spatial ecology of animals. To appropriately scale the size of conservation units to a species needs in ecosystem management, a thorough understanding of the factors that influence variation in home range size is required. Despite considerable work on the drivers of home range size in carnivores, questions remain regarding inter-seasonal and inter-sexual differences in home range variation.

In this study we used two-tier hierarchical variance partitioning as well as multivariate generalized mixed models (GLMM) on standardized predictor variables to determine how a suite of biophysical, ecological and anthropogenic factors contribute to and influence variation in home range size in the African lion (*Panthera leo*). Using a large telemetry dataset from the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) in southern Africa we measured the independent and joined effects and evaluated the differences between sex and season. In this semi-arid environment male and female home range size was primarily driven by the availability of water both in the dry and wet season. Anthropogenic variables had little effect on home range size of either sex in any season, except for female's response to cattle in the dry season. This suggests that human persecution or anthropogenic reduction of prey density is not strongly affecting the size of lion home ranges, especially of male lions, and of both sexes in the wet season. Home ranges of both sexes in both seasons were generally smaller in areas with higher soil nutrients and in areas with lower extent of woodlands and higher extent of grasslands. However, the effects of these factors seemed to vary seasonally for males, such that wet season home ranges were larger and more influenced by extent of woodlands, and less influenced by soil productivity.

Key Words:

Drivers of home range size, Lion *Panthera leo*, Variance partitioning, Kavango Zambezi Transfrontier Conservation Area

Introduction

The home range is a fundamental concept in animal ecology describing a spatial extent containing all the resources an animal requires to survive and reproduce (Burt, 1943). Identifying the size and location of animals' home ranges can provide critical insights into demography, population regulation (Wang and Grimm, 2007), and spatial ecology (Rhodes et al., 2005), and may help identify the appropriate scale of protected areas and guide ecosystem management (Woodroffe and Ginsberg, 2000).

Home range size is typically influenced by resource availability and dispersion (Mitchell and Powell, 2007), metabolic rate (Tucker et al., 2014) and energetic requirements of an individual, (Carbone et al., 1999) and can therefore be described as a trade-off between obtaining sufficient resources (resource maximization) while keeping energy expenditure at a minimum (area minimization; (Mitchell and Powell, 2004).

While drivers of home range size are generally well understood for herbivores (Bremset Hansen et al., 2009; van Beest et al., 2011; Morellet et al., 2013), they are more complex and less understood amongst the order Carnivora. This is due to carnivores' reliance on resources that are not fixed in time and space, and because carnivores are generally highly mobile and sparsely distributed. Despite considerable work on the drivers of home range size in carnivores (Mcloughlin et al., 2000; Kelt and Van Vuren, 2001; Grigione et al., 2002; Loveridge et al., 2009b; Šálek et al., 2015) questions remain regarding inter-seasonal and inter-sexual differences in home range variation.

Prey abundance (driven by habitat productivity) is considered to be one of the main drivers of variation in home range size for carnivores (McLoughlin and Ferguson, 2000; Grigione et al., 2002; Nilsen et al., 2005; Loveridge et al., 2009b). However, prey distribution is often significantly influenced by seasonal changes and the relative influence of prey on home range selection is dependent upon the sex, age and stage of the individual predator, due to differences in the factors that optimally produce the trade-off between resources, energetic cost and mortality risks among demographic groups (Elliot et al., 2014a). For most carnivores, female home range size is generally expected to closely track prey density, whereas male home range size is expected to be governed by the distribution of females in addition to prey (Sandell, 1989; Herfindal et al., 2005).

Semi-arid savannahs often exhibit strong seasonality between the dry and the wet season which leads to variation in biomass availability over large spatial areas. Annual fluctuations in water availability influence seasonal vegetation dynamics, spatial composition and the distribution of woody vegetation. With net primary productivity regulating herbivore biomass in the absence of anthropogenic influences, (Owen-Smith and Ogutu, 2003; Ogutu et al., 2008) climatic factors related to habitat productivity are therefore thought to influence carnivore abundance directly (Loveridge et al., 2009a).

While inter-seasonal and inter-sexual differences in home range size of carnivores have been described in depth (Ferguson et al., 1999; Begg et al., 2005; Henry et al., 2005), their intrinsic drivers have rarely been formally quantified. Furthermore, in modern multiple-use landscapes carnivore distribution is often influenced not only by natural factors but direct and indirect human interference, such as agricultural and urban development, bushmeat poaching, trophy hunting and human-wildlife conflict (Treves et al., 2004; Randa and Yunger, 2006; Henschel et al., 2011; Loveridge et al., 2017b). To quantify drivers of home range size in carnivores in a human-dominated environment it is therefore essential to include both natural and anthropogenic factors. As the dominant predator in the ecosystem, the lions of the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) a multi-use landscape in southern Africa, are ideal candidates to study the influence of environmental and anthropogenic factors on home range size.

To correctly represent the complex interactions of effects underlying home range selection, it is preferable to evaluate their relative contributions and interactions, and how they vary according to sex and season rather than looking at single effects in isolation. Quantifying the relative importance and interaction of multiple predictors on ecological responses is a fundamental challenge to research, and of particular relevance to understanding the effects of different factors on lion home range size.

A number of methods have been used to separate the independent and interactive effects of multiple predictors on ecological responses (Smith et al., 2009). Among these hierarchical variance partitioning (e.g. (Cushman and McGarigal, 2002)) is particularly attractive given it can fully account for and describe all independent and shared variance components, thereby providing a full accounting of the interactive, confounded and unique explanatory ability of multiple datasets. However, for some datasets with complex, nonlinear and multicollinear relationships variance partitioning may not produce a clear and unbiased measure of independent and interactive effects. In those cases other methods are needed, such as comparing the magnitudes of standardized regression coefficients, which, while not measuring independent or interactive effects, do provide a robust and unbiased measure of the full marginal influences of each variable (Smith et al., 2009). Therefore, in this study we used two-tier hierarchical variance partitioning (Cushman and McGarigal, 2002) as well as multivariate generalized mixed models (GLMM) on standardized predictor variables to determine how a suite of biophysical, ecological and anthropogenic factors contribute to and influence variation in home range size in the African lion. Using a large telemetry dataset from the KAZA TFCA we measured the independent and joined effects and evaluated the differences between sex and season to test the following hypotheses:

1) In this semi-arid environment, variation in male and female lion home range size is closely associated with the availability of waterholes (and therefore prey) in the dry season but not in the wet season.

2) Due to their different reproductive strategies, we expect that access to resources in the form of water and prey (for which we use primary productivity as a proxy) is the

key driver for variation in female home range size but is less important for male home range size.

3) Anthropogenic covariates are a limiting factor to home range size for both sexes, but more so for females as they have been shown to be much more averse to human disturbance (Elliot et al., 2014b).

Materials and Methods

Study site

The study was carried out in a ~70.000 km^2 section of the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) between 17°47' – 20°15'S and 23°32' – 27°44'E (Figure 3. 1). It encompasses 6 national parks, 10 forest reserves and a host of other land uses such as wildlife management areas and mixed communal areas. The majority of the area is semi-arid, tree or shrub savannah, characterized by dystrophic soils with the vegetation dominated by the genera *Combretum, Acacia* and *Terminalia* as well as *Colophospermum mopane* and *Baikiaea plurijuga* interspersed by open grassland (Ben-Shahar, 1993). Two seasons are distinguished in this study: dry season, lasting from April to October, and a rainy season, from November to March. Average annual rainfall ranges between 400 mm and 680 mm (Mazvimavi, 2010; Batisani & Yarnal, 2010). During the dry season, very little natural surface water is available and animals rely on a series of artificial waterholes, in addition in the perennial Chobe and Zambezi Rivers to the north and the Okavango Delta in the western portion of the study area. Human settlements are absent from most of the area and largely limited to the rivers in the north and the communal areas east of Hwange National Park in Zimbabwe.

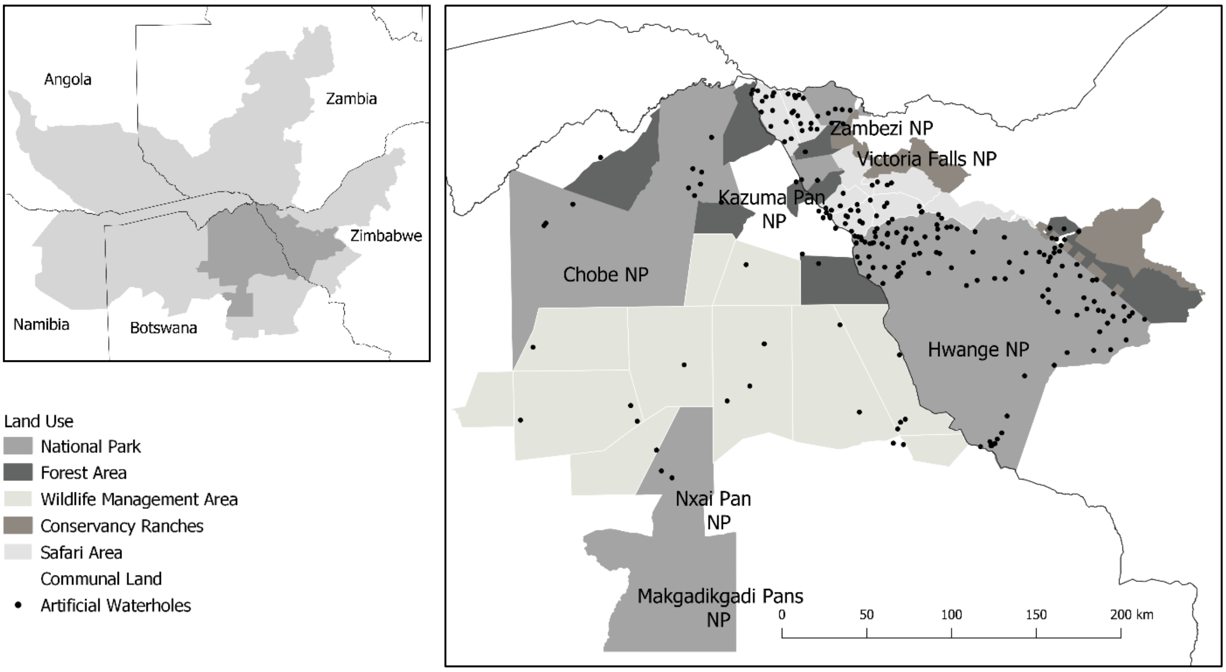


Figure 3. 1. Study area with land-uses and its extent (in dark grey) within the KAZA TFCA (light grey) (top left)

Covariates

Based on *a priori* identification of natural and anthropogenic variables potentially influencing lion home range size (e.g. (Woodroffe, 2000; Loveridge et al., 2009a; Mosser et al., 2009; Henschel et al., 2016)), we assembled a suite of 14 predictor variables in three categories (biophysical, ecological and anthropogenic) to explain variability in lion home range size (Table 3. 1). In our analysis, biophysical variables consist of climate and water, ecological variables are related to soils and vegetation, and anthropogenic variables consist of land use categories and cattle densities (Elliot et al., 2014b). We accounted for covariates associated with climate (*Precipitation & Temperature*) and water by calculating distances to the nearest waterhole or perennial river *(Distance to Water)* and relative kernel density of waterholes per 100m^2 (*Water Density*) using the heatmap plugin in QGIS v.2.14 (QGIS Development Team, 2016). We generated layers relating to soil (*Carbon & Nitrogen*) and vegetation such as Normalized Difference Vegetation Index (*NDVI*), percent canopy cover (*VCF*) and included habitat classification maps for *Grassland*, *Savannah/Shrubland* and *Woodland* (Elliot et al., 2014b). We included the number of cattle per 1km^2 (*Cattle*) as a proxy for human disturbance and calculated the relative percentage of home ranges inside national parks (*PRNP*) and other protected areas (*PRPA*).

Table 3. 1. Covariates hypothesized to influence home range size

Covariate	Description	Resolution	Source
	Biophysical		
Climate			
Precipitation	Mean seasonal precipitation	1km	(Maidment et al., 2017)
Temperature	Mean seasonal temperature	5km	MODIS MOD11C3 https://modis.gsfc.nasa.gov
Water			
Distance to Water	Distance to nearest available surface water	100m	this study - euclidean distance to the nearest waterhole (rivers treated as series of waterholes spaced 100m apart)
Water Density	Relative density of surface water per 100m^2	100m	this study - kernel density estimation algorithm with 10.000m radius and a quartic (biweight) kernel
	Ecological		
Soil			
Carbon	Organic carbon concentration in g/kg soil	250m	(Hengl et al., 2015)
Nitrogen	Total nitrogen in g/kg soil	250m	(Hengl et al., 2015)
Vegetation			
NDVI	Mean seasonal Normalized Difference Vegetation Index	250m	MODIS MOD13Q1 https://modis.gsfc.nasa.gov
VCF	Vegetation Continuous Fields	250m	MODIS MOD44B http://glcf.umd.edu/data/vcf
Grassland	Closed to open Shrubland (+/-15%)	500m	(Elliot et al., 2014b)
Savannah/ Shrubland	Forest and Shrubland (50%) /grassland (50%)	500m	(Elliot et al., 2014b)
Woodland	>40%forest	500m	(Elliot et al., 2014b)
	Anthropogenic		
Cattle	Number of cattle per km^2	1km	(Robinson et al., 2014)
Protected Areas			

PRNP	Percentage of home range in National Park	this study
PRPA	Percentage of home range in otherwise protected area	this study

Lion data

From 2011 to 2016 we captured and fitted 19 pride males and 23 females over the age of four years with GPS-telemetry collars. Lions were immobilized by qualified veterinarians or highly trained staff using calling stations or when located opportunistically during the day. The date of birth was determined through physical examination of each animal during the collaring process or from project records of known age lions. Positional data was recorded at five-hour intervals with a mean GPS fix success rate of >98%. To improve accuracy in locational data while retaining the maximum number of locations, we only retained GPS fixes with a low Positional Dilution of Position (PDOP<10) (Lewis et al., 2007; Frair et al., 2010).

Home range delineation

We defined home ranges as the 95% volume contour of location data using a bivariate plug-in Matrix (Sheather and Jones, 1991) to calculate separate bandwidths for each individual lion with at least three months of positional data. While the correct choice of kernel density estimator is still debated, second generation estimators such as “solve-the-equation” plug-in are now widely recommended (Sheather, 2009; Venables and Ripley, 2013) and perform better with large datasets of auto correlated data (Gitzen et al., 2006; Walter et al., 2011). For each individual we separated the telemetry data per year and season (dry season from 1st of April until 31st of October; wet season from 1st of November until 31st of March) which resulted in 54 discrete dry season home ranges (21 male, 33 female) and 63 discrete wet season home ranges (28 male, 35 female).

