Concurrent spatiotemporal ecology of African lions and Spotted hyenas and the potential for inter- and intraspecific interactions in semi-arid and wetland ecosystems

by

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As the candidate's supervisor, I have approved this thesis for submission.

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ABSTRACT

Intraguild interactions among apex predators can potentially influence carnivore population densities and distribution, which may have profound effects on trophic processes within ecosystems. Coexisting carnivores are able to mitigate such interactions through behavioural mechanisms that promote spatiotemporal separation. Despite increasing research which highlights the occurrence and prevalence of competitive interactions between African lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), studies that incorporate the effects of such interactions on lion and hyena space use patterns are limited. Interactions among sympatric carnivores reveal how predators utilize spatial and temporal partitioning strategies within jointly used areas, and elucidate the spatiotemporal patterns enabling species co-existence between them. Thus, an understanding of how inter- and intragroup interactions drives the movement responses of apex predators has important implications for the structure and function of large carnivore communities, and their conservation. We used remote tracking data to investigate aspects of the ecology and behaviour of lions and spotted hyenas, with an emphasis on the spatiotemporal patterns among coexisting populations. Both lions and spotted hyenas mediated the potential for interference competition through subtle differences in temporal activity, fine-scale habitat use differentiation, and localized reactive-avoidance behaviours. Recursivity to, and duration of time at, locales of high competitor probabilities, were similar among female lions and both sexes of hyenas, but different for male lions. Our findings of lion space-use patterns across arid and mesic environments indicated the seasonal influences of competitive interactions with competitors (spotted hyenas), in that lions selected for, and chose to move through areas with a lower probability of competitors during the dry season. Dyadic interactions among lions and spotted hyenas illuminates how hyenas effectively reduced their potential of interactions with lions by utilizing spatiotemporal partitioning strategies and local reactive avoidance behaviours within shared space use areas. Quantifying the types of movement behaviour between competitors highlights the type of interaction occurring in a dyad and enhances our understanding of the potential effects of interspecific interactions among large carnivore space-use patterns within an apex predator system. Both lions and spotted hyenas exploit different behavioural strategies resulting in fine-scale spatiotemporal segregation among shared space-use areas enabling the two species to co-exist, and show adaptability across heterogeneous and homogeneous environments. Such findings are essential in understanding the behavioural choices made by members of a guild that subsequently affects population dynamics and community structure of multi-species food networks.

PREFACE

The work described in this thesis was carried out in the Okaukeujo and Halali regions of the Etosha National Park in northern Namibia, and in the region encompassing the floodplains of the Chobe National Park and the Linyanti Conservancy in northeastern Botswana, including the NG32 concession of the Okavango Delta. This work was conducted through the School of Biological and Conservation Sciences, and the School of Mathematical Sciences, University of KwaZulu-Natal, Westville, Durban, from September 2012 to January 2018, under the co-supervision of Professors Rob Slotow and Wayne M. Getz for Namibia, and under the co-supervision of Professors Rob Slotow, Wayne M. Getz, and Kathleen A. Alexander for Botswana.

The author of the thesis collected data in the field from September 2012 to February 2015 in Namibia, and from February 2015 to January 2018 in Botswana. These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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DECLARATION 1 – PLAGIARISM

I, Nancy Ann Barker, declare that

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DECLARATION 2 – PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, in press and published and give details of the contributions of each author to the experimental work and writing of each publication).

Publication 1

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Author contributions:

NAB obtained funds and equipment sponsorship, secured the relevant permits, conducted all field work, collected, processed and analyzed the data, and designed and wrote the paper. FGJ, MK, GS assisted in collecting the data. VS assisted in processing and analyzing the data. KAA supplied the IACUC approval for Botswana. WMG supplied the IACUC approval for Namibia, and contributed to the design of the study. WMG and RS provided funds for the study, guidance on analysis of the data, and provided valuable comments on the manuscript.

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Author contributions:

NAB obtained funds and equipment sponsorship, secured the relevant permits, conducted all field work, collected, processed and analyzed the data, and designed and wrote the paper. FGJ, MK, GS assisted in collecting the data. VS assisted in processing and analyzing the data. KAA supplied the IACUC approval for Botswana. WMG supplied the IACUC approval for Namibia, and contributed to the design of the study. WMG and RS provided funds for the study, guidance on analysis of the data, and provided valuable comments on the manuscript.

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Author contributions:

NAB contributed to the design of the study, obtained funds and equipment sponsorship, secured the relevant permits, conducted all fieldwork, collected, processed, and analyzed the data, and wrote the paper. VS assisted in processing and analyzing the data. LLV developed the relative-motion method, calculated the 95% CI and provided the graphics describing the method. KAA supplied the IACUC approval for Botswana. WMG supplied the IACUC approval for Namibia, and contributed to the design of the study and developments of new methods to analyze the data. WMG and RS provided funds for the study and guidance on analysis of the data. WMG, RS, and KAA provided valuable comments on the manuscript.

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CHAPTER ONE

General Introduction

1.1. Background

Interactions between carnivore species has profound implications in shaping community structure and population dynamics (Linnell & Strand 2000). Large carnivores benefit multi-species community networks of which they are a part, through modulating the total effect of the predator guild on prey species (Terborgh et al. 1999), and in suppressing the release of smaller carnivore species (Soulé & Noss 1998). This results in more species being able to utilize a certain habitat, and increases the biodiversity of species in certain areas (Miller et al. 2001). Sympatric guild members who share the same limiting resource frequently face competition (Linnell & Strand 2000), and this is evident with interspecific competition among carnivores in which competition for prey resources is a limiting ecological factor on their survival (Creel 2001, Caro & Stoner 2003).

Caro and Stoner (2003) demonstrated that the average African carnivore shares part of its geographic range and habitat with 26 other carnivore species, which suggests a high probability of competition. Carnivores may also have to share food resources with 22 other carnivore species, and may be vulnerable to predation by 15 other species, although they are unlikely to be consumed by other carnivores (Caro & Stoner 2003, Moleón et al. 2017). The prevalence of competition has also been documented between carnivores through range and habitat overlaps (Palomares et al. 1996, Fedriani et al. 2000, Tannerfeldt et al. 2002), dietary overlaps (Jones & Barmuta 1998, Mitchell & Banks 2005, Azevedo et al. 2006), as well as agonistic interactions between species (Venkataraman 1995, Palomares et al. 1995, Fedriani et al. 2000); including among African carnivores (Creel & Creel 1996, Mills & Gorman 1997, Gorman et al. 1998, Durant 2000a, b, Creel 2001, Honer et al. 2002, Breuer 2005, Trinkel & Kastberger 2005, Hayward 2006).

Intraguild predation has been documented, and is prevalent among communities of mammalian carnivores, with interspecific killing accounting for up to 68% of known mortalities in some carnivore species, although the ecological and behavioural factors influencing such intraguild competition are poorly understood (Palomares & Caro 1999). As a result, such high costs of competition and intraguild predation among sympatric guild members can potentially influence species viability through population reduction or extinction, and has important implications for the structure and function of large carnivore communities (Palomares & Caro, 1999). Therefore, interactions between carnivores can adversely affect carnivore distributions and population demographics (Palomares & Caro 1999, Caro & Stoner 2003), with cascading effects on species at lower trophic levels (Estes 1991, Palomares et al. 1995, Crooks & Soulé 1999).

Despite the prevalence of interspecific competition in carnivores, carnivore species continue to coexist, and several studies have attempted to unravel the ecological processes driving the mechanisms for the coexistence of a large predator guild (Voigt & Earle 1983, Karanth & Sunquist 1995, Fedriani et al. 1999, Neale & Sacks 2001, Scognamillo et al. 2003, Glen & Dickman 2005, Nelson et al. 2007, Atwood & Gese 2010, Chetri et al. 2017), including those in Africa (Mills & Biggs 1993, Durant 1998, Trinkel & Kastberger 2005, Hayward & Kerley 2008, Périquet et al. 2015b, Dröge et al. 2017, Kushata et al. 2018, Périquet et al. 2021, Davis et al. 2021, Searle et al. 2021). Recent developments in studies of species interactions has demonstrated that species can respond to the presence of a competitor or predator in either proactive or reactive ways, resulting in food-mediated or stress-mediated costs (Creel 2018). With the emergence of such studies, subordinate carnivore species have been found to respond reactively (Broekhuis et al. 2013) or proactively (Davies et al. 2021) to the risk from dominant competitors. Given the ongoing global decline in large carnivore populations (Estes et al. 2011, Ripple et al. 2014), understanding the interactions among sympatrically occurring large carnivores can provide insight as to how and why they are able to coexist, and is of paramount importance for the maintenance of biological diversity and ecosystem processes (Ripple & Beschta 2004, Elmhagen et al. 2010).

The African lion (*Panthera leo*) and the spotted hyena (*Crocuta crocuta*), two of Africa's largest carnivores, exist mainly within protected areas in Africa and occupy a similar trophic niche (Sales et al. 2021). As apex predators, lions and spotted hyenas co-exist at the local scale within a competition-centered niche (MacArthur & Levins 1967, Sales et al. 2021), and compete for the same limiting resources throughout much of their range (Mills & Biggs 1993, Trinkel & Kastberger 2005, Hayward 2006). Lions are able to exploit a wide range of habitats except tropical rain forests, and they can persist in arid areas along drainage lines and can survive for long periods without drinking water (Apps 2000). Spotted hyenas are opportunistic and flexible carnivores capable of inhabiting such diverse habitats including semi-deserts, savannahs and open woodlands, dense dry woodlands, and mountainous forests up to 4000m above sea level (Kruuk 1972, Estes 1991, Mills & Hofer 1998). Lions and spotted hyenas acquire most of their food through active predation (Kruuk 1972, Schaller 1972), and demonstrate significant overlaps in their dietary composition of prey (Hayward 2006, Hayward & Kerley 2008). Lions kill and eat a variety of prey species, from young elephants to porcupines, but eat mainly medium-sized and large ungulate prey. Lions will also eat birds, reptiles, fish, and even insects (Apps 2000).

Lions frequently scavenge and steal kills from other carnivores, and sometimes attack and kill other carnivores but rarely eat them (Cooper 1991, Honer et al. 2002). Studies analyzing the diets of spotted hyenas have shown them to overlap extensively with lions (Hayward 2006), but are very generalist, consuming more non-mammalian food sources than other carnivores (Mills & Biggs 1993). This is primarily due to its highly opportunistic and flexible foraging nature in which they may scavenge or actively hunt for prey (Kruuk 1972). Spotted hyenas are presumed to be more efficient scavengers than lions as they are able to utilize dried meat, skin and bones from carcasses (Kruuk 1972), and, thus, often scavenge food from lions. Spotted hyenas have successfully appropriated kills from lions in the Ngorongoro Crater (Honer et al. 2002) and in the Savuti areas of Botswana (Cooper 1991), although they were never seen to appropriate kills from lions in the Etosha National Park (Trinkel & Kastberger 2005).

Consequently, many of the interactions between lions and hyenas are centered around kills/carcasses and are often of an aggressive nature, with both species frequently stealing kills from each other (Cooper 1991, Honer et al. 2002). Spotted hyenas will aggressively induce lions to leave certain areas through mobbing behaviour (Trinkel & Kastberger 2005, Lehmann et al. 2017), and lions are a critical factor contributing to hyena mortality in some areas (Henschel 1986, van Jaarsveld 1993, Watts & Holekamp 2008, 2009). Despite intense competition between the two species, both species continue to coexist in many ecosystems (Mills & Biggs 1993, Ogutu & Dublin 1998, Trinkel & Kastberger 2005, Hayward & Kerley 2008, Kissui 2008, Watts & Holekamp 2008, Webster et al. 2010, Pangle & Holekamp 2010, Watts et al. 2010, Broekhuis et al. 2013, Périquet et al. 2016, Kittle et al. 2016, Lehmann et al. 2017, Dröge et al. 2017, Kushata et al. 2018), with nearly 95% of the lion's range overlapping with that of the spotted hyena's (Périquet et al. 2015a). Consequently, the pervasiveness of such interspecific competition between lions and spotted hyenas has not resulted in the competitive exclusion of the other at the population level.

As remaining habitats are often subjected to increasing land-use competition, coupled together with insufficient funding for conservation efforts, the need to conserve a maximum number of species diversity is further constrained by the available minimum areas (Gurd et al. 2001, Restani & Marzluff 2002). Therefore, an understanding of the dynamics influencing the spatiotemporal relationship among sympatrically occurring competing species is of paramount importance for the effective conservation planning of carnivores, whose large spatial requirements have made them most susceptible to habitat loss, and equally difficult to conserve (Linnell et al. 2001, Lindsey et al. 2004). Carnivores are often nocturnal, cryptic, wide-ranging and occur at low densities (Gese 2001). The huge home ranges of many carnivores also makes it likely that the true population value will be overestimated. Therefore, advances in a variety of methodological techniques can prove useful tools in understanding carnivore distributions and ranging patterns and in estimating their population densities. Global Positioning System (GPS) satellite collars together with accelerometers provide excellent tools for identifying behavioural modes and in assessing fine-scale movements on a landscape scale (Nathan et al. 2012). Predator movement should be sensitive to the spatial patterns of interspecific competitors, and it is possible that at the fine scale, there may be a negative association between these predators that indicate possible temporal avoidance or localized habitat shifts. To ascertain the mechanisms of competition and coexistence, one should assess (1) how individuals are distributed spatially, (2) whether habitat segregation occurs between species, (3) how a species' habitat use is influenced by the presence of the other species, and (4) whether the spatial distributions of the different species are positively or negatively correlated, or independent of each other. Few theoretical or empirical studies have examined the interplay between predator behavioural responses to each other to account for patterns of predator spatial and temporal overlap. To our knowledge, there have yet to be any studies that have quantified the simultaneous fine-scale movement characteristics and behavioural patterns of sympatrically occurring lions and spotted hyenas that utilize much of the same resources. Understanding these types of dynamic interactions may prove crucial for the conservation of coexisting large carnivores and the promotion of biodiversity, especially in the light of ongoing habitat destruction and fragmentation.

In this study, I examined the spatiotemporal relationship between the African lion and the spotted hyena simultaneously, using a mixed fine-scaled sampling interval of 30 min from dusk to dawn, and of 5 min during peak activity periods. Specifically, I aimed to determine the specific influences of interspecific competition on lion and spotted hyena interactions. To achieve this, I provide an overview of factors that might influence the outcome of these behavioural responses. I first measured the spatial overlap of lion and spotted hyena ranges within utilized areas to establish the presence of interaction. I then established the presence of a competitor as one of the drivers for altered spatiotemporal patterns of resource use and movement decisions. Finally, I illuminated the effects of such interactions, in which encounters with the other species induces patterns of behavioural changes with altered movement characteristics.

1.2. Thesis outline

As studies increasingly demonstrate the effects of interactions among sympatric and competing carnivores and their implications for carnivore conservation, it becomes crucial to discern the underlying factors that govern the spatiotemporal behaviour driving the space use patterns of apex predators. Specifically, a method is required for both identifying and quantifying the movement patterns, and to understand temporal and spatial differences between two species. By doing so, it will be possible to discern and explain the types of interactions among carnivore species that potentially shape the guild, and understand the relationships that drive this. In this thesis, I examine the spatio-temporal ecology of, and the interactions between two of Africa's large carnivores, the African lion and the spotted hyena, in Namibia's Etosha National Park, Botswana's Chobe National Park / Linyanti Conservancy, and in the NG32 concession of the Okavango Delta. In the current context of ecological interactions, space-use decisions by lions and spotted hyenas regulates the spatial overlap between the two species, which in turn affects predation and encounter rates, and subsequently predator populations and community dynamics. Given the role that predator-prey relationships holds in ecological studies, much is known about the space-use patterns of either predator, whereas very little is known about the behavioural ecology of the joint space use of lions and spotted hyenas (Périquet et al. 2015a). Hence, this study is the first of its kind to analyze the simultaneous fine-scale spatiotemporal patterns of coexisting large carnivore species across two distinct ecosystems on a landscape scale.

Thus, in each chapter I have analyzed the influencing factors driving the joint space use patterns of lions and spotted hyenas while incorporating measures of interactions in these analyses. Each chapter therefore complements each other and lends support to the objective of the thesis in effectively identifying and understanding the role that such interactions among lions and spotted hyenas have in their space use patterns and movements. In chapter 2, I assessed the differences between species in the space use patterns of lions and spotted hyenas. I also developed a preliminary framework to establish for the presence of potential interactions between the two species that affects their spatial patterns in the context of time-use metrics. Then in chapter 3, I incorporated interaction covariates to resource selection function (RSF) and step selection function (SSF) models, with which I modelled lion habitat selection and movement. I subsequently identified the effects of both interspecific and intraspecific interactions on the selection and movement responses of lions. Thereafter in chapter 4, I reiterated the presence of interactions among lion and spotted hyena individuals using the hull association metric technique, and also applied a relative-motion method to identify the types of interaction occurring between lion and spotted hyena dyads. Taken together, each chapter lends support to the evidence for the presence of interactions between lion and spotted hyena individuals, and addresses how such interactions may dictate or shape the spatial and movement patterns of both lions and spotted hyenas in response to the effects of competitive interactions. I have written chapters 2 to 4 as independent peer-reviewed scientific papers, each with its' own reference list, and I have presented a synthesis of my findings in chapter 5. Below I briefly discuss each chapter.

First, I utilized an increased mixed sampling rate of both 30 min and 5 min GPS fixes during the nocturnal period from tracking collars deployed on both species to obtain a fine scaled record of both species' movement behaviour. This information was corroborated against activity measures obtained from the accelerometers to identify when and where periods of heightened activity occurred on a landscape scale. The objective of this study was to provide an overview of factors that drive the space-use patterns of lions and spotted hyenas, with a focus on understanding the dynamic interactions between the two species as a potential source of competition. Such fine scale analyses provide insight into the behavioural dynamics of lions and hyenas; and whether there exists a spatio-temporal mechanism in predator movement decisions which facilitates coexistence between the two species. This thesis is written as a series of independent papers for publications, and a brief explanation for each of the following chapters is outlined below.

In Chapter 2, I analyzed the mechanisms facilitating coexistence between lions and spotted hyenas with the aim of understanding the environmental and bioclimatic factors influencing the spatiotemporal patterns of lions and spotted hyenas, and to determine whether these patterns were primarily influenced by interspecific or intraspecific competitors. I compared and contrasted the movement characteristics, individual home ranges and core areas, and activity patterns of these two predators to discern the differences between species and among ecosystems. I examined the differences and similarities in the speed, distance travelled (step lengths), and path tortuosity (turning angles) of lions and spotted hyenas over various times of the day, between diel cycles and across seasons (Gurarie et al. 2016, Edelhoff et al. 2016). I assessed whether lion and hyena movement metrics differed across sex (Funston et al. 2001, Boydston et al. 2001), age classes (Funston et al. 2003, Boydston et al. 2005), body condition scores (Kolowski & Holekamp 2008), group sizes (Cooper 1991), and including antibody titres to anthrax for Etosha individuals (Bellan et al. 2012). I further evaluated the relationship between the activity patterns of lions and spotted hyenas to the lunar cycle and with respect to competitor and conspecific core areas (Trinkel & Kastberger 2005, Packer et al. 2011, Cozzi et al. 2012, Périquet et al. 2015a). I attached ecogeographical variables and interaction covariates to all lion and spotted hyena relocations and used the *K*-prototype (Huang 1998), hierarchical and PAM clustering algorithms (Kaufman & Rousseeuw 1990) to explore the patterns of recursions and extended stays within an individual's range (Berger-Tal & Bar-David 2015). I also applied the factorial analysis of mixed data (FAMD) method to assess which variables contributed significantly to an individual's time-use patterns, and compared these across species.

In Chapter 3 the objective was to incorporate the effects of inter- and intraspecific interactions on lion habitat selection and movement responses to investigate the influences of heterospecific and conspecific interactions on lion habitat use and movement. I first examined the range use, movement metrics and activity patterns of lions. I used the kernel density estimator (KDE, Worton 1989) and the time localized convex hull method (T-LoCoH, Getz & Wilmers 2004, Lyons et al. 2013) to construct seasonal home ranges and core areas to compare and contrast across circadian cycles and seasons. I used the location data in conjunction with ecogeographical variables to address the second and third order selection (Johnson 1980) of an individual's home range and habitat use within the individual's home range. I identified home ranges and core areas for each lion individual, and created species utilization distributions which were converted into probability of use values (Kittle et al. 2016). I obtained the simultaneous distance measure of each individual to all other collared individuals to serve as a proxy of competition through potential inter- and intraspecific interactions. These variables were included along with other bioclimatic covariates, landscape features and individual factors as predictors in the resource selection function (RSF, Manly et al. 2002) and step selection function (SSF, Fortin et al. 2005) models to explain for species range use and movement decisions. I examined whether variables of inter- and intra- specific interactions were selected by a backward stepwise procedure to be included as predictors in the globally saturated model. From these analyses, we ascertained the most likely factors influencing lion space use between the two ecosystems.

In Chapter 4, I assessed the joint space use, movement and proximity characteristics of lions and spotted hyenas with the objective of quantifying the spatiotemporal separation among lion and hyena interactions. The purpose of this undertaking was to demonstrate for the presence, and prevalence of interactions among lion-hyena dyads, and to ascertain the effects of inter- and intraspecific competitors on lion and hyena movement responses. I investigated the range use of lions and spotted hyenas with both the kernel density estimator (KDE, Worton 1989) and the time localized convex hull method (T-LoCoH, Getz & Wilmers 2004, Lyons et al. 2013) to ascertain for whether spatial and temporal overlaps were occurring between the two species within their home ranges and core use areas. I used the hull association metrics within the spatially and temporally overlapping hulls of an individual's range to inspect for the presence of interactions between species pairs and individual pairs. The fine-scaled sampling rate was designed to illuminate patterns in an individual's fine scale movement behaviour as they come into contact with one another during periods of spatial overlap in home range use and during periods of temporal overlap in activity periods. This information further provided the context from which analyses into the dynamic interaction between the species was developed using the heading and direction of an individual's movement path towards the other individual. These interaction measures of approach and retreat behaviours allowed us to contextualize the effects of interspecific interactions in species' movement patterns. I used these measures to determine which individual was following or tracking whom, and compared these across species and individual pairs to evaluate the frequency of these types of interactions.

In chapter 5, I present a recap of my findings, and summarize the results of this work. I also provide a general conclusion which synthesizes the information of the three chapters. In addition, I discuss the implications and findings of this work for carnivore ecology and conservation, and identify areas for future research.

1.3. General methodology

In each chapter, I provide a description of the relevant methodologies. In summary, I used satellite tracking collars with accelerometers to obtain lion and spotted hyena relocations and activity measures within the Etosha National Park, the Chobe National Park, the Linyanti Conservancy and the Okavango Delta. I evaluated these data against various landscape features in ArcGIS (ESRI ArcMap v.10.0, Redlands, CA, USA) and Google Earth Engine using remotely sensed data. I analyzed these data to illustrate the differences in the movement and activity patterns between the two species across different environmental gradients. To understand the role of interference competition as an influential factor driving the space use patterns of co-existing lions and spotted hyenas, I constructed individual home ranges and analyzed the areas and proportion of overlaps between individual ranges. For each individual, I generated a revisitation/duration (RD) space in which I identified areas of high use intensity (revisitations) and locales of extended stays (visit durations) within home ranges and attached ecogeographical covariates (including covariates of inter- and intra-specific interactions) to these sites for cluster analyses. I applied a factorial analysis of mixed data and three different clustering methods to designate the variables that best explained the patterns of recursion and extended stays within an individual's range. In addition, I modelled resource selection and step selection functions using frequentist inference of lions across two ecosystems to ascertain the factors influencing lion habitat selection and movement. I used a multi-stage approach with the first models consisting of landscape features, bioclimatic factors and individual variables. Then, interaction covariates were included in the best selected models to examine whether inter- and intraspecific factors improved the models. Finally, I repeated the modelling process with interaction covariates included and applied a backward stepwise procedure to obtain the most parsimonious model. I then investigated whether landscape features, bioclimatic factors, individual variation or inter- and intraspecific interactions influenced the habitat selection and movement of lions. Furthermore, for each pair of individuals that had overlapping ranges within their constructed T-LoCoH utilization distributions, I examined the properties of intersecting hulls using hull association metrics. In collaboration with colleagues, a novel method was developed to quantify approach and retreat movements that occurred during fine-scale sampling intervals to understand the types of interaction between pairs of individuals. All analyses were conducted in R version 3.5.1 (R Core Team, 2018).