To improve home range estimates we excluded any unusual (non-residential) movements, such as a male pride takeover, by applying a biologically informed threshold model (Weston et al., 2013). We calculated the average expected and maximum ranging distances of ten breeding and therefore resident females from the centroids of their home ranges. We compared the seasonal movement data of each individual against the female threshold model by calculating net squared displacement (NSD; (Bunnefeld et al., 2011)). Movement was determined non-residential if an individual exceeded the maximum ranging distance and did not return within expected ranging distance for a period of one month. All positional data determined non-residential were subsequently excluded from further home range analysis.

Variance partitioning

We extracted mean values for covariates at a home range-level and used linear regression-based variance partitioning analysis (Borcard et al., 1992) to assess how variation in home range size was best explained by sets of covariates per sex and season. Variance partitioning provides the means to measure the effects of independent and confounded sets of explanatory factors on a common response variable and has been successfully applied in ecological studies (Watling et al., 2015; Timm et al., 2016).

In Variance partitioning, all combinations of possible regression models are calculated and then hierarchically classified to determine the relative contribution of independent variables or groups of variables. The total variance explained is then decomposed into the contributions of those independent variables/groups of variables as well as joint contributions (Mac Nally, 1996).

We used a two-tier hierarchical variance partitioning approach (Cushman and McGarigal, 2002) to first measure the variation in home range size explained by main effects defined as biophysical, ecological and anthropogenic sets of covariates and second to measure the independent and joined effects of covariates nested within the first tier decompositions following the structure in Figure 3. 2**Error! Reference source not found.**. Using the "varpart" function in the R package "vegan" (Oksanen et al., 2013; R Core Team, 2018) we extracted first-tier decompositions and then partitioned their conditional and marginal effects (*sensu* (Cushman and McGarigal, 2002)) at the second tier. This resulted in nine discrete components explaining variation in home range size at the second tier (i.e., *climate* & *water* and their joint effect, *soil* & *vegetation* and their joint effect and *cattle* & *protected area* and their joint effect; Figure 3. 2).

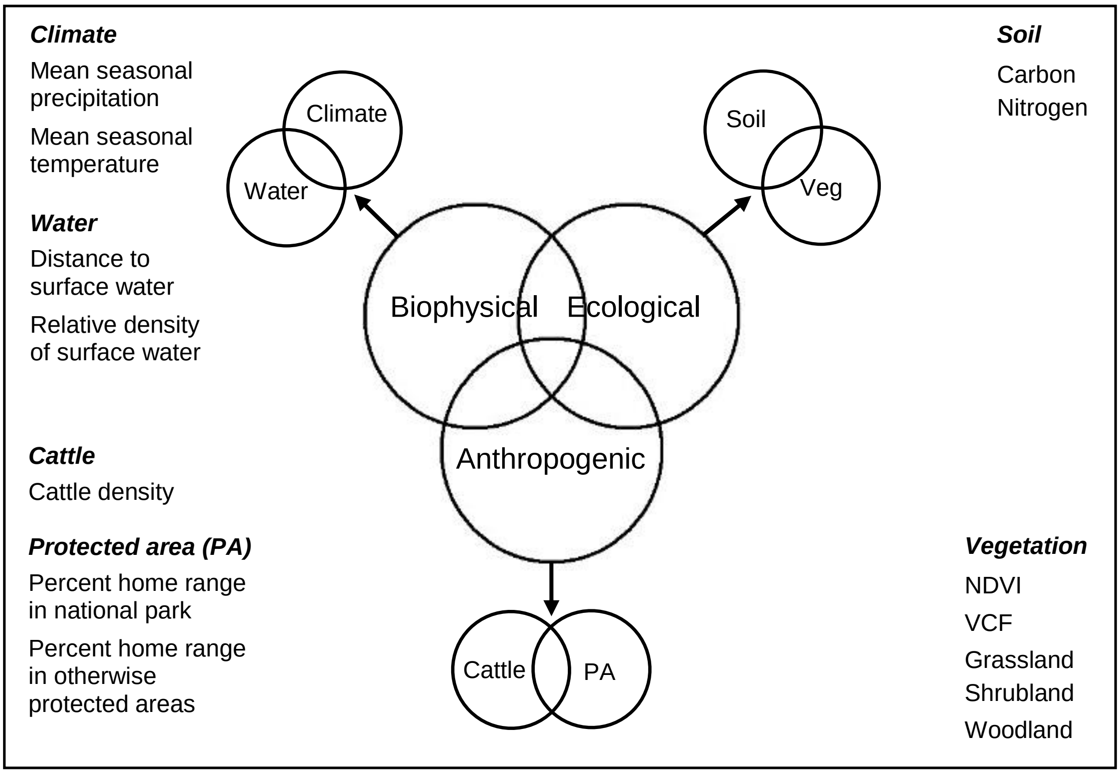


Figure 3. 2. Two-tier hierarchical variance partitioning of drivers of lion home range size

Generalized Linear Mixed Models

To investigate effect size and sign of individual variables best explaining home range size for each sex and season we used univariate generalized linear mixed models (GLMMs) with a gamma distribution and a log-link function to evaluate the direction and magnitude of relationships between home range size and covariates. We incorporated a random factor into our models to account for repeated sampling from individuals and used a gamma error distribution as home ranges assume continuous, non-negative values and often show positively-skewed errors (Kenward, 2000). Using the “lme4” package in R (Bates et al., 2014) we created separate home range models per sex and season, including all candidate variables as fixed effects, considered polynomial relationships and tested for collinearity between variables using Variance Inflation Factor (VIF). All variables were standardized to zero mean and unit standard deviation, allowing direct comparison of effect sizes. We stepwise eliminated covariates with the highest VIF values until the remaining ones dropped below the value of 5. We assessed the significance of each fixed effect term by dropping each higher-level term from the global model, using likelihood ratio tests (LRT).

Results

With 454.8 ± 62.6 km^2 in the dry season and 430.1 ± 53.2 km^2 in the wet season, our results showed no significant difference in average home range sizes for females between seasons (GLMM: $\beta_{wet} = 0.04$, SE = ±0.11, t = 0.39, p = 0.69) or males in the dry season (356.9 ± 50.9 km^2). At 575.2 ± 74.5 km^2 average male home range size in the wet seasons was significantly larger and showed more variation than female home range size in both seasons and male home range size in the wet season (GLMM: $\beta_{wet} = 0.39$, SE = ±0.15, t = 2.57, $p < 0.05$).

Variance partitioning

Female dry season

A large majority of the total variation in dry season female home ranges size was explained by all covariates (74.4% with 25.6% of the variation unexplained). The total variation explained by the three different sets of variables showed a moderate degree of collinearity (Figure 3. 3). The marginal explanatory power, or total effect not excluding covariation with other factors, of

(1) biophysical covariates was 48.5% of total variation in home range size, (2) ecological covariates was 26.9% and (3) anthropogenic variables was 6.7%. In contrast, their conditional effects, the amount of variance explained uniquely by that set of variables after removing the variance jointly explained by other variables, was (1) 38.3% for biophysical variables, (2) 16.5% for ecological variables and (3) 13.8% for anthropogenic variables. Note that logically the conditional effect cannot be smaller than the marginal effect, as the conditional effect is a component of the marginal effect and variance explained cannot be negative. The smaller marginal effect of anthropogenic variables is due to calculated negative variance explained in the interactive components, which can occur when there is complex nonlinearity or collinearity among variable sets (Legendre, 2008).

At the second tier of partitioning of female dry season home range variance, we interpret only the conditional components of the second tier not removing the covariation with the other groups (conditional-marginal), given the many negative variance values in the conditional-conditional components. Water completely dominated the effect of biophysical variables both marginally (in interaction with anthropogenic and ecological variables) and conditionally (after removing the variance jointly explained by anthropogenic and ecological variables). This suggests that climatic variation has negligible influence on female dry season home range, but that water availability is highly important.

Among ecological variables, both soils and vegetation had substantial explanatory ability, with soil having roughly twice the independent effect of vegetation, but about half the effect of water. Among anthropogenic variables cattle density had a much larger independent effect than did protected area extent (approximately 2.5 times more variance explained), but less than the independent effects of vegetation (proportionally 80% as explanatory) or soils (49.7% as explanatory). The strong relationship between home range size and water was mainly driven by average distance to surface water (*Distance to Water*), with larger home ranges further from water sources (Figure 3. 4). For ecological factors home range size decreased with an increase in soil productivity (increase in *Carbon* and *Nitrogen* levels) and an increase in the proportion of *Savannah*/*Shrubland* per home range. Home range size was lowest for moderate *NDVI* values and highest for very low and very high levels of *NDVI* which correspond to very dry habitat and dense woodland. Amongst anthropogenic factors cattle accounted for the majority of variation explained with home range size smallest in areas with high cattle densities (*Cattle*).

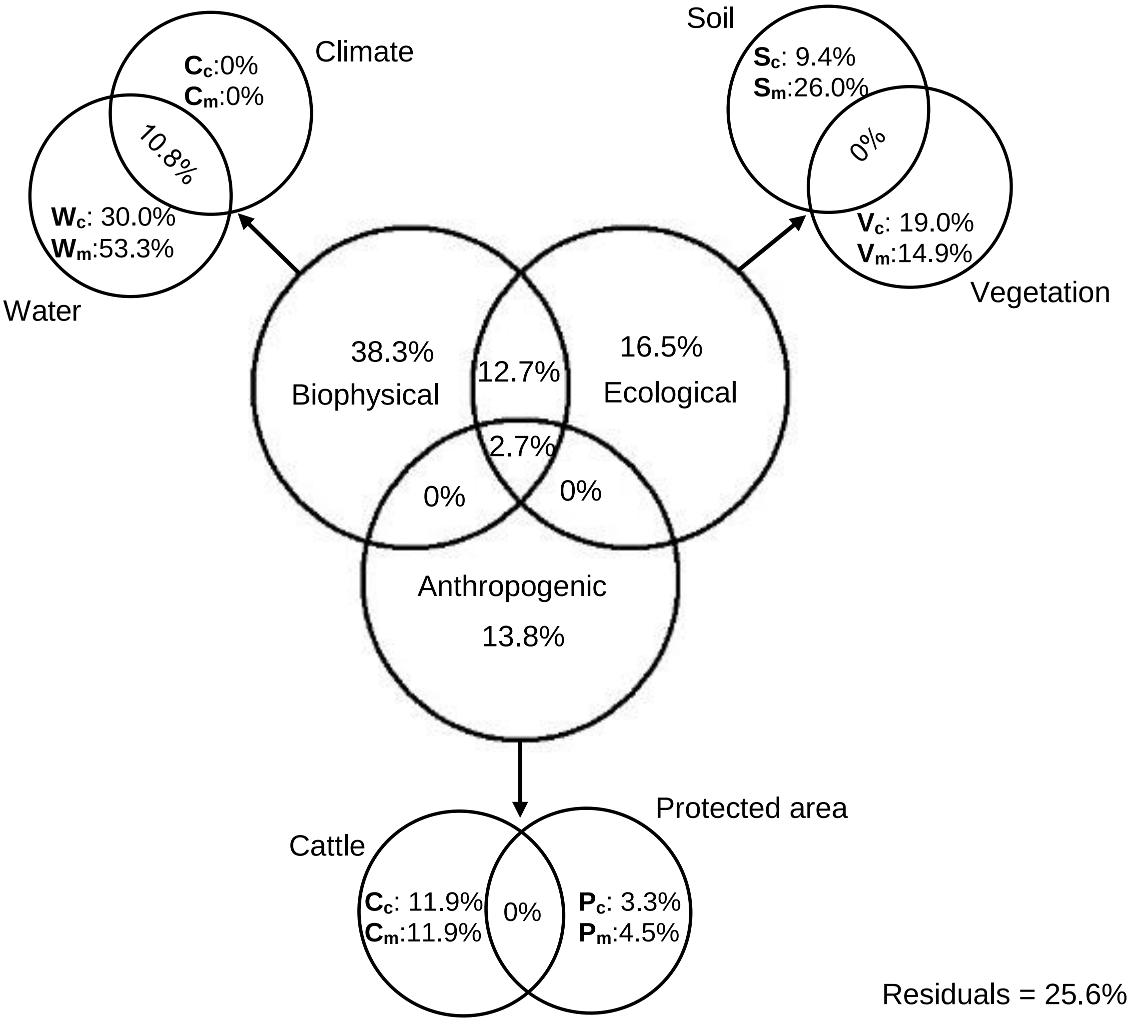
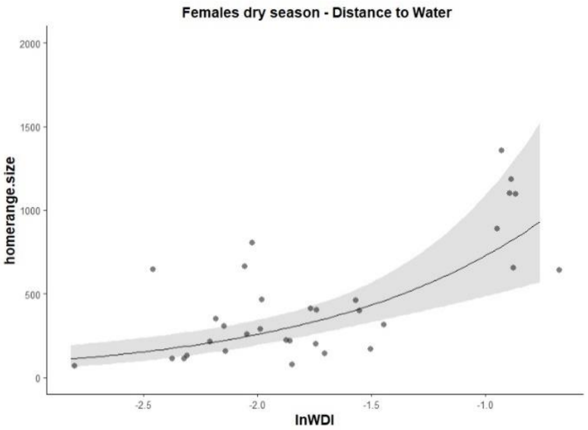
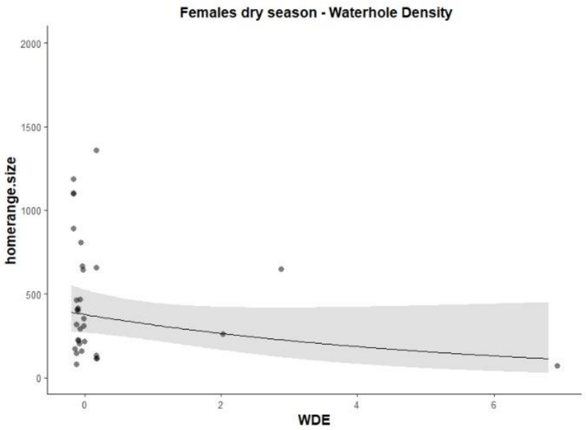


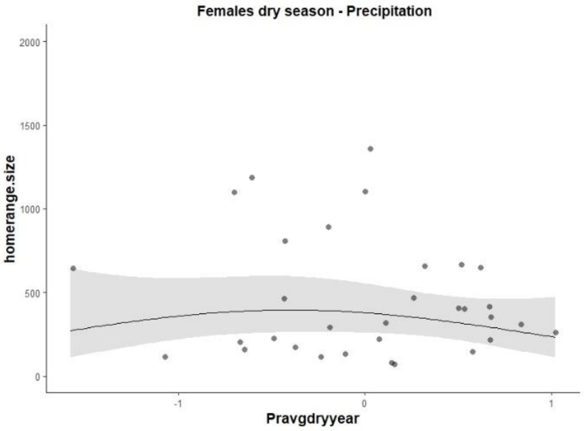
Figure 3. 3. Hierarchical variance partitioning of drivers of female lion home range size in the dry season. Second-tier conditional decomposition at the top, marginal decomposition at the bottom