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CHAPTER TWO

Coursing hyenas and stalking lions: the potential for inter- and intraspecific interactions

2.1. Abstract

1. Resource partitioning promotes coexistence among sympatric guild members, and carnivores reduce interference competition through behavioral mechanisms that promote spatio-temporal separation.

2. We analyzed spatiotemporal movement and activity patterns of sympatric lions *Panthera leo* and spotted hyenas *Crocuta crocuta* to ascertain the mechanisms facilitating their coexistence within both a semi-arid and a wetland ecosystem. We used GPS satellite collars with accelerometers on lions and spotted hyenas from the Etosha National Park in Namibia between 2013-2015, and the Chobe National Park, Linyanti Conservancy, and the NG32 concession in the Okavango Delta, Botswana between 2015-2017. We identified recurrent high use (revisitation) and extended stay (duration) areas within individuals' home-ranges, and correlated environmental variables with movement-derived measures of inter- and intraspecific interactions.

3. Lions and spotted hyenas shared parts of their home ranges across reserves, between seasons, and within diel cycles. Spatial overlaps among competitors and conspecifics occurred at the edge of home ranges, around water-points, and along pathways between patches of high use areas. Areas of overlap between lions and hyenas in the core use areas differed between ecosystems, in that they were larger in arid environments compared to mesic environments, but expanded during the wet season in both. Lions from arid ecosystems shared more of their home ranges with spotted hyenas, while lion conspecifics shared more of their home ranges in mesic environments than in arid environments. Despite shared space use, we found evidence for subtle temporal differences in the movement patterns and nocturnal activity periods between the two predators, suggesting a fine localized-scale avoidance strategy. Time-use patterns (revisitation frequency and duration) within individual home ranges were influenced by land cover categories and the time of day, with interspecific interactions the next most important factor. Additional factors for lions were intraspecific interactions and, for hyenas, moon illumination and probability of encountering foraging ungulates attracted to old anthrax carcass sites in Etosha, and distance to permanent water in Chobe/Linyanti.

4. *Synthesis and applications.* Our results suggest that both lions and spotted hyenas mediate the potential for interference competition through subtle differences in temporal activity, fine-scale habitat use differentiation, and localized reactive-avoidance behaviours. In addition, the recursion rate and duration of time at specific locations, according to locales of competitor probabilities, were similar among female lions and both sexes of hyenas, but different for male lions. These findings enhance our understanding of the potential effects of interspecific interactions among large carnivore space-use patterns within an apex predator system, and show adaptability across heterogeneous and homogeneous environments. Future conservation plans should emphasize the importance of inter- and intraspecific competition within large carnivore communities, particularly moderating such effects within increasingly fragmented landscapes.

2.2. Introduction

Spatio-temporal partitioning helps stabilize multi-species communities in which more than one species use the same resource (Schoener 1974a, Chesson 1985, Edwards et al. 2015). More specifically, species whose ranges overlap forage different types of food, feed at different temporal schedules (Mills & Biggs 1993, Scognamillo et al. 2003, Sinclair et al. 2003, Radloff &

Du Toit 2004, Périquet et al. 2015b, Herrera et al. 2018), demonstrate habitat separation, exhibit nonsynchronous spatial overlap or temporal partitioning (Mitchell & Banks 2005, Nelson et al. 2007, Berger & Gese 2007, Hayward & Slotow 2009, Pereira et al. 2012, Bender et al. 2017). Environmental heterogeneity provides temporary refugia where the risk of competition and injury is reduced (Pereira et al. 2012, Llaneza et al. 2018). In addition, when there is an abundance of surplus resources the amount of food attracts numerous competitors, such that the energy required to exclude them becomes costly, and, therefore, competition ceases (Maher & Lott 2000). Resource use varies widely among sympatric carnivores (Fedriani et al. 2000, Neale & Sacks 2001, Andheria et al. 2007, Nelson et al. 2007, Sollmann et al. 2012, Chetri et al. 2017, Zielinski et al. 2017, Bender et al. 2017, Astete et al. 2017), including African carnivores (Valeix et al. 2010, Cozzi et al. 2012, Vanak et al. 2013, Swanson et al. 2014, Périquet et al. 2015b, Edwards et al. 2015, Périquet et al. 2016, Swanson et al. 2016, Dröge et al. 2017, Ramesh et al. 2017, Davies et al. 2021), and is presumed to promote coexistence (MacArthur & Levins 1967, Schoener 1974b, Chesson 2000, Di Bitetti et al. 2010).

Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) are mainly crepuscular and nocturnal predators that demonstrate at least an 80% overlap between their daily activity budgets (Hayward & Slotow 2009). Although both species are sometimes active during cool winter days (Kruuk 1972, Schaller 1972, Mills 1990), they do not appear to use temporal partitioning to avoid interference competition (Hayward & Hayward 2007). The population densities of both lions and spotted hyenas are primarily influenced by the abundance of prey, and are, thus, positively correlated in some areas (Hayward et al. 2007, Loveridge et al. 2009). As increasing prey abundance leads to an increase in the densities of both predators, however, the potential for interference competition increases with the likelihood of interspecific encounters (Périquet et al.

2015b). Nonetheless, it appears that spotted hyenas derive benefits from sharing areas with lions. Hyenas appropriated up to 100% of lion kills in the Ngorongoro Crater when adult male lions were absent (Honer et al. 2002). In the Amboseli National Park, hyenas did not avoid lion sounds from audio-call stations, and sometimes even approached these stations in response to lion roars (Watts et al. 2010). This type of behaviour likely persists because avoiding lions may cost hyenas missed scavenging opportunities, given the high degree of overlap in their diets (Hayward & Kerley 2008).

The ecological dynamics between lions and spotted hyenas are thus complex, and coexistence may be occurring because of the spatiotemporal partitioning of resources at fine spatial and temporal scales. Avoidance of potential competitors may be possible through small differences in the temporal use of habitats and shared resources (Karanth & Sunquist 2000). Competitor avoidance is a behavioural strategy that reduces the probability of encounters within the foraging range of potential deadly rivals, thus enhancing the survivorship and fitness of the individual (Lima & Dill 1990, Durant 2000a). However, avoidance of competitors is likely to invoke costs, such as a reduction in activity, a reduction in foraging rate or efficiency, or an increase in the use of refugia due to the perceived risk of predation (Ward et al. 1997, Durant 1998, Hilborn et al. 2018).

Lions and hyenas appear to reduce some of the competitive effects of a shared diet by hunting prey of different sizes or ages (Kruuk 1972, Mills 1984, Mills & Biggs 1993, Périquet et al. 2015a). Lions are able to hunt larger prey than spotted hyenas (Purchase 2004), but large groups of hyenas have adapted to hunting migratory prey populations in the Serengeti with the use of a unique commuting system (Hofer & East 1993). Despite the lack of evidence for definite temporal partitioning in the activity periods of lions and hyenas, they exhibit slight differences during periods of activity. In several sites within Southern Africa and Tanzania, spotted hyenas were active for one continuous period during the night, while lions' were active for two or three periods (Hayward & Slotow 2009), whereas in the Southern Rift Valley of Kenya, hyenas were active after sunset and from the middle of the night to sunrise, with lions active throughout the night from 22h00 to dawn and after sunrise (Schuette et al. 2013). Therefore the two predators may actually be avoiding each other by utilizing the same prey abundant areas but at different times. In addition, food competition among lions and hyenas may be alleviated during periods of high resource availability, such as in the case of ungulate carcasses during anthrax outbreaks (Getz 2011). Furthermore, both species employ differences in their hunting behaviour, with hyenas mainly hunting large groups of prey and selecting target animals from rushing herds (Kruuk 1972), while lions mainly employ stalk-and-ambush tactics of small herds of prey (Schaller 1972). Thus, lions have the advantage in closed habitats while hyenas are likely to benefit from open habitats because of their cursorial nature. Lions tend to select for habitats with tall grass or steep embankments that promote hunting success and increases the catchability of prey (Van Orsdol 1984, Funston et al. 2001, Hopcraft et al. 2005), while hyenas seemingly appear to be able to utilize any type of habitat as habitat generalists (Kruuk 1972, Mills 1990).

Although many studies have focused on the factors underlying spatio-temporal patterns in species distributions and resource use, few studies have examined the relationship between predator movement responses to each other to explain spatial overlap patterns. To our knowledge, studies have yet to elucidate fine scale movement and behavioural patterns in sympatric lions and spotted hyenas occurring in large scale natural systems that share much of the same resources, as mechanisms facilitating coexistence between these two predator species.

This study fills this gap, by analysing fine-scaled movement data obtained from two different ecosystems subject to seasonal influxes of resources, to discern the behavioural differences that allow lions and spotted hyenas to co-exist. In particular, co-existence was assessed at the arid and mesic extremes of their environment, and the spatiotemporal or behavioural differences in their space use and activity patterns examined.

Data were collected using Global Positioning System (GPS) satellite telemetry collars and activity accelerometers outfitted on 19 lions and 14 spotted hyenas located in both a large fenced National Park and within free-ranging areas of two distinct ecosystems. These data were analysed with the following objectives in mind: (1) to ascertain the environmental and bioclimatic factors influencing the spatiotemporal patterns of lions and spotted hyenas related to the age, sex, and condition of individuals; and, (2) to determine whether these were primarily influenced by heterospecific or conspecific competitors. We proceeded by first assessing the differences among the range use, movement characteristics, and activity patterns of the two species. We then compared and contrasted species movement patterns at various distances to competitors and conspecifics. To assess whether lion and hyena space-use patterns signify avoidance competition, we identified areas across lion and spotted hyena ranges with locations of higher-than-expected revisitation rates or locales of long-duration visits, and assessed whether these shifted in response to the presence of, or proximity to competitors. We also related these patterns to the distribution of resources at a landscape scale, including anthrax endemic areas in the arid environment. Finally, we evaluated the relative roles of environmental variables versus inter- and intraspecific interactions in determining lion and hyena spatial distributions and movements. We expected that the space use patterns of lions and spotted hyenas would be driven by certain landscape features linked to the availability of potential resources. We expected lions and hyenas to frequent and remain within areas of high Normalized Difference Vegetation Index (NDVI) correlated to high prey density, and to frequent and to remain close to water sources. While we expected environmental variables to be key drivers on lion and hyena space use patterns, we also expected that social interaction variables would also be important. We expected intraspecific competitors to elicit a stronger behavioural response than interspecific competitors, and we also expected that hyenas would reactively avoid lions while still utilizing habitats of extended lion use, so as to benefit from potential resources (i.e., scavenging from carrion of lion kills). Although we expected lions and hyenas to overlap spatially, we expected that they would adopt temporal mechanisms to facilitate coexistence and to avoid competition. Thus, we expected lions and hyenas to actively avoid each other by seeking out areas of low competitor probabilities and at far distances from competitors.

2.3. Methods

2.3.1. Ethics statement

Relevant permits required to carry out the research were obtained from the Ministry of Environment and Tourism, Namibia (Research/Collecting Permits 1724/2012, 1834/2013, 1956/2014) and from the Department of Wildlife and National Parks, Botswana (Research Permit EWT 8/36/4 XXVIII (35)). All animal handling procedures were conducted with the ethical clearance of the Animal Research Ethics Committee of the University of KwaZulu-Natal, South Africa (009/13/Animal), and the Institutional Animal Care and Use Committee of University of California at Berkeley (IACUC Protocol #R217-0512B) and Virginia Tech (IACUC Protocol # 15-012). Namibian specimens were shipped to RSA and Germany under

CITES permits for the Regulations of Threatened or Protected Species (Permit/Certificate No. 0045192 and 157940).

2.3.2. Study area

In brief, the study area covered 19,200km^2 within the protected areas of the Southern Africa region: the Etosha National Park, a semi-arid savanna in northern Namibia; the Chobe National Park, Linyanti Conservancy, and the NG32 concession of the Okavango Delta, which comprises the Kalahari floodplains of northern Botswana (Fig. 2.1, see Supplementary materials for additional details on these sites). In the Etosha National Park, certain regions are subject to an influx of seasonal resources from annual anthrax outbreaks (Lindeque & Turnbull 1994). The bacterial pathogen, *Bacillus anthracis*, is endemic as a major disease of various game species (Berry 1993), and provides a significant subsidy of ungulate carcasses to predators and scavengers (Getz 2011). The Chobe-Linyanti region, hereafter “Chobe”, experiences a seasonal influx of migratory ungulate prey during the dry season in which they congregate around the perennial river (Sianga et al. 2017). Situated within the southeastern floodplains of the Okavango Delta, the NG32 concession is subject to an unimodal, annual flood pulse characterized by high variability in interannual flooding (Murray-Hudson 2009), and typically comprises a higher prey abundance during the dry season (Bartlam 2010). All study sites, therefore, have a season pulse in prey availability, although through different mechanisms.

2.3.3. Data collection

A total of 19 lions (13 females and 6 males) and 14 spotted hyenas (10 females and 4 males) were fitted with GPS satellite telemetry collars with dual-axis accelerometers

(IridiumTrackM, Lotek Wireless Inc., Newmarket, Ontario, Canada) (Appendix S2.1; see Supplementary materials for additional details of collared animals and capture and sampling protocols). Collars were programmed to record GPS fixes on a schedule that consisted of a fix every 30 min during nocturnal periods (18h00 – 6h00 for Etosha individuals, and 17h00 – 8h00 for Botswana individuals), a fix every 5 min for two hours twice daily, once after sunset (19h00 – 21h00) and once before sunrise (4h00 – 6h00), and single diurnal fixes both at 10h00 and 14h00. For each datum, activity was averaged from acceleration collected in 8 second bursts over a duration of 240 seconds, and given a relative range between 0 and 255 (activity monitor values [AMVs]) to characterize the mean activity/acceleration. Relocation and activity data were downloaded from retrieved collars at the end of the study, with a subset of relocation data obtained from the satellite uplink of unretrieved collars via the Lotek web service (see Supplementary materials for details on data from unretrieved collars). Etosha lions comprises of 11 individuals from 8 prides and 3 male coalitions, while Botswana lions comprises of 8 individuals from 5 prides and 3 male coalitions. Prides consisted of adult females with subadult males and females. Etosha spotted hyenas comprises of 8 individuals from 8 clans during the dry season, and 7 individuals from 7 clans during the wet season. Chobe spotted hyenas comprises of 4 individuals from 4 clans in the dry season, and 5 individuals from 5 clans in the wet season.

We retrieved 63% of all possible relocations while collars were deployed, due to the loss of collars from individuals that were killed, or for which we were unable to retrieve the collar (n = 3 lions and 6 hyenas). From the retrieved relocations (n = 575,418) over all study sites, 73% were from lions with 27% from spotted hyenas. This dataset is roughly split between the two ecosystems with 43% of relocations from Etosha and 57% from Botswana. However, our relocation records from Etosha are significantly more complete (99.6% for lions and 84.1% for hyenas) compared to our relocation records from Botswana (53.3% for lions and 35.8% for hyenas). All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018), and all Geographic Information System (GIS) applications were conducted in ArcGIS (ESRI ArcMap v.10.0, Redlands, CA, USA). See Table 2.1 for a list of expectations and key results.

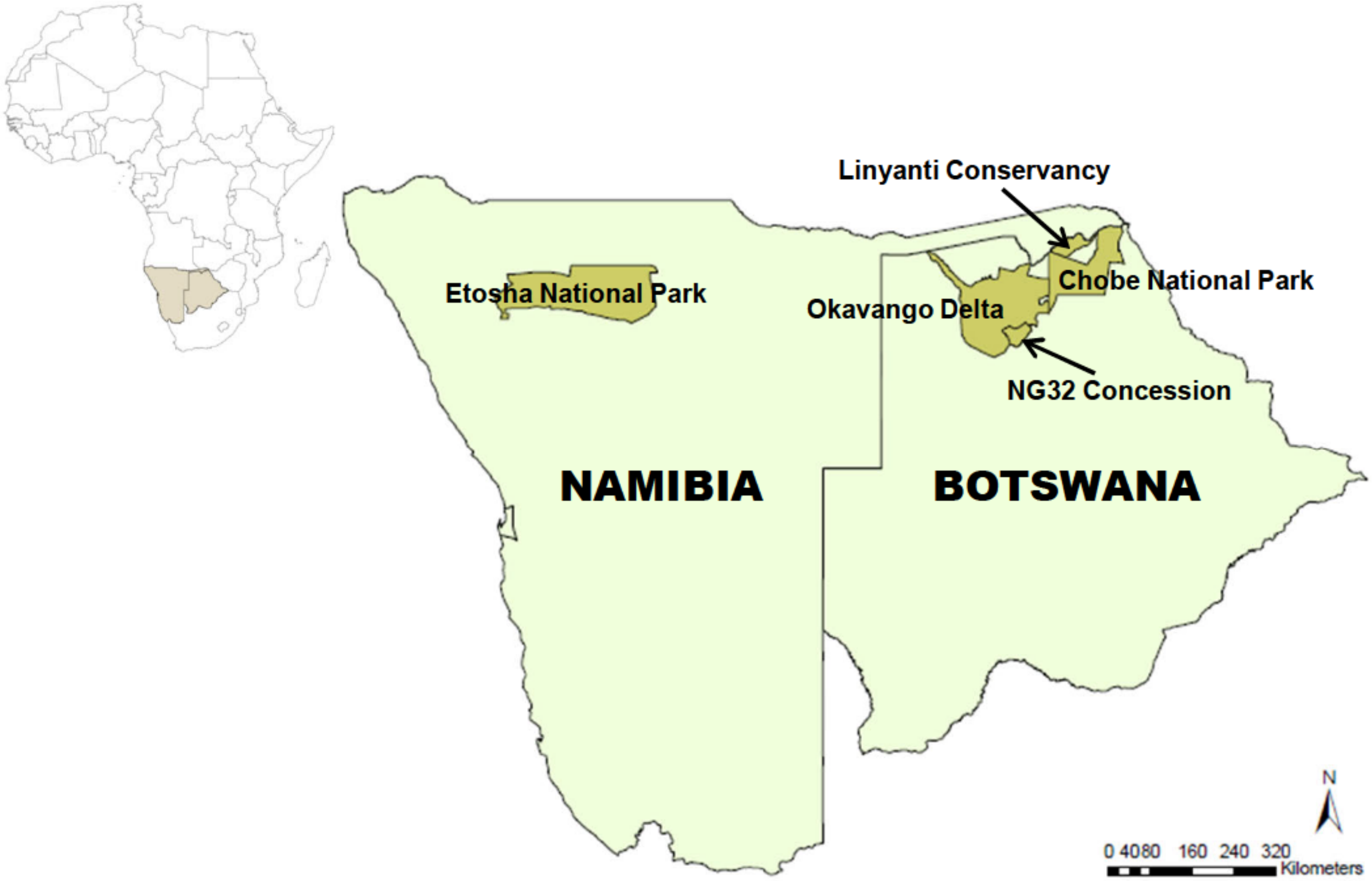

Figure 2.1. Location of the study areas. The map of the African continent shows the countries of Namibia and Botswana shaded, and the protected areas within these countries where the study was conducted. Maps were generated with ArcGIS (ESRI ArcMap v.10.0).

Table 2.1. Expected behavioural patterns for lions and spotted hyenas, based on literature, for analyses undertaken in this study. The analyzed context is listed in the column on the far left, with the summarized key results on the right. Key results that were not in agreement with the expected patterns are emphasized in bold.

Context	**Source**	**Expected behavioural patterns**		**Key results**
		Lion	**Spotted hyena**	
Range use	*(Boydston et al. 2003a, Kolowski & Holekamp 2009, Périquet et al. 2016, Kittle et al. 2016, Zehnder et al. 2018)*	individuals will have larger home ranges and core areas during nocturnal periods and in the wet season, and in arid environments		- **no differences in sizes of home ranges and core areas across reserves and diel cycles;** - lions had larger home ranges and core areas in wet season; - hyenas had larger core areas in wet season
		home ranges and core areas of lions and hyenas will overlap more in mesic environments		- **lions and hyenas shared more of their core areas in Etosha than in Chobe;** - lions in Etosha shared more of their home ranges with hyenas than they did with other lions;
		lions will have smaller home ranges and core areas than hyenas	hyenas will have larger home ranges and core areas than lions	- **no differences in sizes of home ranges and core areas between species**
Activity patterns	*(Kolowski et al. 2007, Hayward & Slotow 2009)*	individuals will exhibit increased activity during the night, in the wet season, and with lower activity during the day, in the dry season		- lions and hyenas had increased activity during the night, **but no differences across seasons**; - hyenas had higher activity than lions
Movement characteristics	*(Funston et al. 2001, Boydston et al. 2003b, Hopcraft et al. 2005, Stratford & Stratford 2011, Vanak et al. 2013, Périquet et al. 2015a, 2016)*	lions will move at slower speeds, have smaller step lengths and net-squared displacements, and have more tortuous movement paths than hyenas	hyenas will move at faster speeds, have larger step lengths and net-squared displacements, and have straighter movement paths than lions	- hyenas moved at faster speeds and had larger step lengths and net-squared displacements than lions; - lions had more tortuous movement paths than hyenas during nocturnal periods; - **Chobe hyenas had more tortuous movements than Chobe lions after sunrise (from 6h00-10h00)**
Age	*(Funston et al. 2003, Boydston et al. 2005, Elliot et al. 2014)*	older individuals will have larger home ranges and core areas		- **no relationship between age and home ranges or core areas**
Gender	*(Funston et al. 1998, 2001, Boydston et al. 2001, 2005, Packer et al. 2005)*	males to have larger home ranges and core areas than females	females to have larger home ranges and core areas than males	- **no differences between male and female lion home ranges and core areas;** - female hyenas had larger home ranges and core areas than male hyenas during the wet season
Body Condition	*(Otali & Gilchrist 2004, Kolowski & Holekamp 2008)*	individuals with higher conditions will have smaller home ranges / core areas, and move in slower, more tortuous movement paths	individuals with higher conditions will have smaller home ranges / core areas, and move in faster, straighter movement paths	- **no relationship between body condition scores and home range or core areas;** - male lions with low body condition scores moved at higher speeds and had more directional movements than females; - **female lions with high body condition scores moved at higher speeds** and had more tortuous movements **than males;** - hyenas with low body condition scores had more tortuous movements, while hyenas with high body condition scores had more directional movements