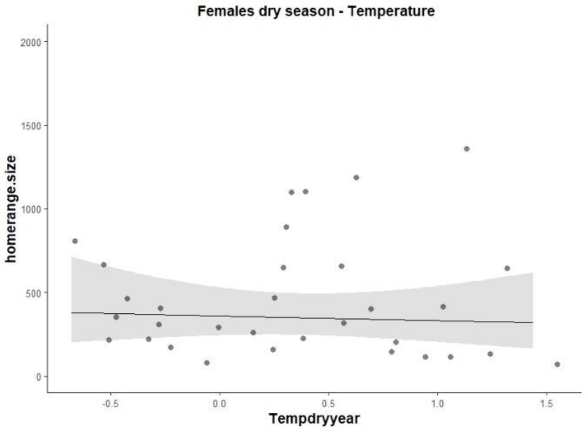
Water



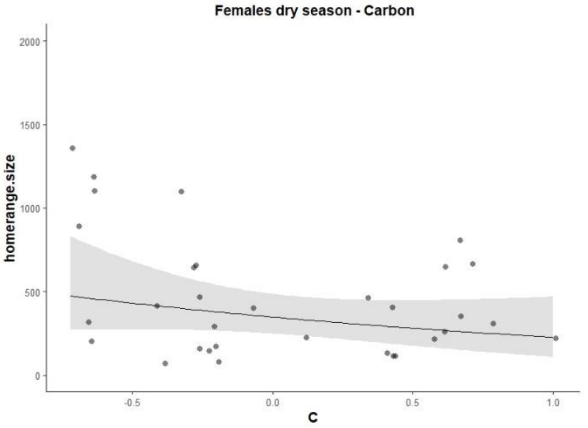


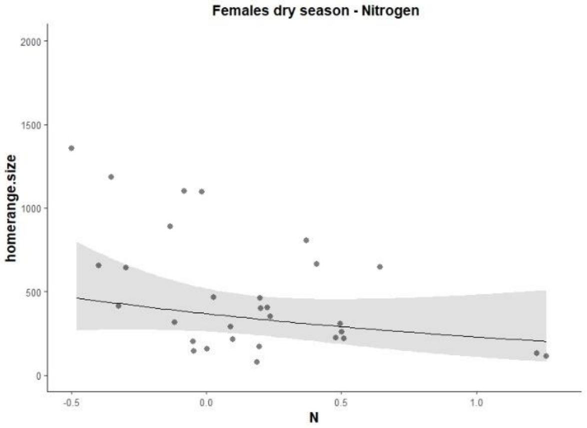
Climate



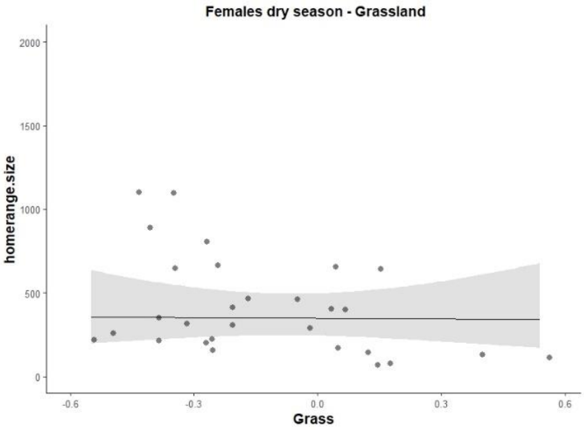


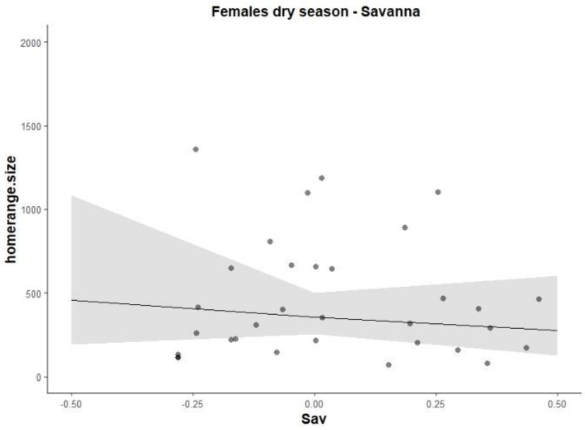
Soil

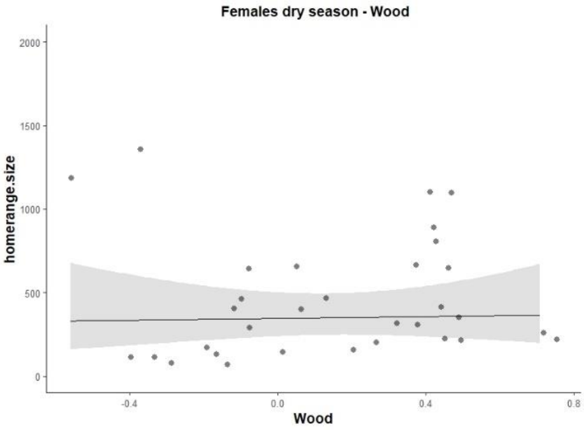


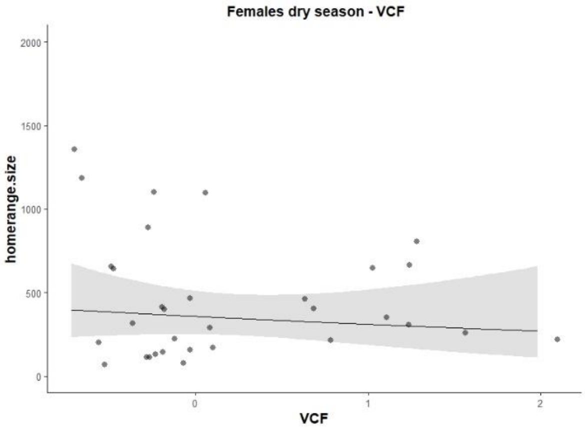


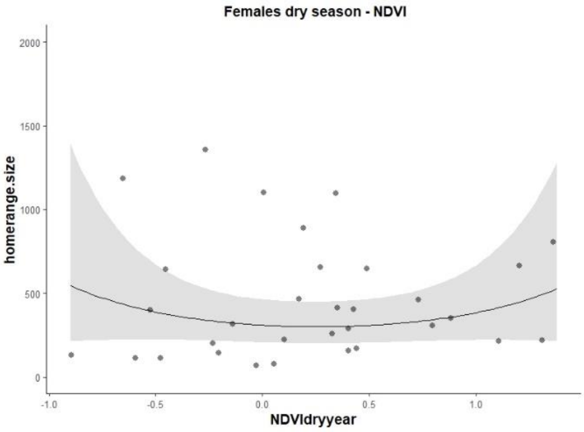
Vegetation



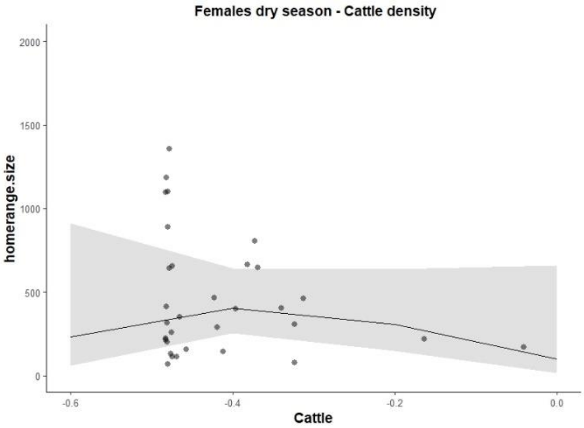


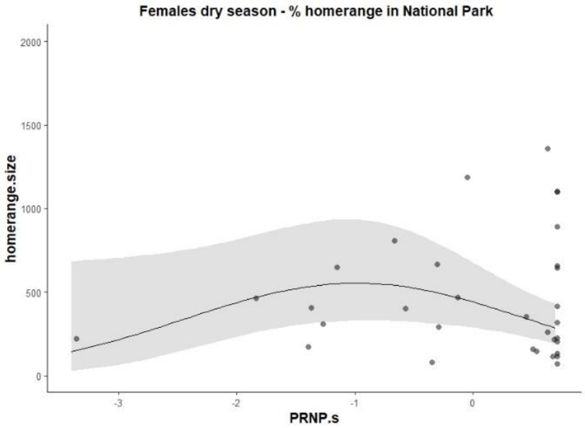






Cattle/Protected Area





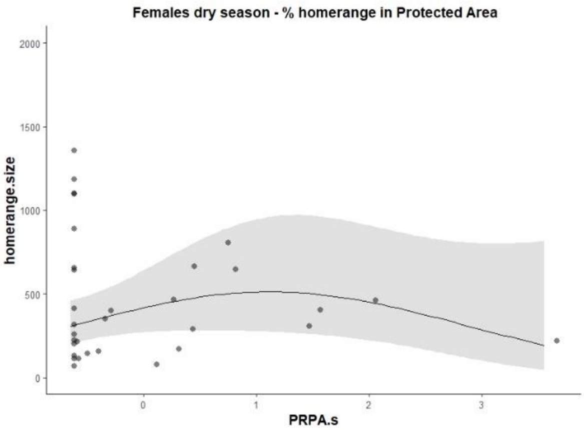


Figure 3. 4. Direction and magnitude of relationships between standardized covariates included in variance partitioning and female home range size in the dry season

Female wet season

A total of 69.2% of the total variation in female wet season home range size was explained by the full set of predictor variables, which was 5.2% lower than the total variation explained by same set of variables for the dry season. The first tier partitioning for females in the wet season is difficult to interpret given several large negative components of explained variance. Interpreting the conditional, or independent, components, biophysical variables had the largest effect, followed by anthropogenic (with explanatory ability 32.7% as great as biophysical variables), and ecological variables (explanatory ability 16.6% as great as biophysical variables).

At the second tier of female wet season partition, again we interpret only the conditional-marginal terms (conditional at the second tier but including variance jointly explained by variables in other first tier groups). As in the dry season model, water dominated the effects of biophysical variables, with climate having only 8.8% of the explanatory ability as water. Among ecological variables, soil and vegetation were similar in their independent explanatory ability, and were much less explanatory than water (8.8% and 12.2% as explanatory, respectively). Neither cattle density nor protected area extent had any positive variance explained in the second tier conditional-marginal partitioning.

Female wet season home rage size increased with growing *Distance to Water* and decreased with *Waterholes Density* (Figure 3. 6). Average home range size decreased with an increase in highly productive *Grassland* and increased with an increasing proportion of nutrient poor *Woodland* per home range. Home range size correlated negatively with cattle density (*Cattle*) and to lower degree was dependent on protection status when comparing with dry season.

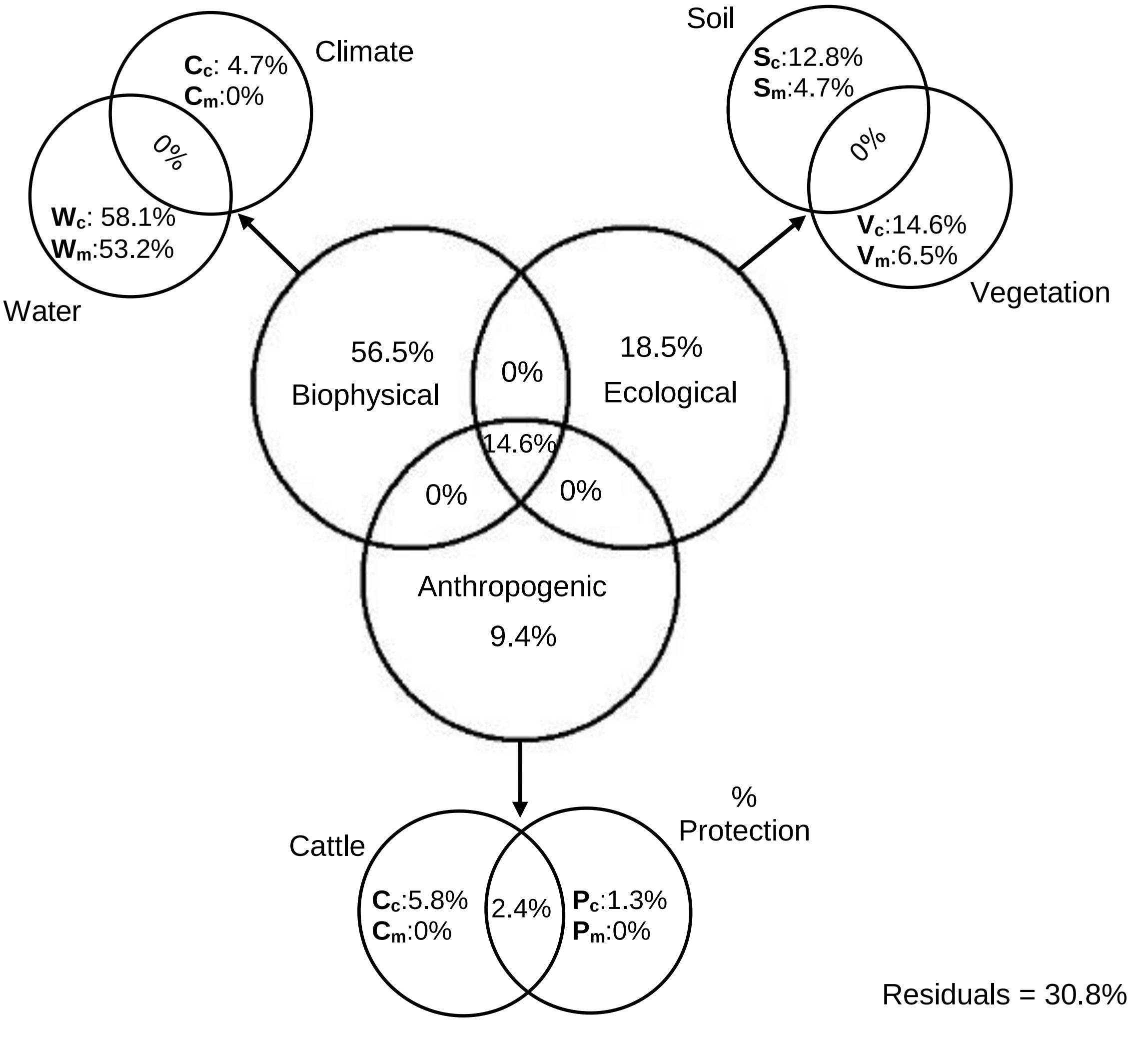
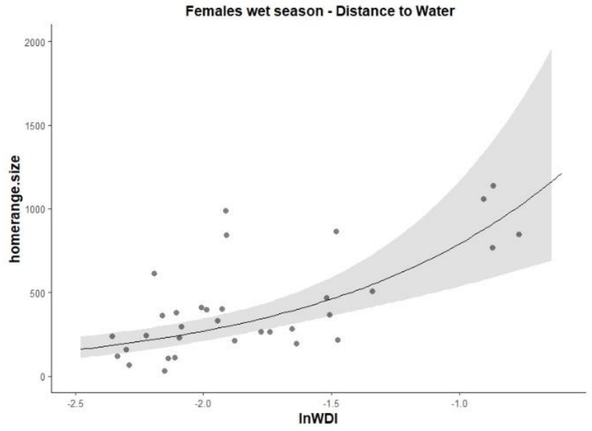
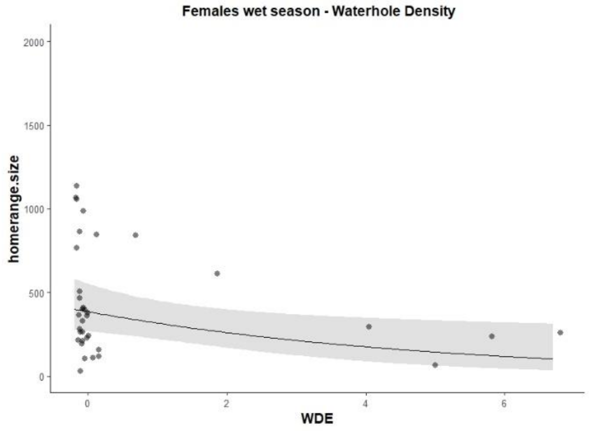