Group Size	*(Cooper 1989, 1991, Holekamp et al. 1997, Mosser & Packer 2009, Loveridge et al. 2009)*	individuals from larger groups will have smaller home ranges and core areas		- **no relationship between pride or clan sizes and home ranges or core areas**
Anthrax areas	*(Good et al. 2008, Bellan et al. 2012, Dougherty et al. 2020)*	Etosha individuals will shift home ranges to encompass anthrax areas, and will have slower speeds and more tortuous paths in anthrax endemic areas		- 73% of Etosha lions and 75% of Etosha hyenas shifted their home ranges to the anthrax endemic areas during the wet season; - **no difference in speed or tortuosity of Etosha lions** - Etosha hyenas had more tortuous movements in anthrax areas with higher probabilities of site-attracted foragers, and had more directional movements in areas with low probabilities of site-attracted foragers
Lunar cycle	*(Theuerkauf et al. 2003, Packer et al. 2011, Cozzi et al. 2012, Broekhuis et al. 2014)*	individuals will have higher activity, slower speeds, and more tortuous paths in low moonlight conditions	individuals will have higher activity, faster speeds, and straighter movement paths in bright moonlight conditions	- lions had higher activity during low moonlight conditions, and hyenas had higher activity during brighter moonlight conditions; - **Botswana lions had** larger step lengths on new moon nights, with **more tortuous movements on full moon nights;** - Etosha lions and Chobe spotted hyenas had more tortuous movements on new moon nights; - **Etosha hyenas** had larger step lengths and **were more tortuous in nights preceding full moon nights**
Competitor / conspecific core use areas	*(Cooper 1991, Trinkel & Kastberger 2005, Périquet et al. 2016, Lehmann et al. 2016)*	individuals will have higher activity, faster speeds, straighter paths inside competitor / conspecific core areas, and lower activity, slower speeds, more tortuous paths outside competitor / conspecific core areas		- Chobe lions and Chobe hyenas had higher activity inside competitor core areas; - hyenas moved at faster speeds inside of competitor core areas; - **Etosha lions had more tortuous movements,** while Chobe lions had more directional movements **inside competitor core areas** - Chobe lions were more directional inside conspecific core areas; - **Etosha hyenas had more tortuous movements inside conspecific core areas;** - **Chobe hyenas had lower activity and moved at slower speeds inside conspecific core areas**
Distance to nearest competitor / conspecific	*(Cooper 1991, Trinkel & Kastberger 2005, Périquet et al. 2015b, a, Lehmann et al. 2016, Kittle et al. 2016)*	individuals will have higher activity, faster speeds, straighter paths at closer distances to competitors / conspecifics, and lower activity, slower speeds, more tortuous paths at further distances to competitors / conspecifics		- Chobe hyena had higher activity at closer distances to competitors; - Etosha hyenas moved at faster speeds at closer distances to competitors; - **Etosha lions had more tortuous movements at closer distances to competitors** - **Lions and Etosha hyenas had higher activity, and Etosha lions moved at faster speeds at closer distances to conspecifics than to competitors**

Revisitation & Duration (RD) – bioclimatic factors	*(Hayward & Hayward 2007, Hayward & Slotow 2009, Cozzi et al. 2012, Schuette et al. 2013, Edwards et al. 2017, Sogbohossou et al. 2018)*	individuals will have increased recursivity during the night, in cool temperatures, during the wet season, and will have extended stays during the day, in hot temperatures, and during the dry season		- individuals had increased recursions during nocturnal periods, and **varied between revisitation and duration across temperatures and seasons**
		individuals will have increased recursivity in low moonlight conditions, and extended stays in bright moonlight conditions	individuals will have increased recursivity in bright moonlight conditions, and extended stays in low moonlight conditions	- **Etosha hyenas had increased recursivity during low** and bright **moonlight conditions,** with extended duration between new and full moons - **moonlight conditions had no effect on lion RD patterns**
Revisitation & Duration (RD) – landscape features	*(Kolowski & Holekamp 2009, Valeix et al. 2010, de Boer et al. 2010, Roever et al. 2010, Latham et al. 2011, Bellan et al. 2012, Abrahms et al. 2015, Edwards et al. 2015, Dickie et al. 2016, Davies et al. 2016, Kushata et al. 2018)*	individuals will have higher recursions to areas of high NDVI, to anthrax endemic areas, carcass sites, water sources, and roads; and will have extended stays in areas of high NDVI, in anthrax endemic areas, at carcass sites, water sources, and far from roads		- land cover categories was one of the most important factors explaining for RD patterns in all individuals; - Etosha hyenas had higher recursions to, and longer durations in areas with higher probability of site-attracted foraging ungulates; - **Chobe hyenas had higher recursions to locations far from water** and had extended stays in areas closer to water sources
Revisitation & Duration (RD) – interaction covariates	*(Cooper 1991, Durant 1998, Honer et al. 2002, Funston et al. 2003, Höner et al. 2005, Trinkel & Kastberger 2005, Watts & Holekamp 2008, 2009, Holekamp & Dloniak 2010, Watts et al. 2010, Benhamou et al. 2014, Périquet et al. 2015b, a, 2016, Lehmann et al. 2016, Swanson et al. 2016, Dröge et al. 2017, Kushata et al. 2018)*	individuals will have higher recursions to areas far from competitors / conspecifics, in areas with a low probability of encountering competitors / conspecifics, and inside competitor / conspecific core areas; and will have extended stays in areas far from competitors / conspecifics, in areas with a low probability of encountering competitors / conspecifics, and outside competitor / conspecific core areas		- **female lions and hyenas** had longer durations in areas of low competitor probabilities, at far distances to competitors and outside competitor core areas, and **had increased recursions to areas of high competitor probabilities, at close distances to competitors and inside competitor core areas;** - **male lions had longer durations in areas of high competitor probabilities** - **lions were equally split between revisitation and duration in areas of high and low conspecific probabilities;** - **hyenas had longer duration in areas of high conspecific probabilities,** and had higher recursions in areas of low conspecific probabilities, at far distances to conspecifics, and outside conspecific core areas

2.3.4. Species range use

The movement dataset of the lions and spotted hyenas were collected over a four year period split between the two study areas. From this dataset, we removed individuals with less than 30 tracking days, and created different subsets of sampling intervals to ensure for scale appropriateness in subsequent analysis (Thurfjell et al. 2014). Sampling intervals occurred every 30 or 5 min (depending on the sampling frequency over that sampling period, see above). The regularly sampled data downloaded from the collars all had some incidences of missed fixes (mean ± standard error (SE): lion 0.57 ± 0.03%, hyena 0.44 ± 0.06%), while the relocation fixes uploaded via satellites transmitted only a subset of locations during the study period in order to conserve collar batteries. Where collars were unable to be retrieved, movement data was downloaded from the Lotek web service, which consisted of relocations once every third fix of the programmed schedule (15 min fixes during the 5 min schedule, and 90 min fixes during the 30 min schedule). Thus the satellite data for some individuals (n = 3 lions, n = 6 hyenas) had missed fixes that ranged between 5 and 1040 minutes. Therefore, for analyses that included satellite individuals, we removed data that had a time difference in GPS fixes greater than 15 min from the 5 min schedule, and greater than 90 min from the 30 min schedule (which tended to occur towards the end of the study as a result of failing batteries). We then applied the continuous-time movement modelling "*ctmm*" R package (Calabrese et al. 2016) to fill in the missing coordinates in the schedule where required.

The data for analyses comprised of relocations from both collared individuals and relocations uploaded via satellite filled in with the ctmm method. From this data, nocturnal periods of relocations every 30 min were organized to include only fixes obtained during times of 18h00–6h00 or 17h00–8h00, and split into dry and wet seasons for the construction of home ranges and core areas. We filtered out 4 h locations over a 24 h period (maximum 6 fixes per day) from the relocation data, which were also split into dry and wet seasons to use for a comparison of nocturnal and diurnal ranges using the t-test.

We constructed two types of Utilization Distributions (UDs) for each individual's overall and seasonal ranges. First, we used the Home Range Estimation "*adehabitatHR*" R package kernel density estimator (KDE) with the reference bandwidth as the smoothing factor (Calenge 2006). Second, we used the *a*-LoCoH (local convex hulls) adaptive method (Getz et al. 2007, Lyons et al. 2013), which facilitates the identification of regularly revisited sites, such as dens, waterholes, or riverbanks (Getz et al. 2007). We used the 95% and 50% UDs (both methods) to represent respectively the home ranges and core use areas of individuals. We used the *t*-test in R v.3.5.1 to compare the sizes of home ranges and core areas among competitors (lions and spotted hyenas) with regards to location (Etosha versus Chobe), seasons, and segments of diel cycles. Within the kernel density ranges and utilization distributions, we used the intersection function from the Interface to Geometry Engine "*rgeos*" R package (Bivand et al. 2020) to compute the areas of overlap between neighbouring individual ranges, and used the *t*-test to determine the significance of differences in species' overlapping ranges among ecosystems, across seasons and diel cycles.

2.3.5. Species movement patterns

To analyze the movement patterns of lions and spotted hyenas, we used the Analysis of Animal Movements "*adehabitatLT*" R package (Calenge 2006) to calculate the movement metrics of the two species. We calculated the speed and distance travelled (step length), path tortuosity (turning angle), and net-squared displacement (NSD) for each individual, and combined these individuals into species groups. Since turning angles range continuously on a circular scale from -180 to 180, we used the Circular Statistics "*CircStats*" R package (Agostinelli & Lund 2018) to calculate the vectorized mean turning angle, which treats each observation as a vector on the unit circle to indicate the direction of the resultant vector (Jammalamadaka & Sengupta 2001). Note that for CircStats, Watson's two sample test is significant at $p < 0.10$ (Agostinelli & Lund 2018). We then compared and contrasted the seasonal, sex-specific movement metrics of lions and spotted hyenas from each of the two ecosystems with the t-test and using the Watson's two sample test for turning angles. We also assessed these differences over various times of the day, between diel cycles, land cover types, and across seasons. In addition, we used the analysis of variance (ANOVA) to assess these differences in relation to the lunar cycle.

2.3.6. Species activity patterns

We further analyzed the seasonal activity patterns of lions and spotted hyenas according to the full moon and new moon phases of the lunar cycle, as in Cozzi et al. (2012). We defined full moon nights when ≥95% of the lunar disc was illuminated and new moon nights were when moonlight intensity was ≤5%. For each day during full moon and new moon phases, we divided each 24 h period into seven different sections (afternoon, dusk, night, nadir, night-end, dawn, morning) to reflect the main activity periods for lions and spotted hyenas (Hayward & Slotow 2009). We used Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase "*suncalc*" in R (Thieurmel & Elmarhraoui 2019) to calculate the times of periods for each day with dusk lasting from sundown to the end of evening astronomical twilight and dawn from the end of morning astronomical twilight to sunrise. The period between the end of evening twilight to the beginning of morning twilight was divided into three equal intervals in minutes to reflect night, nadir, and night-end. The day period from sunrise to sundown was divided from noon into morning and afternoon periods. We then calculated the proportion of the averaged activity measures that occurred during each of these periods. We used the t-test to compare the average activity of lions and hyenas from different periods, and we used the ANOVA to test whether predator activity differed across lunar phases.

Other factors such as age, sex, body condition scores, and group size, were analyzed to determine their effects, if any, on the spatial use patterns of lions and spotted hyenas across both ecosystems. As our sample sizes were small, we grouped lions together from all areas (*n* = 19), and did the same for the hyenas (*n* = 13). We used the Spearman's correlation to analyze for relationships between home range size and the ages of animals, or the sizes of the group. We used ANOVA to assess whether lion and hyena movement metrics differed according to the body condition score of individuals. We also used ANOVA to assess whether the movement metrics of the Etosha predators (lions, *n* = 11; hyenas, *n* = 8) differed according to the probabilities of site-attracted foragers in locations that consisted of anthrax positive carcasses from previous years (see Supplementary materials for details of the probability layer of site-attracted foragers).

For those individuals that had relocations within the core use area (or 50% isopleth) of either competitors or conspecifics, we assessed whether such proximity had any effect on the activity patterns as well as the speed and tortuosity of the focal animal. We assigned a value of 1 to each individual's location that occurred within the core use area of a competitor's or conspecific's UD, and assigned a value of 0 to each individual's location not within a competitor or conspecific core use area. We averaged the activity measures and movement metrics for each individual occurring inside and outside the core use areas of competitors and conspecifics. We then tested whether the average activity and movement metrics of lions and spotted hyenas differed significantly from when they were inside and outside of the core use areas of competitors and conspecifics with the ANOVA. We also used the t-test to compare whether movement metrics differed when at close distances to competitors or conspecifics.