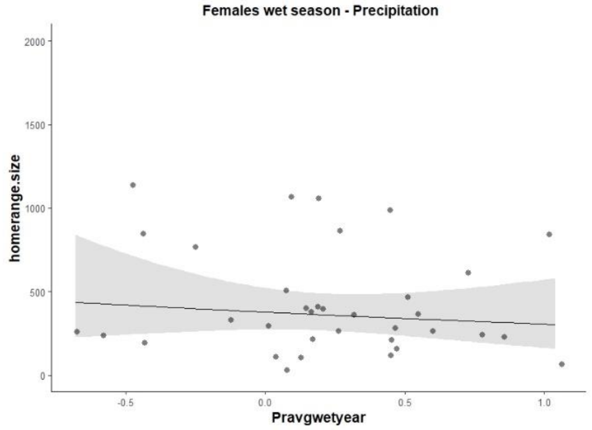
Figure 3. 5. Hierarchical variance partitioning of drivers of female lion home range size in the wet season. Second-tier conditional decomposition at the top, marginal decomposition at the bottom

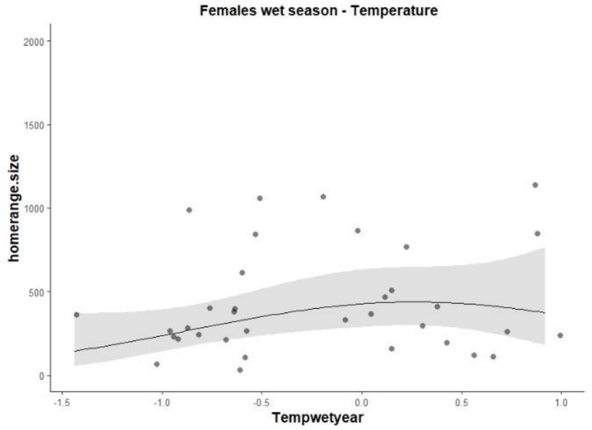
Water





Climate





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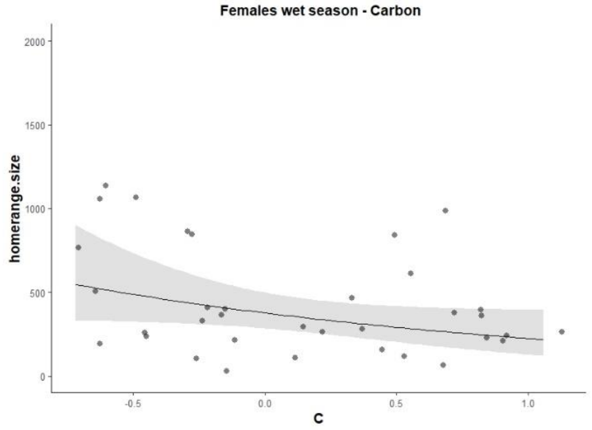
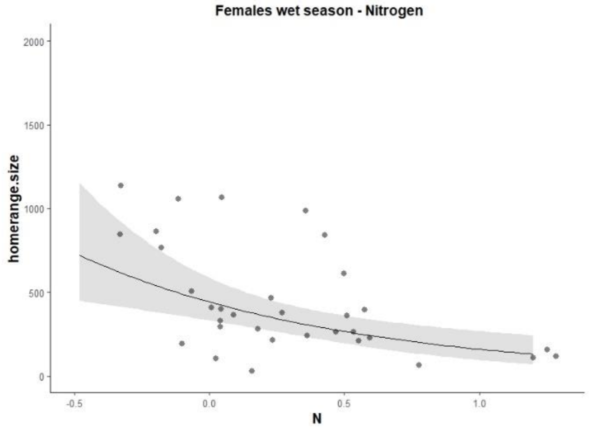
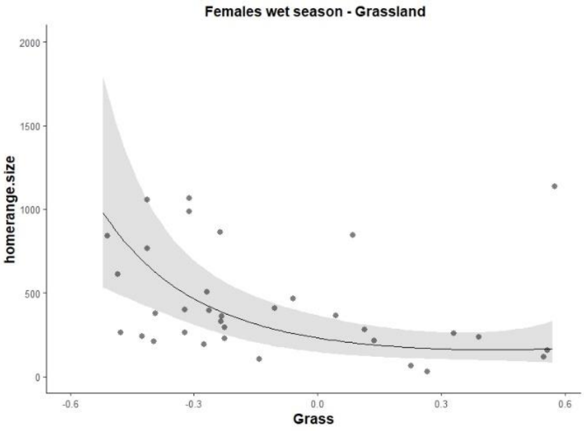
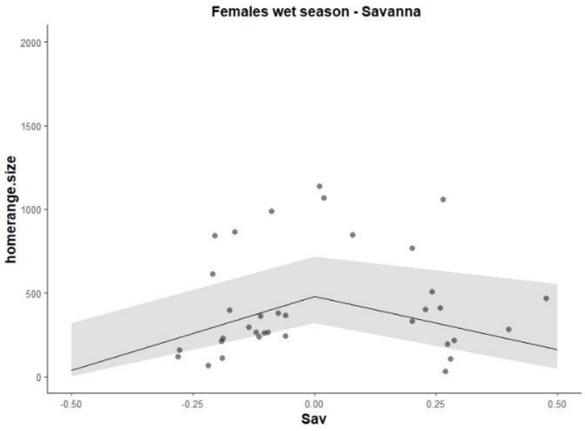
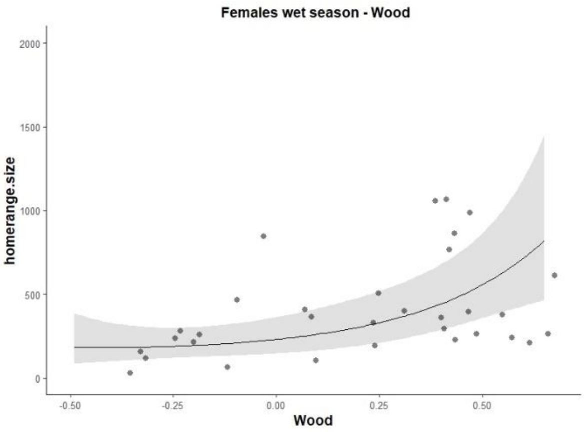


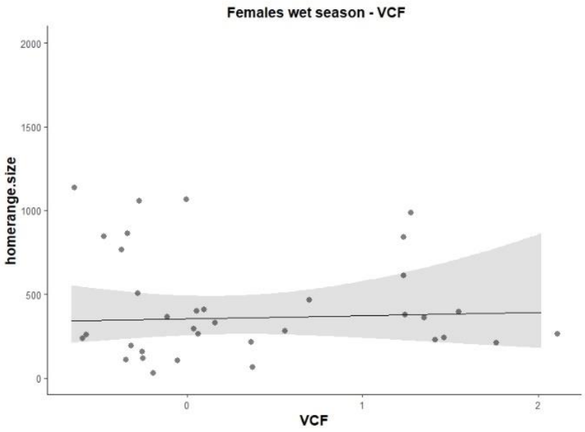


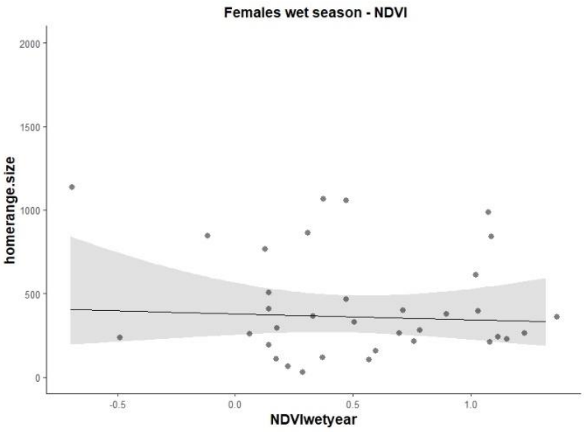
Vegetation



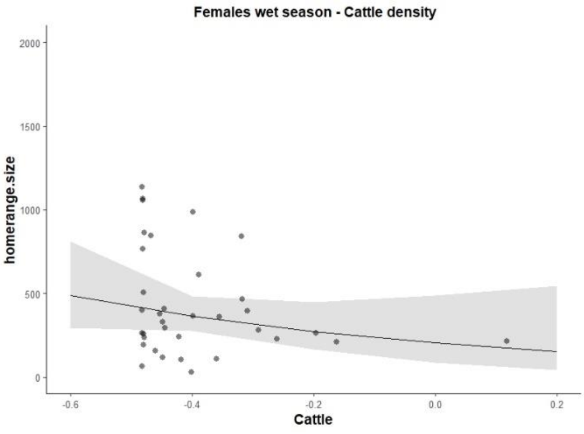


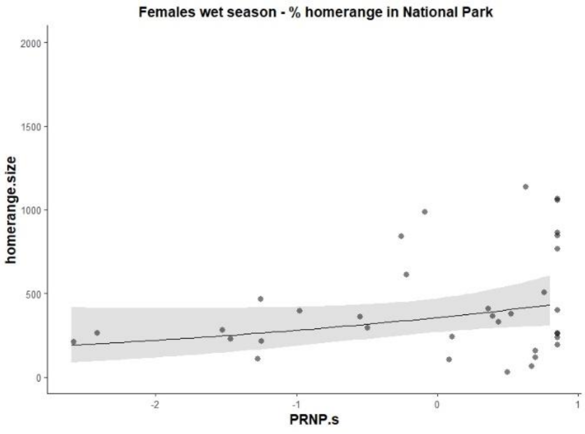






Cattle/Protected Area





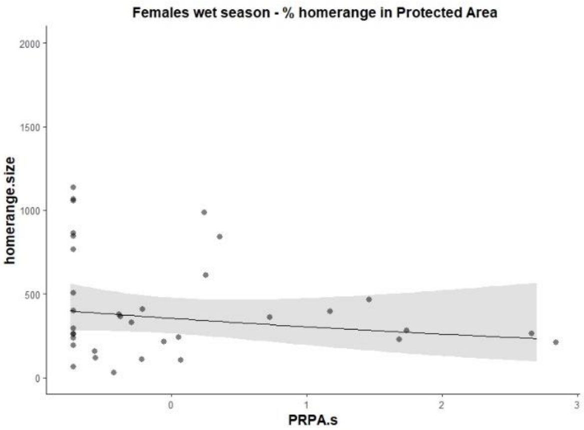


Figure 3. 6. Direction and magnitude of relationships between standardized covariates included in variance partitioning and female home range size in the wet season

Male dry season

The total variation in male dry season home range size explained by all covariates (66.4%) was markedly lower than for females in the same season. As in the case of females in the wet season, due to substantial negative variance components in the first tier, we only interpret the independent (conditional) first tier components. As in the case of females in both seasons, biophysical factors had the largest effect, (37.6% independent explanatory ability). However, unlike either of the female wet season models ecological variables also had substantial explanatory power (30.5% total variance explained, and 81% as explanatory as the independent effect of biophysical variables). Anthropogenic variables had the smallest independent effects (31.6% as explanatory as independent effects of biophysical variables.

At the second tier, again interpreting the conditional-marginal effect, we see that the there is no independent explanatory ability of climate, and water fully dominates the explanatory power of biophysical variables. Among ecological variables soil is approximately twice as explanatory as vegetation, and neither cattle density nor protected area extent had a positive explanatory ability (Figure 3. 7).

Home range size increased substantially with an increase in average distance to surface water (*Distance to Water*) and steeply declined with an increase in surface water availability

(*Water Density*) (Figure 3. 8). Similar to female home ranges in the dry and wet season, male dry season home ranges declined with an increase in soil productivity (*Carbon* and *Nitrogen*).