2.3.7. Interaction variables

We included interaction variables to examine the influence of competitors and conspecifics on the rates of revisitations and visit durations of lions and spotted hyenas within their ranges. We measured distances between collared individuals and constructed GIS layers representing areas with a probability of competitor and conspecific use to analyze for interactive effects. To obtain the distances between collared individuals, we developed a temporally aligned matrix of each individual that overlapped with each other during the collaring period. For each sampling record of collar overlap, we measured the minimum Euclidean distance of that individual to all other collared individuals at all locations over the same times.

Individual seasonal UDs were overlaid and pixel cell values averaged to generate a total combined lion UD and a total combined spotted hyena UD for each of the dry and wet seasons. We converted the combined kernel UDs to volume UDs to obtain probability of use values for each cell. We subtracted volume UD values from 100 as in Kittle et al. (2016), to obtain a more intuitive value with low use cells reflected by low values and high use cells reflected by high values. UD pixel values were then extracted and assigned to each locational point as a probability of competitor use area in ArcGIS v.10.0. We also repeated the process as above for a probability of conspecific use area. To construct the layer of the potential conspecific range, we overlaid the seasonal UDs of all other individuals of the same species, while excluding the individual the layer was being created for.

The Etosha lion UD was constructed from 52,547 relocations for the dry season and 65,428 relocations for the wet season. The Chobe lion UD (excluding the Okavango individuals) was constructed from 30,016 relocations for the dry season and 43,356 relocations for the wet season. Etosha spotted hyena dry season UD was constructed from 57,211 relocations, with the wet season UD from 70,724 relocations. Chobe spotted hyena dry season UD was constructed from 14,546 relocations, with the wet season UD from 15,335 relocations.

2.3.8. Ecogeographical variables

Ecogeographical variables (EGVs) such as distance to water, land cover types, and precipitation that have been statistically associated with species distribution (Varela et al. 2009, Durant et al. 2010, Abade et al. 2014), and were attached to each point within the revisitation duration (RD) space to evaluate their influences on lion and spotted hyena revisitations and visit durations (Table 2.2). We used ArcGIS (ESRI ArcMap v.10.0, Redlands, CA, USA) to measure the minimum Euclidean distance from all location points to various geographical features and landscape attributes, including distance to carcasses in Etosha (see Supplementary materials for additional details on the collection of Etosha carcass data).

Digital elevation maps of the four study areas were obtained from Landsat 8 images, courtesy of the U.S. Geological Survey, using a spatial resolution of 30 m. We derived the slope and aspect from these digital elevation maps in ArcGIS. Open-source land cover maps generated from LandSat thematic mapper data were downloaded for Namibia and Botswana (2010 Scheme II) via the RCMRD GeoPortal (http://geoportal.rcmrd.org), to which we assigned arbitrary values to reflect discrete land cover categories. We overlaid site-specific individual seasonal UDs onto the country's raster land cover map and obtained the outermost boundary line, from which we constructed a polygon of the study area that was inclusive of all individual UDs for that study site. We then used the land cover values assigned to each pixel to calculate the percent available land cover classes for each site. We compared this against the frequency of relocations from lions and hyenas to determine whether individuals preferred certain land cover types. We used Google Earth Engine's (Gorelick et al. 2017) Normalized Difference Vegetation Index (NDVI) 8 day composites from the duration of the study period to obtain the mean NDVI values for each of the four study areas for each of the dry and wet season. As a measure of vegetation productivity (Gaitán et al. 2013, Madonsela et al. 2018, May et al. 2018, Fern et al. 2018), NDVI has been used as an index of prey availability (Gavashelishvili & Lukarevskiy 2008, Abade et al. 2014), with areas of increased vegetative cover correlated to increased ungulate and herbivore biomass (Bårdsen & Tveraa 2012, Hurley et al. 2014, Stoner et al. 2016, Albon et al. 2017, Ciach & Peksa 2018). These Landsat 8 composites are generated from Tier 1 orthorectified scenes, using the computed top-of-atmosphere reflectance. All the images from each 8-day period are included in the composite, with the most recent pixel as the composite value. NDVI values ranged from -1 to 1, with negative values corresponding to clouds and water, values near zero representing rock and bare soil, moderate values of 0.2 – 0.3 representing shrub and grassland, with high values close to 1 indicating temperate forests and tropical rainforests. Using ArcGIS, we calculated the mean center for each individual's range, from which we obtained the relevant sunrise/set and moonrise/set times (Astronomical Applications Department of the U.S. Naval Observatory, from https://aa.usno.navy.mil), and interpolated the average precipitation from available CMAP Precipitation data (Climate Data and Resources, NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from https://www.esrl.noaa.gov.psd/). The Lunar Phase and Distance, Seasons and other Environmental Factors "*lunar*" package in R version 3.5.1 (R Core Team, 2018) was used to assign moon phases and moon illumination values (ranging from 0 = new moon to 1 = full moon) to all locations, according to each location's unique timestamp. For any location points collected between moonset and moonrise, the moon illumination was assigned a false logical vector.

Table 2.2. Description of ecogeographical variables (EGVs) used for cluster analyses. EGVs were included in cluster analyses of the revisitation and duration (RD) space for each lion and spotted hyena individual within Etosha National Park, Namibia and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana.

Ecogeographical Variables	**Description**	**Data Resolution/Type**
Bioclimatic variables	Time of day	each relocation
	Temperature	each relocation
	Season	binary variable
	Moon illumination	probability index, 0-1
	Precipitation amounts	pentad average
Landscape features	Slope	30m x 30m
	Land cover categories	30m x 30m
	NDVI	30m x 30m, seasonal mean
	Anthrax carcass probability	UD value
	Distance to nearest available carcass	Euclidean, in m
	Distance to nearest permanent water source	Euclidean, in m
	Distance to nearest seasonal water source	Euclidean, in m
	Distance to nearest road	Euclidean, in m
Human disturbances	Distance to nearest anthropogenic feature	Euclidean, in m
*Interspecific interactions**	Distance to nearest competitor	Euclidean, in m
	Competitor probability	UD value
	Competitor core	1 = inside core, 0 = outside core
*Intraspecific interactions**	Distance to nearest conspecific	Euclidean, in m
	Conspecific probability	UD value
	Conspecific core	1 = inside core, 0 = outside core

** not included in cluster analyses of lions from Okavango Delta, Botswana.*

2.3.9. Time-use metrics

To assess how lions and spotted hyenas adjust their movements over time and across seasons, we quantified the time-use metrics (i.e., revisitation rates and visit duration) from the Time-Local Convex Hull (T-LoCoH) hull parent points for each individual's seasonal trajectories. We used the T-LoCoH Development "*T-locoh.dev*" R package (Lyons et al. 2013) to identify sites of repeated visits (nsv, number of separate visits to each cell) and sites of average visit durations (mnlv, mean number of locations per visit to each cell). A lion and spotted hyena whose ranges overlapped in Etosha is shown in Fig. 2.2a, with all other individuals shown in Appendix S2.4 (Supplementary materials). As we were interested in the period of time which both lions and spotted hyenas overlap in their activity periods (Hayward & Slotow 2009), we chose to use an inter-visit gap (IVG) of 12 hours (one nocturnal period) to distinguish locations with more than 12 hours of time between them as separate visits. From this, we created density plots of each individual's time use metrics on the landscape, which we refer to as Revisitation and Duration (RD) space (Fig. 2.2b). We then obtained the local values of various ecogeographical and interaction variables (see below) and associated these covariate vectors to each point within the RD space.

We used a factor analysis of mixed data (FAMD) to test for a statistically significant relationship between our selected ecogeographical and interaction variables with points in our constructed RD space. From the principal dimensions identified by our FAMD that describe >80% of the cumulative variation, we chose the variables with the highest scores in each dimension as the most important covariate. From this analysis, we determined the appropriate covariate combinations prior to clustering. We then performed a cluster analysis on the points within the RD space for each individual. We built mixed data type cluster models according to the FAMD results, and applied three different clustering algorithms for 2-8 clusters. We used a *k*-prototypes clustering algorithm (Huang 1998) from the Clustering for Mixed Variable-Type Data "*clustMixType*" R package, which is based on *k*-means for mixed data. Because of the stochasticity of the *k*-prototype algorithm, each model configuration was recomputed 50 times with random initializations to obtain a model of minimum total distance. We also calculated a dissimilarity matrix using the "gower" metric in the daisy function from the Cluster Analysis "*cluster*" R package, which we used in the agglomerative hierarchical and PAM (partitioning around medoids) (Kaufman & Rousseeuw 1990) clustering algorithms for further clustering. We colour-coded the points on the map according to the clustered results, and examined whether the points within a range of revisitation (R) and duration (D) values from the RD space fell mainly within the identified clusters. We then visually inspected the results of the clustering analysis and determined the appropriate clustering method. We chose the clustering method according to the distribution of the FAMD selected covariates for each cluster and the percentage of categories occurring in each cluster. We chose the *k*-prototype clustering algorithm as it resulted in more defined clustered groups within the individual's RD space, and was more distinctive in the distribution of the clusters according to the covariates. An example is shown in Fig. 2.3 for a lion and spotted hyena whose ranges overlapped in Etosha. We used the multivariate *t*-distribution algorithm from the Data Visualization "*ggplot*" R package to draw ellipses around the clustered points, and subsequently chose the number of clusters according to how the points were clustered together in the RD space.