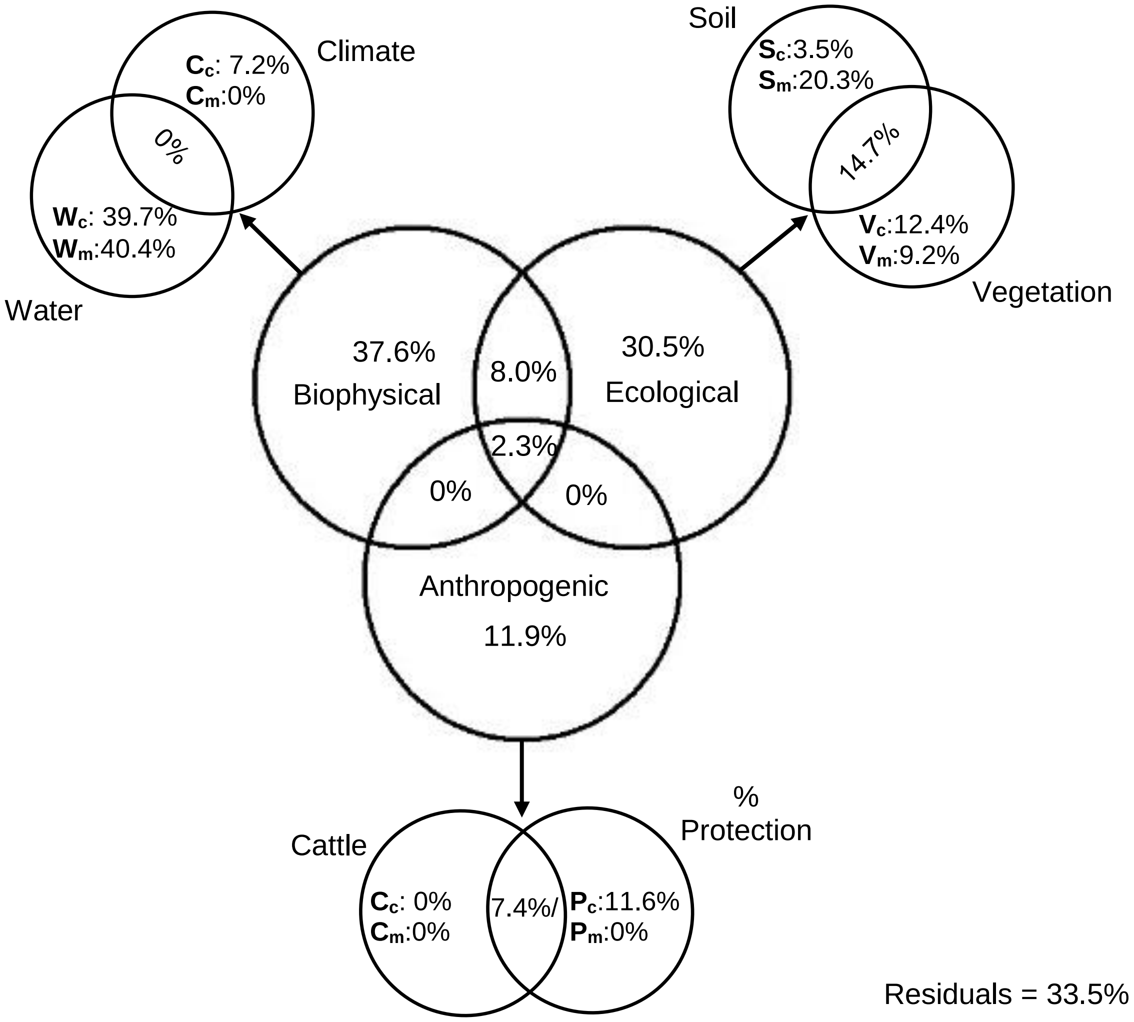
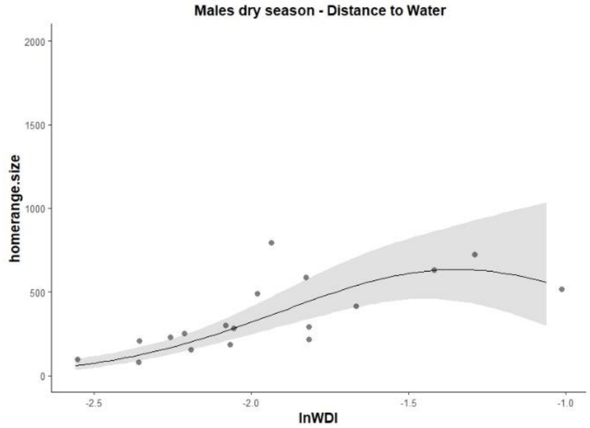
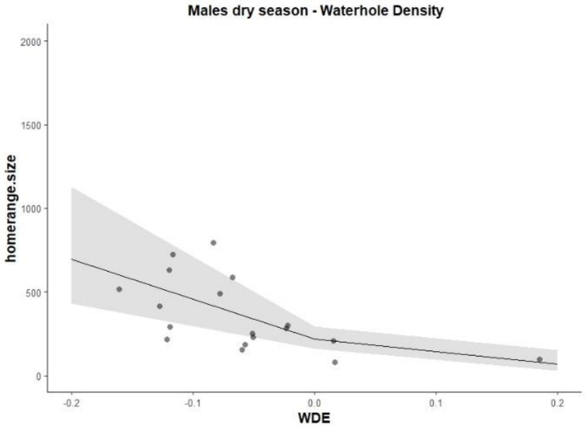


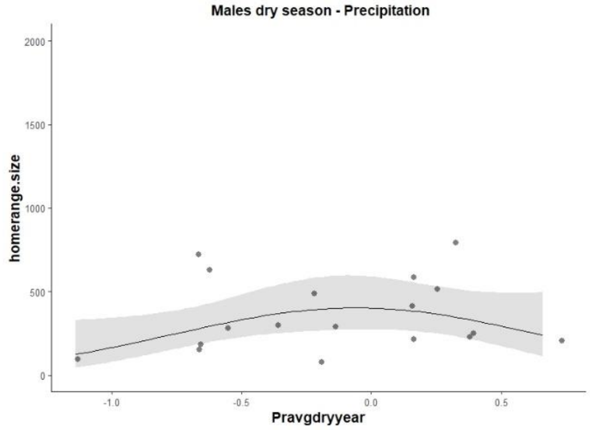
Figure 3. 7. Hierarchical variance partitioning of drivers of male lion home range size in the dry season. Second-tier conditional decomposition at the top, marginal decomposition at the bottom

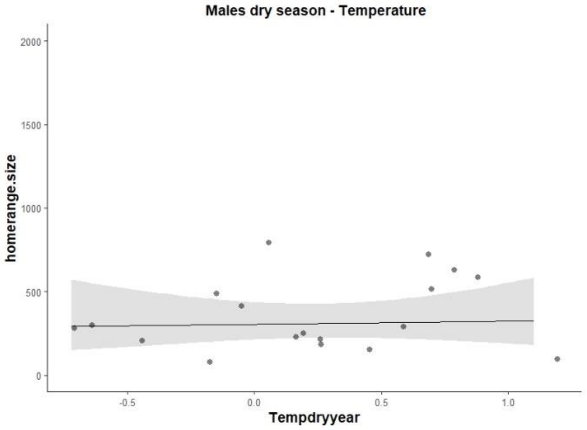
Water


Males dry season - Distance to Water

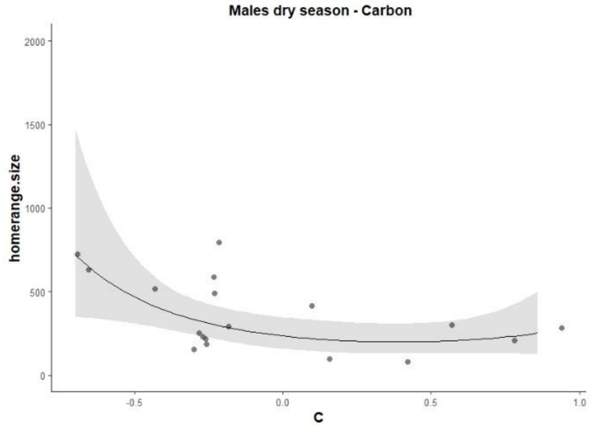

Males dry season - Waterhole Density

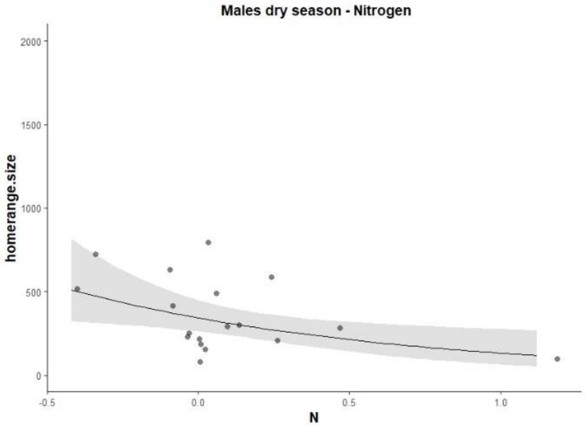
Climate


Males dry season - Precipitation

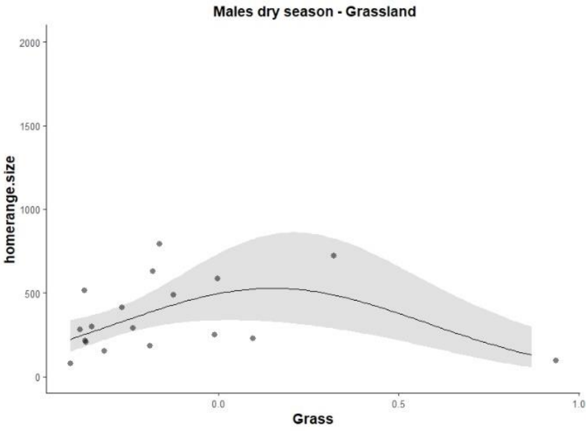

Males dry season - Temperature

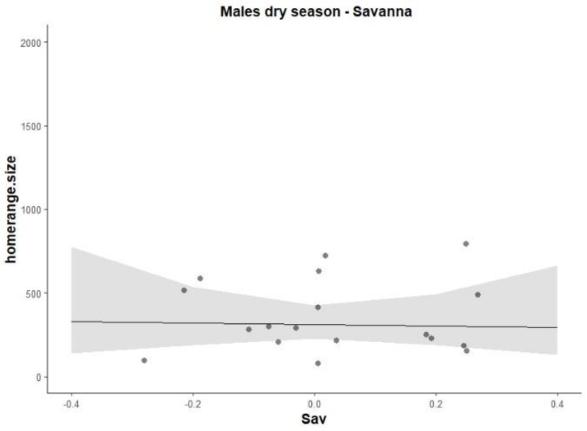
Soil

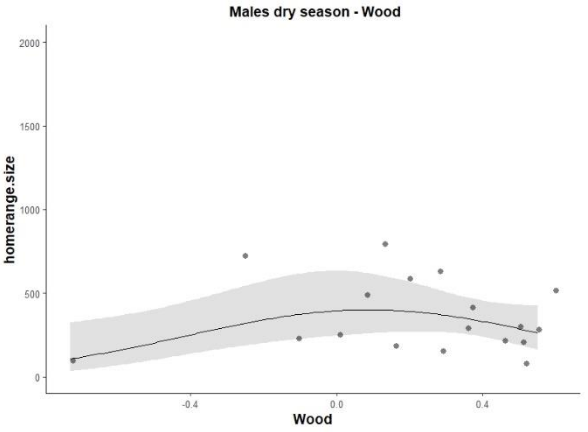

Males dry season - Carbon

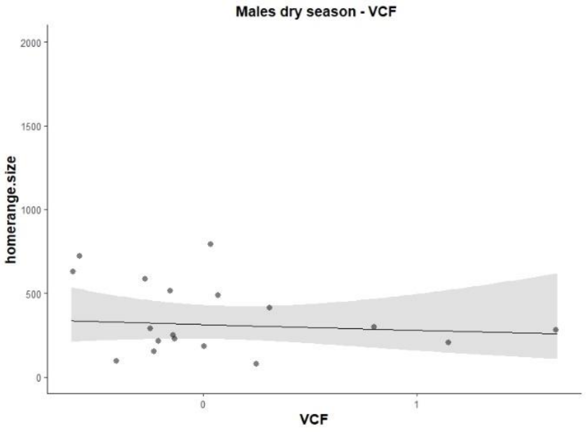

Males dry season - Nitrogen

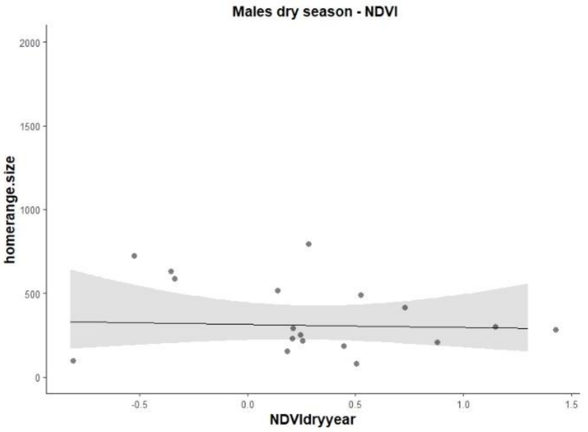
Vegetation



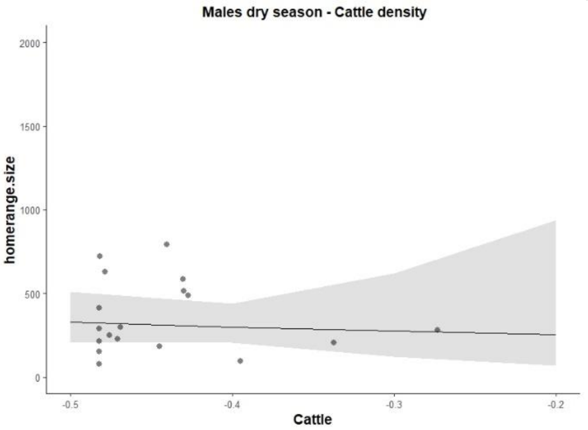


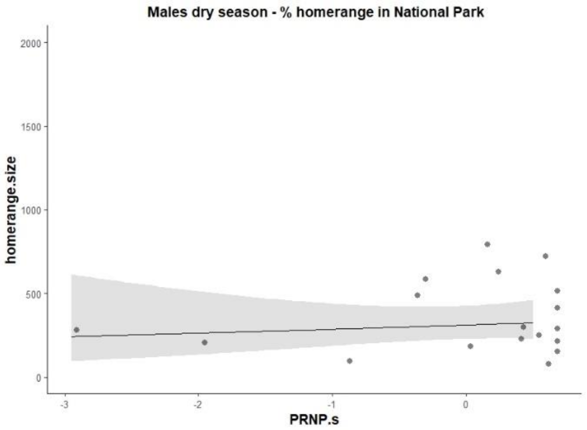






Cattle/Protected Area





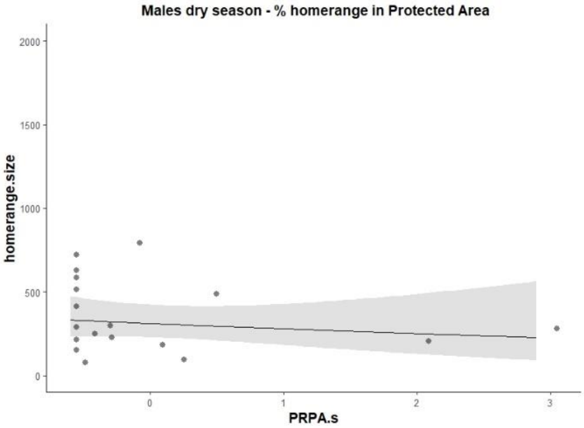


Figure 3. 8. Direction and magnitude of relationships between standardized covariates included in variance partitioning and male home range size in the dry season

Male wet season

The total variation in home range size explained for the wet season was 73.1% with 26.8% of the data unexplained. Biophysical and ecological covariates jointly explained 50% of variance in males wet season home ranges (Figure 3. 9). In addition, the conditional (independent) explanatory ability of biophysical variables was 17.9%. Anthropogenic and ecological variables had no independent (conditional) explanatory ability at the first tier of the partitioning, but as noted above, ecological variables jointly explained 50% of home range size along with biophysical variables.

At the second tier of the male wet season partitioning, again only interpreting the conditional-marginal variance components, water again fully dominated the effect of biophysical variables, with no positive variance explained by climate. Vegetation explained approximately twice as much independent variance as soils (in the ecological variables second tier partitioning), and about 2/3 as much as water variables did. Among anthropogenic variables, only protected area extent explained a positive amount of independent variance, and about 10% as much as water variables.