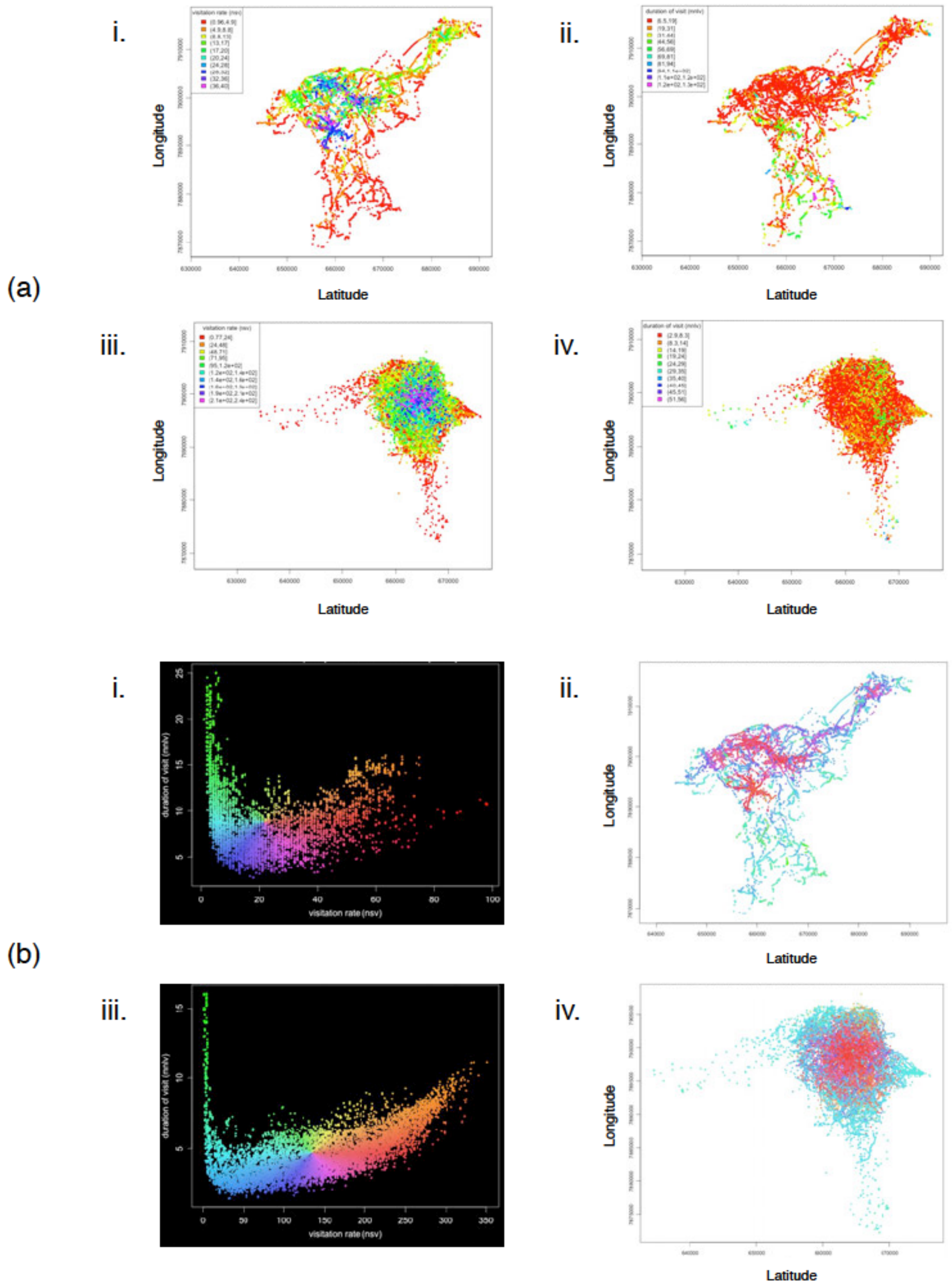

Figure 2.2. Hull parent points for a collared female lion (NU-33865, i & ii, both figures) and female spotted hyena (GO-33869, iii & iv, both figures) whose ranges overlapped in Etosha. (a) Parent points are coloured by visitation rate (nsv, number of separate visits; i & iii), and duration of visit (mnlv, mean number of locations in the hull per visit; ii & iv). (b) RD space scatterplots (i & iii) with X-axis = visitation rate (nsv), and Y-axis = duration of visit (mnlv), provide a legend for revisitation/duration (RD) values for the maps (ii & iv). Points in the RD space have been jiggled to better see point density, and each point within the RD space represents a hull (i) n = 9160, (iii) n = 11898. Points on the maps (ii & iv) are coloured by their location in the RD space. Separate visits defined by an inter-visit gap period ≥ 12 h. Hulls were created using the adaptive method. Duplicate points are offset by 1 map unit.

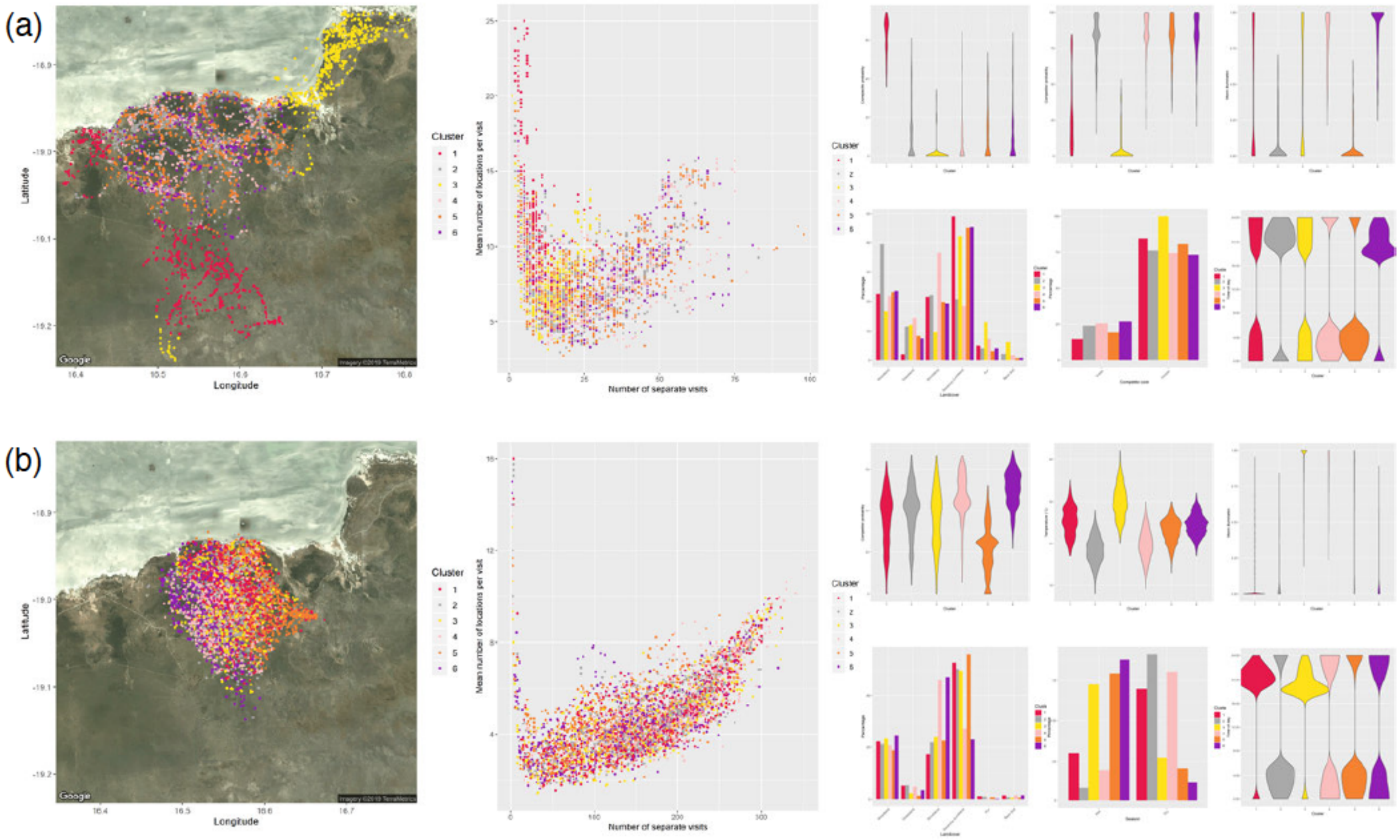

Figure 2.3. Maps (left panels) depict the individual relocations of a collared (a) lion (NU-33865) and (b) spotted hyena (GO-33869) whose ranges overlapped in Etosha. Relocations are colour-coded according to the clusters indicated by the range of revisitation (number of separate visits) and duration (mean number of locations per visit) values in RD space plots (central panels). Clusters in the RD space were determined with the *k*-prototype algorithm and are based on ecogeographical variables attached to each relocation. The smaller plots (right panels) present the distribution and percent category of each cluster for each of the ecogeographical variables selected from the FAMD analysis.

2.4. Results

2.4.1. Species range use

Lions and spotted hyenas used the same types of habitat and occurred most frequently within similar land cover types between the two ecosystems. In Etosha, both species demonstrated higher frequencies of relocations within grassland habitats, whereas in Botswana sites, the most prevalent land cover types utilized by both species were shrublands (Table S2.1, Supplementary materials). Kernel density UDs of lion and spotted hyena home ranges exhibited a high degree of spatial overlap within both Etosha and Chobe (Fig. 2.4). Seasonal UDs for all individuals are presented in Appendix S2.2 and Table S2.2 (Supplementary materials). During the dry season, all lion core use areas were anchored by water holes in Etosha or the river in Botswana, whereas only 23% of the spotted hyena core use areas were (Appendix S2.2.3).

Kernel density estimates of lion and spotted hyena home ranges tended to be larger than the *a*-LoCoH estimates, but were not significantly different. Lion home ranges in Etosha estimated with the kernel method were (mean ± SE) 577.2 ± 93.9 km^2, versus the *a*-LoCoH estimate of 362.0 ± 48.4 km^2. In Botswana, lion home ranges estimated with the kernel method were 363.3 ± 119.8 km^2, versus the *a*-LoCoH estimate of 257.3 ± 101.1 km^2. Similarly, spotted hyena home ranges estimated with the kernel method were 718.6 ± 327.9 km^2 in Etosha, and 478.7 ± 354.9 km^2 in Chobe, while the *a*-LoCoH estimated hyena home ranges at 413.5 ± 115.1 km^2 for Etosha and 194.1 ± 82.7 km^2 for Chobe (all *t*-tests, $p > 0.05$; Table S2.2). Using the time-scaled distance measure incorporated into the UDs, there were no significant differences in the sizes of either *a*-LoCoH estimated 95% home ranges and 50% core use areas between lions and spotted hyenas during nocturnal and diurnal periods (mean ± SE lion: nocturnal home range 327.8 ± 49.6 km^2, core area 99.0 ± 17.1 km^2; diurnal home range 287.8 ± 49.8 km^2, core area

95.6 ± 19.7 km^2; hyena: nocturnal home range 331.5 ± 90.3 km^2, core area 74.6 ± 15.8 km^2; diurnal home range 257.5 ± 74.9 km^2, core area 54.5 ± 12.1 km^2; all t-tests, $p > 0.05$; Table S2.2). There were also no significant differences in the sizes of either home ranges or core areas between lions and spotted hyenas in each reserve, regardless of seasons and circadian cycles (all t-tests, $p > 0.05$; Table S2.2). However, when comparing conspecifics across reserves, Etosha lions had larger nocturnal core areas than Botswana lions (mean ± SE: Etosha 127.8 ± 24.4 km^2, Botswana 63.0 ± 17.5 km^2, $t = -2.16$, df = 15.4, $p < 0.05$). Similarly, Etosha hyenas had larger core areas than their counterparts in Chobe (mean ± SE: Etosha 85.2 ± 14.0 km^2, Chobe 38.1 ± 21.6 km^2, $t = -2.77$, df = 10.9, $p < 0.05$; Table S2.2). Additionally, lions overall had larger home ranges and core areas in the wet season than they did in the dry season (mean ± SE diurnal home range: wet season 244.4 ± 42.3 km^2, dry season 121.2 ± 29.7 km^2, $t = -2.38$, df = 28.7, $p < 0.05$; nocturnal home range: wet season 278.4 ± 41.4 km^2, dry season 162.5 ± 36.9 km^2, $t = -2.09$, df = 30.8, $p < 0.05$; diurnal core area: wet season 95.7 ± 23.0 km^2, dry season 42.2 ± 10.7 km^2, $t = -2.11$, df = 22.6, $p < 0.05$; nocturnal core area: wet season 106.1 ± 21.4 km^2, dry season 45.3 ± 11.7 km^2, $t = -2.50$, df = 24.7, $p < 0.05$; Table S2.2), whereas hyenas only had larger core areas in the wet season (mean ± SE: wet 90.5 ± 24.4 km^2, dry 30.2 ± 6.9 km^2, $t = -2.38$, df = 12.8, $p < 0.05$; Table S2.2).

The total area of overlap in the home ranges and core areas of the two predators, both the other's main competitor, are also presented for each pair in Table S2.3 (Supplementary materials). We calculated the proportion of lion home ranges and their core areas overlapped by spotted hyena home ranges and core areas, as well as the proportion of spotted hyena home ranges and their core areas overlapped by lion ranges and core areas (Table S2.4, Supplementary materials). Lions in Etosha shared up to (mean ± SE) 20 ± 4% of their home ranges and 8 ± 2%

of their core use areas with hyenas. Meanwhile, hyenas shared up to 17 ± 3% of their home range and 8 ± 2% of their core use areas with lions in Etosha. Similarly in Chobe, lions shared up to (mean ± SE) 23 ± 5% of their home ranges and 3 ± 1% of their core use areas with spotted hyenas, while hyenas shared up to 23 ± 4% of their home ranges, and less than 1 ± 0.5% of their core use areas with lions. The proportion of overlap in the core use areas between lions and hyenas were larger in Etosha than they were in Chobe (mean ± SE: Etosha 8 ± 2%, Chobe 3 ± 1%, $t = 2.19$, df = 81.0, $p < 0.05$; Table S2.4). In addition, the proportion of overlap in the core use areas between lions and hyenas in Etosha were larger during the wet season than they were for the dry season (mean ± SE: wet season 14 ± 4%, dry season 3 ± 2%, $t = -2.31$, df = 34.7, $p < 0.05$; Table S2.4). Although lions did not differ in the sizes of overlapped areas between conspecifics or competitors, a larger proportion of Etosha lion home ranges overlapped with competitors than they did with conspecifics (mean ± SE: competitors 20 ± 4%, conspecifics 10 ± 2%, $t = -2.35$, df = 103.7, $p < 0.05$; Table S2.4). By contrast, lion conspecifics in Chobe shared significantly more of their home ranges than they did with conspecifics in Etosha (mean ± SE: Etosha 10 ± 2%, Chobe 26 ± 7%, $t = -2.19$, df = 28.9, $p < 0.05$; Table S2.4).