Home range size increased substantially with an increase in average distance to surface water (*Distance to Water*) (Figure 3. 10) and decreased with increase in *Water Density*. Both soil and vegetation covariates had an effect on home range size with average male home range size declining with an increase in habitat productivity. This relationship is reflected by the negative response to high levels of *Carbon* and *Nitrogen* and increasing proportions of productive *Grassland* and *Savannah/Shrubland* per home range and further by an increase in average home range size with an increasing proportion of nutrient poor *Woodland*. Average home range size of wet season male lions increased with increase in cattle density and home ranges were larger in national parks.

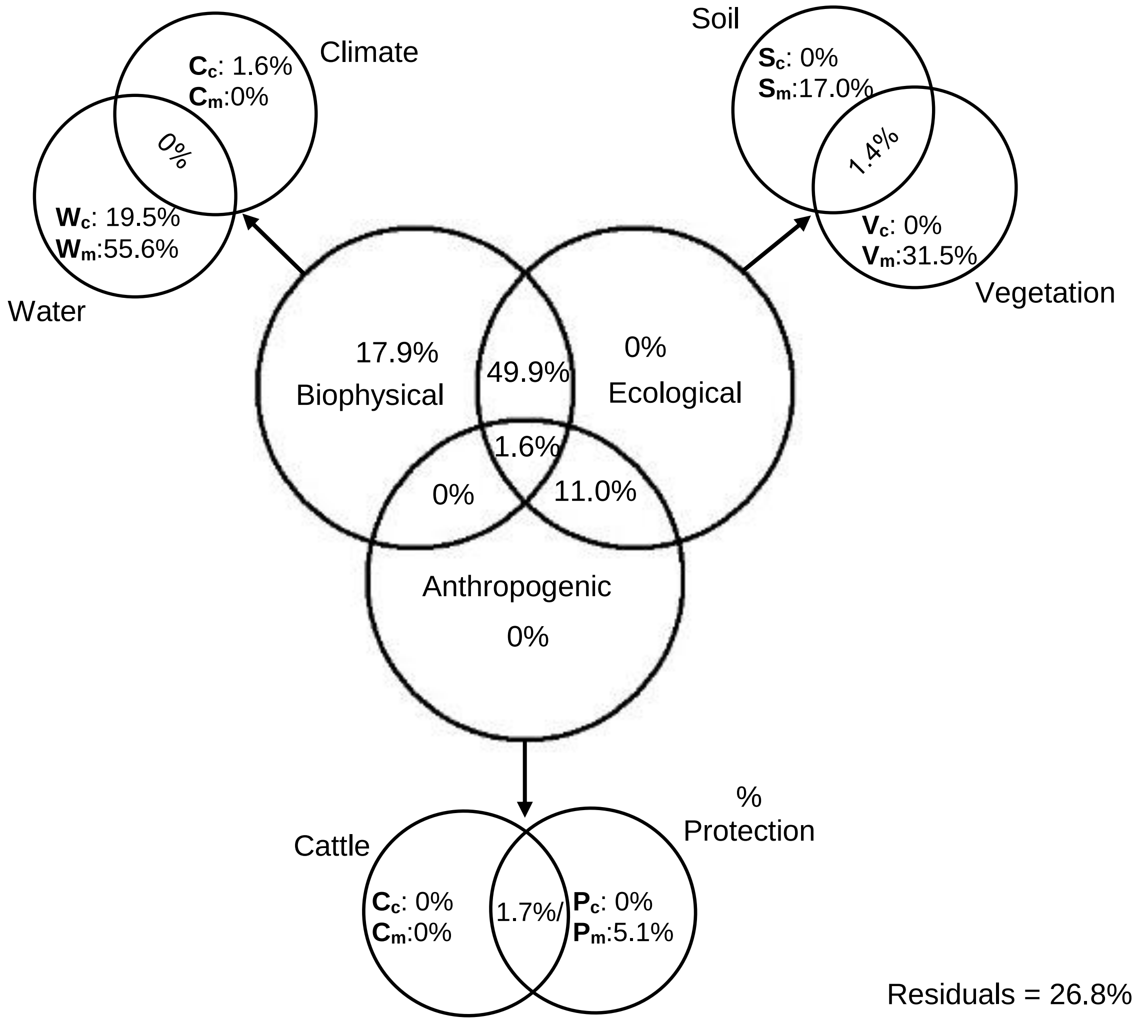
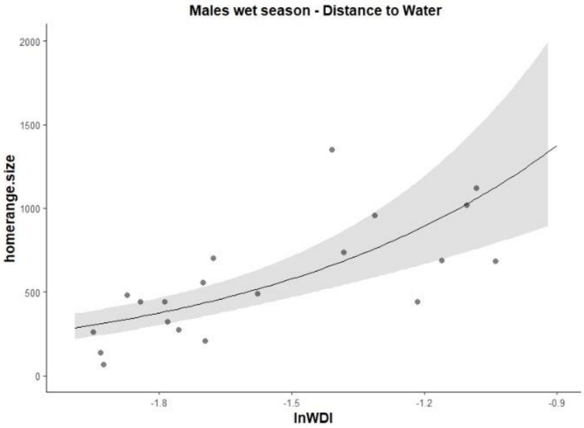
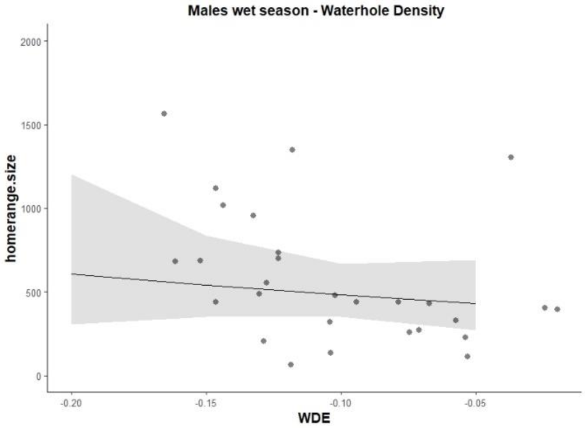


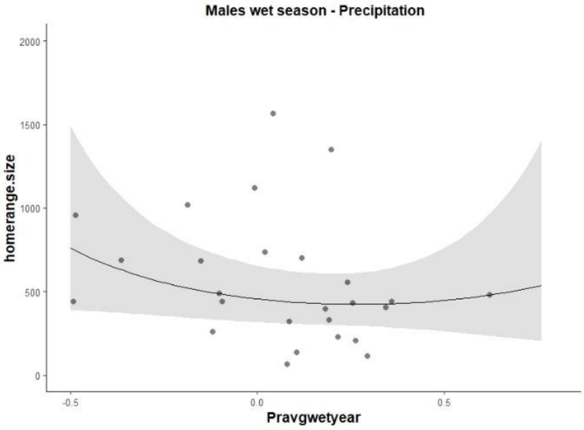
Figure 3. 9. Hierarchical variance partitioning of drivers of male lion home range size in the wet season. Second-tier conditional decomposition at the top, marginal decomposition at the bottom

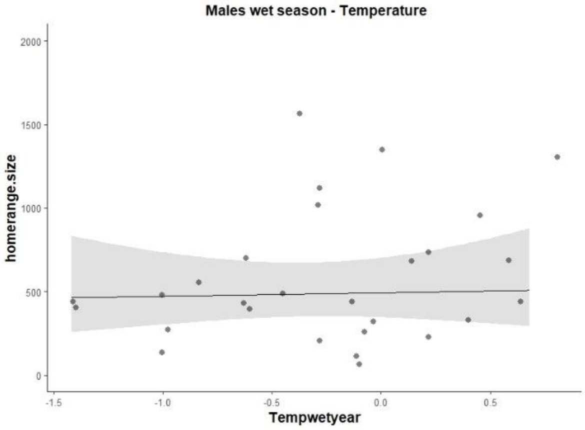
Water



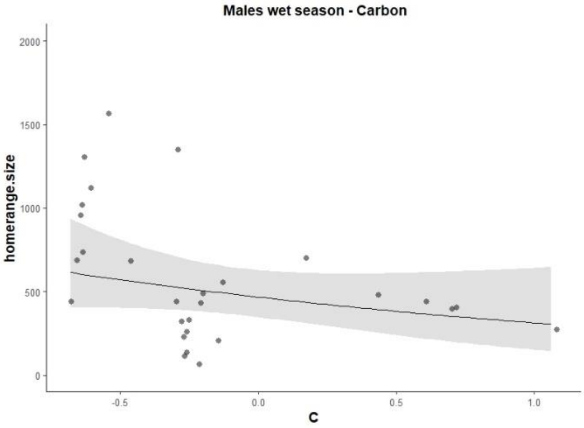


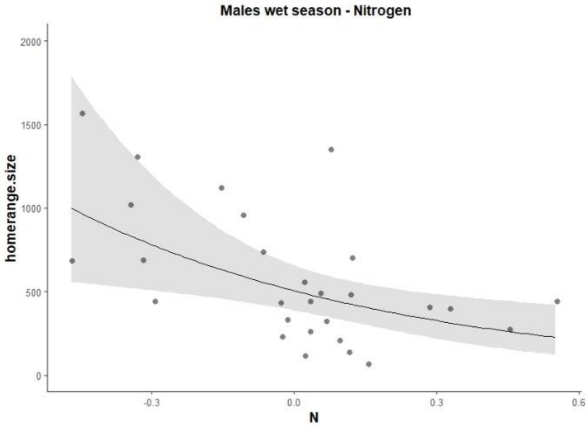
Climate



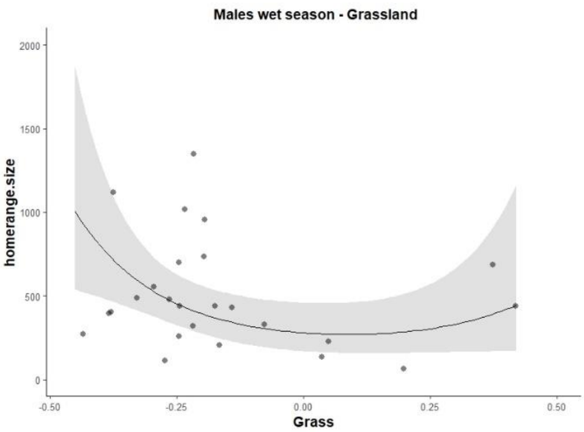


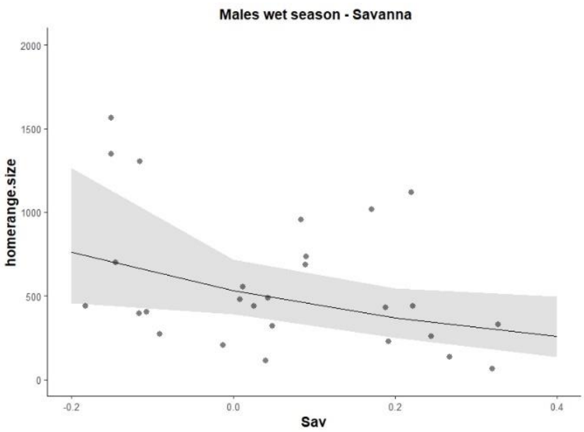
Soil

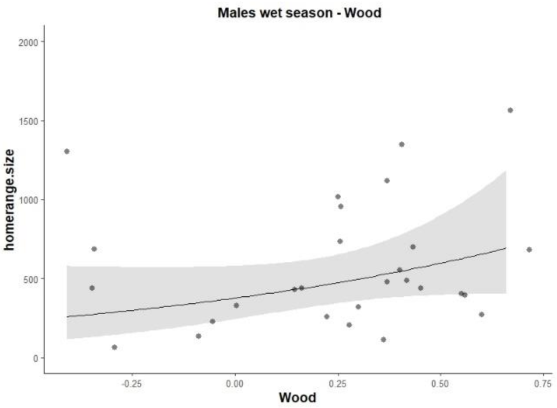


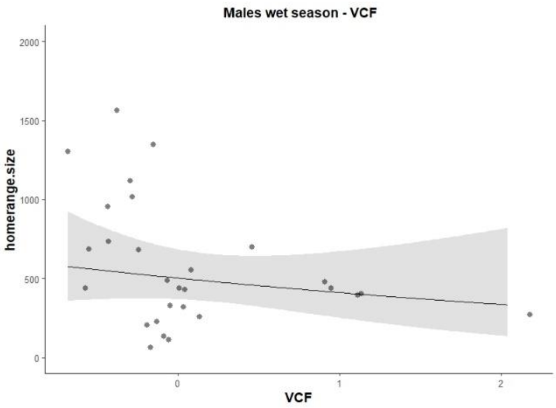


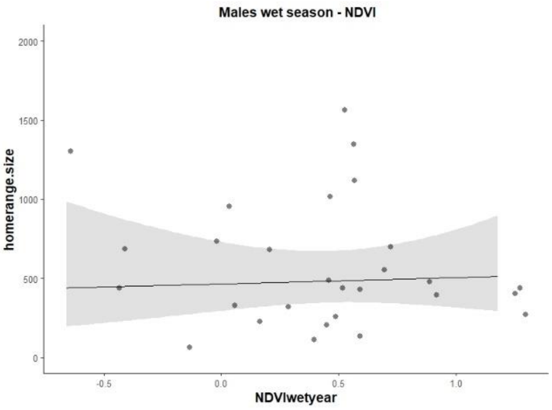
Vegetation



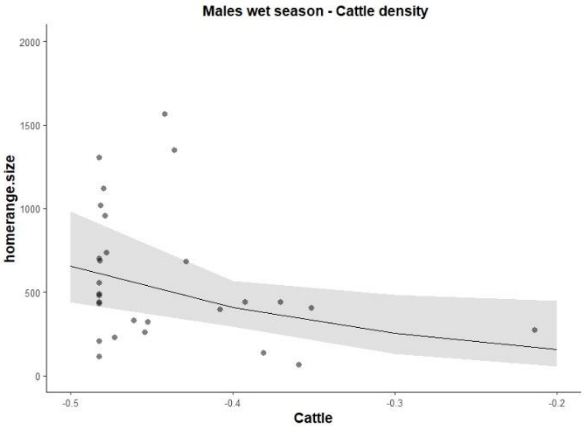


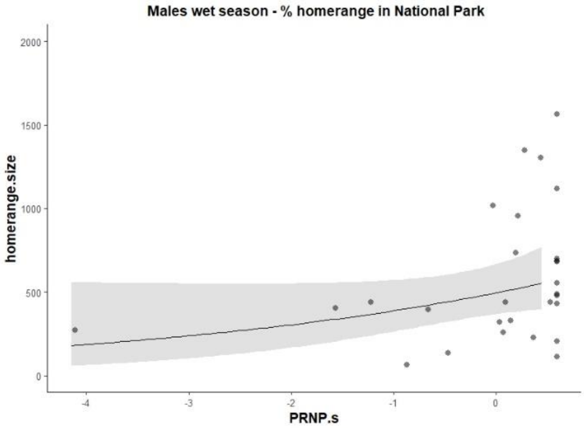






Cattle/Protected Area





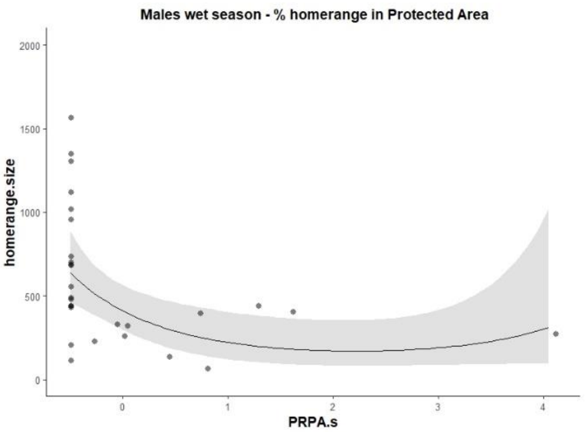


Figure 3. 10. Direction and magnitude of relationships between standardized covariates included in variance partitioning and male home range size in the wet season

Home range size GLMM models

The best multivariate generalized linear mixed-effect models showed large differences in the set of variables retained and the extent of their effects on lion home range size across seasons and sexes. The female home range size in the dry season was best explained by only two variables: *Distance to Water* and *Cattle density* as a quadratic effect (Table 3. 2 **Table 3. 2**), with the home range size non-linearly decreasing with cattle density and increasing with an increase in average distance to surface water. Female home range size in the wet season was best explained by completely different and larger sets of variables including *Temperature*, *Nitrogen*, *VCF* and percentage of home ranges in protected area (*PRPA*). Despite the large contribution of water in the variance partitioning, *Distance to Water* and *Water Density* were not retained in the final model. Home range size showed a moderate non-linear increase with rising average wet season temperature, a strong inverse relationship with increasing soil productivity (increasing nitrogen content) and a positive relationship with the amount of tree cover (*VCF*). The effect of protection status (*PRPA*) was positive but the weakest amongst all variables (Table 3. 3).

The top model for male home range size in the dry season size only included *Water Density* and *Nitrogen* (Table 3. 4), with the negative effect of water density on home range size being eight times stronger when comparing to the positive effect of soil productivity. Water also had a large influence on the size of male wet season home range size, with the top model including, amongst other variables, both *Distance to Water and Water Density* as factors strongly related to increasing home range sizes, with home range size inversely associated with water density and positively associated with distance to water (Table 3. 5). Across all variables, *Cattle* exhibited the highest and negative effect on the male home range size in this season. Furthermore, the home ranges showed moderate decrease in size with an increase in habitat productivity (*Carbon* & *Savannah/Shrubland*) and increased with increasing amounts of *Woodland*.

Table 3. 2. Female dry season: Fixed effects output from generalised mixed-effects model describing home range size as a function of environmental covariates and individual. Estimated effect sizes (β - values are exponential) and their standard errors are presented, with significance of removal of term assessed using likelihood ratio tests

				Likelihood Ratio Test	
	β	SE	df	$\chi 2$	Pr($\chi 2$)
(Intercept)	7.88	0.39			
Distance to Water	1.16	0.21	1	14.84	<0.001
poly(Cattle, 2)1	-0.37	0.21	2	6.54	0.037
poly(Cattle, 2)2	-1.56	0.61			

Model statistics: Marginal R2 0.56, Conditional R2 0.85

Table 3. 3. Female wet season: Fixed effects output from generalised mixed-effects model describing home range size as a function of environmental covariates and individual. Estimated effect sizes and their standard errors are presented, with significance of removal of term assessed using likelihood ratio tests

				Likelihood Ratio Test	
	β	SE	df	$\chi 2$	Pr($\chi 2$)
(Intercept)	5.74	0.19			
poly(Temp,2)1	1.88	0.79	2	10.81	0.004
poly(Temp,2)2	-0.75	0.55			
Nitrogen	-1.31	0.34	1	12.73	<0.001
VCF	1.03	0.29	1	13.46	<0.001
PRPA	-0.41	0.20	1	5.26	0.021

Model statistics: Marginal R2 0.43, Conditional R2 0.85

Table 3. 4. Male dry season: Fixed effects output from generalised mixed-effects model describing home range size as a function of environmental covariates and individual. Estimated effect sizes and

their standard errors are presented, with significance of removal of term assessed using likelihood ratio tests

				Likelihood Ratio Test	
	β	SE	df	$\chi 2$	Pr($\chi 2$)
(Intercept)	4.39	0.26			
Water Density	-17.36	2.68	1	15.52	<0.001
Nitrogen	2.71	0.63	1	9.12	0.002

Model statistics: Marginal R2 0.55, Conditional R2 0.96

Table 3. 5. Male wet season: Fixed effects output from generalised mixed-effects model describing home range size as a function of environmental covariates and individual. Estimated effect sizes and their standard errors are presented, with significance of removal of term assessed using likelihood ratio tests.

				Likelihood Ratio Test	
	β	SE	df	$\chi 2$	Pr($\chi 2$)
(Intercept)	7.02	0.88			
Distance to Water	2.18	0.30	1	30.17	<0.001
Water Density	4.39	1.98	1	4.71	0.029
Carbon	0.91	0.30	1	9.76	0.001
Savannah/Shrubland	1.34	0.75	1	5.09	0.024
Woodland	1.01	0.40	1	6.02	0.014
Cattle	-6.70	1.65	1	14.74	<0.001

Model statistics: Marginal R2 0.75, Conditional R2 0.92

Discussion

Understanding the drivers of space use in animals is crucial to determining the extent of management units that are required for their conservation (Woodroffe and Ginsberg, 2000). As the dominant competitor in the carnivore guild, and therefore least influenced by interspecific competition, lions provide an ideal system in which to identify the drivers of home range size and their interactions.

The results show that there was no statistically significant difference in female home range sizes between seasons, yet average male home range size was significantly larger in the wet season than in the dry season. In this semi-arid landscape variation in home range size of lion females is predominantly determined by access to water and a combination of soil fertility and primary productivity throughout the year and seasonally influenced by cattle. In this study we explored three hypotheses:

1) Variation in male and female lion home range size is closely associated with the availability of surface water (and its associated prey) but the influence changes across the season.

2) Access to resources in the form of water and prey is the key driver for variation in female home range size but is less important for male home range size

3) Anthropogenic covariates are a limiting factor to home range size and influence females more severely than males.

The results strongly support that water availability is critical in the dry season, consistent with our first hypothesis. However, contrary to that hypothesis water availability remained the most important factor affecting home range sizes of both sexes in the wet season, and did not have less effect on home range size in the wet season than the dry season for either sex. This suggests that home range quality across both seasons is dominated by water availability. In the wet season water availability may not limit the movement or prey or of lions, but the overall prey population in the region is likely constrained by total water availability (Redfern et al., 2003; Smit et al., 2007; Smit, 2011; Rozen-Rechels et al., 2015), and so prey densities in the wet season will still be related to water availability and therefore home range size. This reflects, perhaps, the dramatic change in seasonal ecological dynamics that has occurred in southern Africa over the past century, with the collapse of the large herbivore migrations. In centuries past large herbivore populations would seasonally migrate from concentrations along permanent water sources to vast extents in the wet season. Except for greatly reduced numbers in a few remnant locations (e.g. Chobe and Boteti Rivers) (Bartlam-Brooks et al., 2013; Naidoo et al., 2016), the large migrations of ungulates are gone (Harris et al., 2009), and prey populations are now largely non-migratory, except in terms of short distance migration to concentrate on source-point waters in the dry season (Valeix, 2011; Davidson et al., 2013).

Our second hypothesis proposed that due to their different reproductive strategies, access to resources is the key driver for variation in female home range size but is less important for male home range size. This was expected because male home ranges are optimized to both procure resources and to control females (Schaller, 2009). Our results only partly support this hypothesis. In the dry season, female home range size was more strongly affected by each variable set than was male home range size. This suggests that female home range size is more influenced by water and prey availability in the dry season than is male home range size.

However, male home range size was still strongly affected by water availability and soil productivity in the dry season. While the differences in magnitude in explained variance are consistent with the expectation that male home range size is less limited by resources than females, the strong relationship between male home range size and water as well as soils, suggests that resource limitation is still the primary driver of male dry season home range. In the wet season, in contrast, male lion home range was not less related to resource or landscape conditions than was females. An approximately equal amount of variance in home range size was explained by water availability for both males and females in the wet season, and vegetation, in particular, had a much larger effect on male home range size in the wet season than it did on female home range size. This may reflect the fact that male home ranges were substantially larger in the wet season, and those that expanded in areas with high tree cover were larger than those in areas with low tree cover, but high grassland cover, due to the reduced foraging efficiency in woodlands. In African savannah ecosystems, soil nutrients in combination with rainfall determine plant biomass (Scholes, 1990; Fritz and Duncan, 1994) which regulates the distribution and abundance of large herbivores (Fritz et al., 2002; Augustine et al., 2003) and correlate positively with carnivore densities (Celesia et al., 2010).

Forage quality in low rainfall areas is generally highest in grassland dominated by short grass species (Fynn and Bonyongo, 2011). The high nutritional value and digestability attract migratory herbivores in the wet season (Naidoo et al., 2016), increasing prey availability for lions. The woodland in our study area was primarily dominated by combretum and teak forests (*Baikiaea plurijuga*), which are characterized by nutrient poor soils (Gambiza et al., 2008; Chidumayo and Gumbo, 2010) and low wildlife diversity and biomass (Winterbach et al., 2015) with lions likely required to roam further to provide equivalent hunting success.

The third hypothesis we investigated, proposed that anthropogenic covariates are a limiting factor to home range size for both sexes, but more so for females as they have been shown to be much more averse to human disturbance (Elliot et al., 2014b). The results of the analysis generally support this hypothesis for both seasons. In the dry season, male home range size was not related to either cattle density nor extent of protected areas, while female home range size was related to both, with nearly three times more influence of cattle density. In the wet season, however, neither female nor male home range size were strongly related to either cattle density or protected area extent. This is likely because in the wet season prey disperse from source-point waterholes, allowing lions and prey to utilize portions of the landscape with low cattle and human density. Thus in the wet season lions are likely less concentrated in areas with high human activities and thus less likely to be affected by human or cattle densities.

Summary and Conclusions

Females, in both the wet and dry season, had by far the most variance in home range size explained by water availability. Climate variables explained very little variance in home range size for females irrespective of the season. Soil and vegetation explained much more variance in home range size in the dry season than the wet season, and both sets of ecological variables had considerably less explanatory power than water. Anthropogenic variables explained female home range size substantially in the dry season, with cattle having the largest effect, while neither cattle nor protected area status affected home range size of female lions in the wet season.

Male lion home range size was also very strongly affected by water in both seasons. In the dry season ecological variables had a large conditional effect, whereas in the wet season ecological and water variables were highly covarying and jointly explained home range size. Male home range size was not strongly affected by anthropogenic variables in either season. Comparing males and females in the dry season, home range size of both sexes was strongly related to water availability and also, but to a lesser degree, related to soil and vegetation. In the wet season, again both male and female lion home ranges were strongly related to water

These results lead to three main conclusions. First, home range size of both male and female lions in both the wet and dry seasons is primarily driven by water availability. For both sexes in all seasons water availability had much greater influences on home range size than any other set of variables. Home ranges for both sexes in both seasons were larger when water was available at fewer locations and when it was on average farther away. Second, anthropogenic variables had little effect on home range size of either sex in any season, with the exception of female response to cattle density in the dry season. This suggests that human persecution or anthropogenic reduction of prey density does not strongly affect the size of lion home ranges in our study area, especially of male lions and of both sexes in the wet season, although it is known to strongly affect where lions occur and how they move through the landscape (Elliot et al., 2014b). As shown by (Elliot et al., 2014b), male lions are generally less risk averse than females, and thus the lack of impact of anthropogenic variables on their home ranges may indicate lower displacement or modification by human impacts. Female lions in the dry season showed substantial influences of human effects on home range size, perhaps indicating greater sensitivity to human disturbance in that season. The disappearance of that effect in the wet season may be driven by prey populations dispersing over much larger areas. With a large number of waterholes close to the border of Hwange National Park, in the wet season lions are free to roam more marginal areas further away from human settlement and thus experiencing less anthropogenic effect on home range size.

Third, our results show a mixed and varying influence of soil and vegetation variables. Soil and vegetation variables appeared to have a greater effect on female home ranges in the dry season than in the wet season. In contrast, male home range size was approximately equally affected by soil variables in both seasons, and about three times as strongly affected by vegetation in the wet season as the dry season. The standardized regression coefficients and response curve plots clarify this complex relationship with soil and vegetation.

Home ranges of both sexes in both seasons are generally smaller in areas with higher soil nutrients (e.g., Nitrogen) and in areas with lower extent of woodlands and higher extent of grasslands. However, the effects of these factors seem to vary seasonally for males, such that wet season home ranges are larger and more influenced by extent of woodlands, and less influenced by soil productivity.

This may reflect in the wet season prey populations dispersing broadly over the landscape into a range of soil and vegetation conditions, and male lions requiring larger home ranges in areas with high tree cover given that hunting efficiency is decreased in those conditions.

Author Contribution:

I hereby confirm that Dominik Bauer conceived and conceptualized the experiment, analysed the data and wrote the paper.

Hamburg,

Jörg Ganzhorn

Prof. Dr. Joerg Ganzhorn

Discussion

Protecting wide-ranging and migratory species in the midst of unprecedented human population growth (Gerland et al., 2014) is one of the biggest challenges faced by conservation practitioners and policy-makers in the 21st century (Ginsberg, 2001; Sergio et al., 2005; Martin et al., 2007; Buechley et al., 2018). The ever-increasing need for land for livestock and crop production (Rands et al., 2010) rapidly erodes natural habitats (Scholes et al., 2018), reducing the biodiversity and functioning of ecosystems (Folke et al., 1996; Haddad et al., 2015).

As humans alter the environment, animal movement is restricted (Sawyer et al., 2013; Tucker et al., 2018), resulting in limited genetic exchange and increased risk of inbreeding (Carroll et al., 2014; Rhoads et al., 2017). However, traditional conservation management often falls short on addressing the need for connectivity, instead applying a fortress conservation mentality (Jones, 2006), an approach whose effectiveness has come into question in recent years (Brockington, 2002; Benjaminsen and Svarstad, 2010; Büscher, 2016).

Furthermore, protected area selection has historically been biased toward lands of poorer productivity and lower economic worth (Scott et al., 2001). Establishing protected areas has therefore not necessarily favoured the most suitable habitat (Cantú-Salazar and Gaston, 2010) or maximized efforts in biodiversity conservation. In addition, the limited knowledge of fundamental animal ecology has often resulted in protected areas that are too small or ill-suited to cover the resources needed throughout a species life cycle.

A case in point is Botswana's Central Kalahari Game Reserve (CKGR), which suffered a collapse of its ungulate population as a result of limited knowledge of basic ecosystem functions and the resource requirements of its resident herbivores. Established in 1961 as one of the largest protected areas in the world, the CKGR covers more than 50,000 km^2 of xeric, semi-arid shrubland. In the 1960s it was home to more than 300,000 wildebeest (Thouless, 1998), the biggest population outside the Serengeti National Park in Tanzania. In an attempt to fulfil the high standards of veterinary hygiene and disease management required to gain access to the European Union’s beef market, Botswana divided the country into disease control areas to restrict livestock movement. From 1954 the government began to erect a series of veterinary cordon fences (Gadd, 2012) to separate domestic animals from wild ungulate populations in order to limit the spread of foot-and mouth disease. The fences effectively cut off movement from the Central Kalahari Game Reserve to the permanent waters of the Okavango Delta.

Droughts in the 1970s and 1980s resulted in catastrophic wildebeest die-offs when animals tried to cross the veterinary fence (Williamson and Mbano, 1988) to access essential water sources in the north of the country. Since then, numbers have continued to decline and the latest estimates put the population at less than 1000 individuals (Selebatso, personal communication) - a population on the verge of functional extinction.

This example highlights that in semi-arid environments where resource availability can vary widely in space and time, ecosystem integrity is not simply determined by the size of an area, as even large protected areas can fail to provide all the resources an animal will need throughout its life cycle. It also supports the need to diverge from fortress conservation and adopt a landscape-scale approach that maintains ecosystem functions and allows animals to disperse and access seasonal resources. This approach is increasingly being explored (Rabinowitz and Zeller, 2010; McGarigal, 2014; Maiorano et al., 2019) such as in the case of the Jaguar Corridor Initiative (Zeller et al., 2013), a continent-wide attempt by NGOs, local governments and rural communities to protect jaguars across their entire range by securing and connecting core jaguar populations. The resulting cross-border, multi-use landscapes are designed to incorporate whole ecosystems by combining protected core areas with connective corridors that maintain connectivity and protect species from source-sink dynamics (Hansen, 2011). While the harmonisation of environmental management practices across these so called Transfrontier Conservation Areas (TFCAs) can pose significant challenges (Duffy, 2006), TFCAs are now increasingly implemented throughout the world and particularly in southern Africa (Hanks, 2003).

The Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA), officially signed into law by five Heads of State on the 11th August 2011, allows Africa's largest elephant population to move freely across country borders, while aligning the needs of people and wildlife alike. Despite its status as a conservation area it is a multiuse landscape, containing areas of different protective status including multiple human settlements, roads, and high-intensity farming areas. To help navigate land-use planning and conservation in an increasingly complex environment, connectivity models are a useful tool to conceptualise long-term processes over large spatial scales. Relying on these biologically informed models rather than ad-hoc assignments of corridors and dispersal areas based on subjective preconceptions is an advantage for ecosystem management. The results of Chapter 1 have raised considerable interest in the KAZA secretariat, the governing body of the KAZA landscape, and within the framework of the National Spatial Plan 2036 of Botswana.

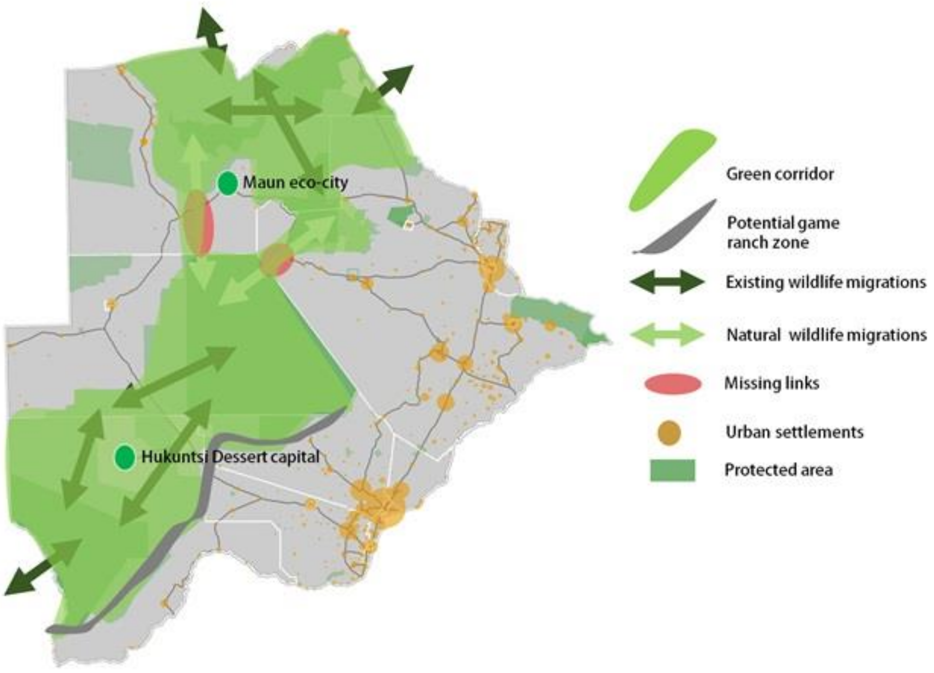


Figure 4. 1. Map of the green corridor concept NSP (© COWI 2036)

The National Spatial Plan (NSP) is a collaborative effort between government ministries, NGOs, and the private sector to create a framework to guide land-use development and investment decisions in Botswana until the year 2036. One of the key concepts that emerged from the process was the development of a contiguous green zone ("green corridor") (Figure 4. 1) in which wildlife and human settlements could be managed together. The results of this dissertation have significantly contributed to the conceptualisation of the green corridor scheme by the NSP development committee. In addition to highlighting these linkages and dispersal areas, connectivity modelling is a useful toolkit to test future land use scenarios (Cushman et al., 2016) by mapping and quantifying the impact of urban and economic development on ecosystem integrity, as already done elsewhere (Kaszta et al., 2019; Kaszta et al., 2020).

Whilst identifying key linkages and dispersal areas is a crucial undertaking, there is still a need to understand elements of the fundamental ecology of lions, including the quantification of the processes that govern their distribution. Understanding how animals adapt to variation and changes in their environment is critical for their current and future management in the face of climate change and rapid human population growth.

The significance and magnitude of environmental and anthropogenic effects on carnivore occurrence have been investigated in a number of studies (Hopcraft et al., 2005; Mosser et al., 2009; Loveridge et al., 2010; Henschel et al., 2016) however, few have included behavioural state and life-history traits (Abrahms et al., 2016; Maiorano et al., 2019). Most commonly, data from individual animals are pooled to allow inference on population-level effects, without accounting for individual or demographic differences in habitat selection (Gillies et al., 2006).

One of the most important life-history strategies in the animal kingdom is dispersal, yet the underlying causes are often poorly understood (Bowler and Benton, 2005). Two different types of dispersal can be distinguished; natal and breeding dispersal (Végvári et al., 2018). Natal dispersal occurs when an individual departs from its birthplace in order to establish a breeding site, whilst breeding dispersal occurs when an individual moves its centre of reproductive activity to a new breeding site.

While natal dispersal in lions is part of the life cycle for all sub-adult males (Packer and Pusey, 1987; Funston, 2011) and is relatively well documented (Elliot et al., 2014a; Elliot et al., 2014b), breeding dispersal in females and adult males is poorly understood. It is often the result of a male take-over with the incoming males evicting the previous pride males, sub-adult females that are too young to breed, and adult females trying to protect their cubs from infanticide (VanderWaal et al., 2009). Furthermore, females may disperse upon reaching sexual maturity whilst their fathers are still the dominant males to prevent inbreeding, or if a pride exceeds its optimal size to guarantee individual reproductive success (VanderWaal et al., 2009).

Whilst adapting to new environmental and social conditions (Smale et al., 1997), these dispersing individuals have significantly different resource needs than individuals exhibiting territorial or residential behaviour (Elliot et al., 2014b). Therefore pooling all locational data irrespective of movement behaviour has the potential to obscure species-habitat relationships (Roever et al., 2014).

To exclude dispersal movement, I applied a threshold model based on the expected movement distances and maximum excursion duration of breeding females following a study of golden eagles in Scotland (Weston et al., 2013). Subsequently, I incorporated random effects in regression models to evaluate drivers of home range selection and highlight differences between the four different demographic categories.

The results of Chapter 2 emphasize the importance of water and how precipitation and surface water regulate animal distribution in a semi-arid environment. In arid and semi-arid environments that often lack natural dry season water sources, artificial waterholes are a common management tool used to influence herbivore movement and distribution (de Leeuw et al., 2001; Chamaillé-Jammes et al., 2007). With lions actively selecting areas of high prey availability (Valeix et al., 2010), artificial waterholes can be used as a management tool to strategically influence population distribution and promote landscape connectivity. The wide-ranging distribution of lions across the central KAZA TFCA generally follows the distribution of artificial waterholes in the landscape, making it part of what is arguably the geographically largest contiguous lion population left in the world, spanning across several hundred kilometres from Hwange National Park in Zimbabwe to the western parts of the Okavango Delta in Botswana (Bauer et al., 2015a).

The addition of water sources in Botswana for hunting purposes and in Hwange National Park for photographic tourism has undoubtedly increased herbivore numbers and their associated predators in otherwise marginal areas (Winterbach et al., 2015), however such fundamental ecosystem changes need to be considered carefully (Beale et al., 2013). With distance to surface water strongly affecting herbivore foraging intensity (Sianga et al., 2017), extensive availability of artificial waterholes promotes habitat homogenization (Beale et al., 2013) due to increased herbivore utilisation pressure in previously inaccessible areas.

In wildlife areas such as Kruger National Park in South Africa, which has a long history of supplementing surface water (Sutherland et al., 2018), the detrimental effects of a large number of boreholes and dams on habitat biodiversity, herbivore distribution, and abundance of rare species (Brits et al., 2002; Purdon and Van Aarde, 2017) (Grant et al., 2002) has led to a revision of its water provision policy and the progressive closure of numerous artificial water sources. This example demonstrates the need to employ artificial waterholes strategically, with consideration for the potentially detrimental effects on habitat biodiversity (Parker and Witkowski, 1999).

The results of Chapter 2 also highlight the importance of prey availability in shaping lion occurrence across the landscape. Abundant prey is a key determinant for large carnivore survival and its depletion is a major cause of carnivore population declines worldwide (Wolf and Ripple, 2017). Efforts to reduce unsustainable bushmeat poaching in order to support a healthy prey base are therefore a prerequisite to maintain healthy carnivore populations.

Resource selection functions can provide valuable insights into the biotic and anthropogenic factors that determine the distribution of carnivores across an extensive landscape. The results contribute to a growing body of knowledge on large carnivore species ecology which is essential for their effective conservation management. The widespread distribution of lions across the study area indicates that the transboundary conservation framework is proving successful in conserving lions in the central KAZA TFCA.

In addition to identifying key resources that shape species distribution, identifying how these resources influence an animals home range is an important aspect in conservation management in order to determine the size of functionally intact protected areas.

Variation in home range size is one of the most studied aspects in animal ecology (McNab, 1963; Gittleman and Harvey, 1982; Börger et al., 2006a; Duncan et al., 2015) as it describes the spatial representation of behaviours related to the maximization of fitness by an individual (Burt, 1943). Within the order Carnivora, home range size can vary significantly both between and within species (King, 1975; Ferguson et al., 1999; Börger et al., 2006b), and is largely determined by energetic constraints, body mass, and the distribution of resources (Kelt and Van Vuren, 2001; Grigione et al., 2002; Mitchell and Powell, 2007).

While the drivers of home range size for carnivores are generally well documented (Ferguson et al., 1999; Loveridge et al., 2009b; Simcharoen et al., 2014), inter-sexual and seasonal differences are generally less well understood. Furthermore, the relative contributions of the drivers influencing carnivore home ranges and their complex interactions have rarely been quantified. The traditional regression methods utilised identify important drivers of home range size, but are unable to quantify independent and confounding contributions. Identifying the size of a species home range, and understanding how the drivers that influence it vary according to sex and season, is essential to scale protected areas (Woodroffe and Ginsberg, 2000) in a rapidly changing environment (Shrestha et al., 2012).

Chapter 3 highlights the environmental and anthropogenic factors and their complex interactions influencing male and female lion home range size in the dry and wet seasons. The results show that there is a strong difference in seasonal variation of home range size between males and females. While female home range size remains stable throughout the year, male home range size increases significantly in the wet season.

In a semi-arid environment, home range size for both sexes is primarily determined by access to water irrespective of the season. In addition to water, soil productivity and vegetation cover affect male and female lion home ranges throughout the year.

Male lion home ranges are more limited by vegetation cover in the wet season, and generally more related to soil productivity in the dry season. This may reflect the fact that in the wet season prey populations disperse broadly over the landscape often into areas with poor vegetation and soil conditions with male lions requiring larger home ranges in areas with high tree cover given reduced forage quality.

While I considered including abundance of prey in the analysis as it is generally one of the key drivers of habitat selection for large carnivores (Carbone and Gittleman, 2002; Valeix et al., 2010), obtaining reliable estimates is often prohibitively expensive and a logistical challenge (Nilsen et al., 2005). Since prey biomass in natural ecosystems is generally closely aligned with primary productivity (East, 1984; Olff et al., 2002; Hopcraft et al., 2010), using environmental factors as proxies for herbivore density is a reasonable alternative (Coe et al., 1976; Bell, 1982; Georgiadis et al., 2007; Borowik et al., 2013). A previous study on drivers of lion density using hierarchical partitioning showed that including prey biomass did not improve explanatory power significantly (most likely because prey itself was strongly influenced by environmental drivers) (Celesia et al., 2010) and I am therefore confident in this approach.

The influence of anthropogenic covariates on the distribution and behaviour of animals is hard to quantify, and they are therefore often excluded when studying drivers of home range size. Few attempts have been made to incorporate anthropogenic factors as determinants for home range size in large carnivores (Dickson and Beier, 2002). The results of Chapter 3 show that anthropogenic variables had little effect on male home range size in both seasons and female home range size in the wet season. However, cattle had a substantial influence on female home range size in the dry season which demonstrates the value of including anthropogenic factors when studying drivers of home range size in a human-dominated landscape.

Conclusion

Due to unprecedented human population growth, few ecosystems remain unaffected by the ever-increasing competition for land in the 21st century. Infrastructure development alters the functionality of natural environments by fragmenting large continuous habitats into smaller, isolated patches. Cutting-edge connectivity modelling is an increasingly important tool to help conservation practitioners to identify crucial population linkages and prioritize appropriate management actions. An additional fundamental requirement for strategic and successful land-use planning includes an understanding of how ecological processes and anthropogenic factors influence the movement and distribution of animals. This dissertation has employed innovative methods to contribute to a growing body of knowledge that is essential to inform effective landscape-scale conservation of a wide-ranging species in a human-dominated landscape.

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Declaration of oath

I hereby declare on oath that the work in this dissertation is my own and that I have not used other than the acknowledged resources and aids.

Oxford, 16th of March 2020

D. Bauer

Dominik Bauer

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