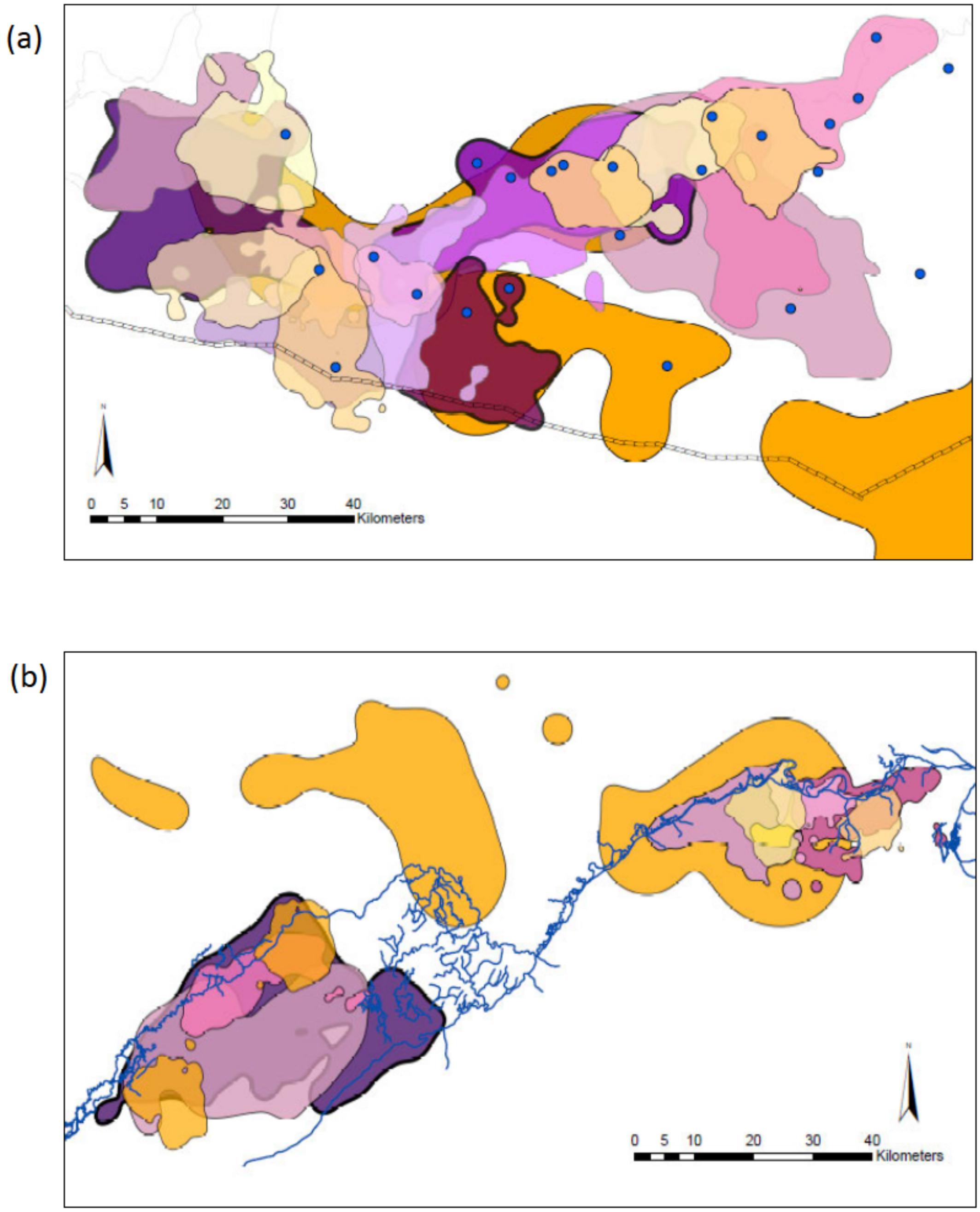

Figure 2.4. Overlapping ranges within study areas as represented by 95% kernel contours. Polygons of dark purple shades with black outlines = male lion ranges. Polygons of lighter purple/pink shades with grey outlines = female lion ranges. Polygons of orange/yellow shades = spotted hyena ranges. Overlapping polygons are set to 20% opacity for easier visualization. (a) Etosha site with the pan to the north and the park's fence along the southern boundary. Blue dots represent permanent water points. (b) Chobe/Linyanti site with the river separating Botswana to the south and Namibia to the north. The river is indicated by blue lines.

2.4.2. *Species movement patterns*

Detailed analyses of lion and spotted hyena movement descriptors are presented in Appendix S2.3 and Table S2.5 (Supplementary materials). Investigations into the movement parameters of the predators revealed that, although hyenas are temporally aligned in their activity periods with lions, they exhibited nearly twice the activity rates of lions (mean ± SE: lion 21.88 ± 10.3 AMVs, hyena 40.20 ± 24.0 AMVs, $t = -2.90$, df = 7.2, $p < 0.05$; Fig. 2.5; Table S2.5.1), moved at characteristically higher speeds than lions in both ecosystems (Etosha mean ± SE: lion 0.187 ± 0.08 m/s, hyena 0.364 ± 0.14 m/s, $t = -5.77$, df = 8.2, $p < 0.001$; Chobe mean ± SE: lion 0.128 ± 0.08 m/s, hyena 0.310 ± 0.16 m/s, $t = -7.73$, df = 6.8, $p < 0.001$; Appendix S2.3.1; Table S2.5.1), and had greater nocturnal mean step lengths (mean ± SE: lion 288.90 ± 99.84 m, hyena 618.12 ± 189.85 m, $t = -7.99$, df = 17.5, $p < 0.0001$; Appendix S2.3.2; Table S2.5.1).

In both ecosystems, spotted hyenas demonstrated overall larger mean step lengths than lions throughout the 4 h periods of the 24 h cycle (Etosha mean ± SE: lion 5.24 ± 2.02 m, hyena 8.37 ± 3.18 m; Botswana mean ± SE: lion 3.74 ± 1.71 m, hyena 7.27 ± 3.46 m), and had consistently larger mean step lengths than lions for each hour throughout the night (Etosha mean ± SE: lion 10.26 ± 4.64 m, hyena 21.65 ± 8.08 m; Botswana mean ± SE: lion 6.94 ± 4.00 m, hyena: 17.62 ± 8.50 m), with some individuals by an order of magnitude (all *t*-tests, $p < 0.05$ for 24 h periods and $p < 0.0001$ for nocturnal periods; Appendix S2.3.3-4; Table S2.5.1). Although there were more lion individuals (61.5%) with a larger mean step length during dawn periods ($\varkappa^2 = 5.33$, df = 1, $p < 0.05$), lions had significantly larger step lengths during dusk periods (mean ± SE: at dusk 64.79 ± 2.29 m, at dawn 50.64 ± 3.87 m; $t = 3.14$, df = 9.7, $p < 0.05$; Appendix 2.2.5). Contrarily, hyena individuals were equally split in whether they had larger mean step length during dusk or dawn periods, and whether they had either small or large differences between the two periods (Appendix S2.3.5).

In addition, spotted hyenas had consistently significantly larger net-squared displacements (NSD) than lions during nocturnal periods, and across all seasons in Etosha (dry season mean ± SE: lion 12.39 ± 0.26 km^2, hyena 27.40 ± 0.32 km^2, t = -2.97, df = 7.8, $p < 0.05$; wet season mean ± SE: lion 12.84 ± 0.20 km^2, hyena 32.69 ± 0.44 km^2, t = -2.52, df = 6.6, $p < 0.05$; Table S2.5.1) and for the dry season in Chobe (mean ± SE: lion 5.21 ± 0.25 km^2, hyena 12.65 ± 0.31 km^2, t = -3.85, df = 6, $p < 0.01$; Appendix S2.3.6; Table S2.5.1). NSDs were generally larger during the wet seasons for both species, although these were not statistically significant (Table S2.5.1). Inspections of the movement parameters over the diel cycle further highlights the similarities between species. Both lions and hyenas typically had larger NSDs during nocturnal than diurnal periods in both ecosystems, although not statistically significant for Chobe spotted hyenas (Etosha mean ± SE: lion, nocturnal 8.25 ± 6.05 km^2, diurnal 2.56 ± 2.16 km^2, t = -6.29, df = 13, $p < 0.0001$; hyena, nocturnal 17.90 ± 15.24 km^2, diurnal 5.17 ± 7.67 km^2, t = -2.71, df = 10, $p < 0.05$; Botswana mean ± SE: lion, nocturnal 2.94 ± 3.23 km^2, diurnal 1.13 ± 1.36 km^2, t = -2.77, df = 8, $p < 0.05$; hyena, nocturnal 6.17 ± 8.90 km^2, diurnal 0.97 ± 1.67 km^2, $p > 0.05$; Appendix S2.3.7; Table S2.5.1).

Spotted hyenas demonstrated relatively more directional movements in the semi-arid Etosha ecosystem, and exhibited increased tortuosity in the wetland ecosystem of Chobe during the 24 h periods for both seasons (dry season mean ± SE: Etosha -2.012 ± 0.89, Chobe 2.660 ± 1.01, Watson's test statistic: 0.217, $p < 0.05$; wet season mean ± SE: Etosha 1.637 ± 0.94, Chobe -2.942 ± 0.90, Watson's test statistic: 0.200, $p < 0.05$; Appendix S2.3.8; Table S2.5.1). Although lions were significantly more directional than spotted hyenas over the 24 h period in Etosha (mean ± SE: lion 0.080 ± 0.62, hyena -2.852 ± 0.82, Watson's test statistic: 0.305, $p < 0.01$), they were significantly more tortuous during the wet season in Chobe (mean ± SE: lion 0.209 ± 0.83, hyena -2.942 ± 0.90, Watson's test statistic: 0.189, $p < 0.05$; Appendix S2.3.8; Table S2.5.1).

However during the nocturnal period, Etosha lions were relatively more directional than Botswana lions, with the Watson's test significant for the dry season only (mean ± SE: Etosha 0.018 ± 0.85, Botswana -0.068 ± 0.86, Watson's test statistic: 0.177, $0.05 < p < 0.10$ (note for CircStats, Watson's two sample test is significant at $p < 0.10$); Appendix S2.3.9; Table S2.5.1). Contrarily for hyenas, they were more directional in Chobe and had increased tortuosity in Etosha during the dusk/dawn periods, with the Watson's test significant for the wet season only (mean ± SE: Etosha 0.012 ± 0.58, Chobe 0.004 ± 0.56, Watson's test statistic: 0.171, $0.05 < p < 0.10$; Appendix S2.3.9; Table S2.5.1). Furthermore, lions were relatively more tortuous than hyenas during dusk and dawn periods (two hours after sunset and two hours before sunrise), although the Watson's test statistic indicated significance only in Etosha (mean ± SE: lion 0.053 ± 0.73, hyena 0.013 ± 0.56, Watson's test statistic: 0.305, $p < 0.01$; Appendix S2.3.9; Table S2.5.1).

A fine-scale scrutiny of seasonal path tortuosity over the 24 h period from both ecosystems reveals lions consistently undertake more tortuous movements than spotted hyenas throughout nocturnal periods, specifically between 18h00-6h00 (Appendix S2.3.10). Although the Watson's two-sample test only showed significance for some of the time intervals (indicated with asterisks in Appendix S2.3.10; Watson's test statistic for Etosha 19h00-20h00, 0.233; 20h00-21h00, 0.250; 21h00-22h00, 0.353; 2h00-3h00, 0.211; 5h00-6h00, 0.211; and Botswana 18h00-19h00, 0.269; 22h00-23h00, 0.215; all p-values < 0.05). Thus, lions were predominantly more tortuous than spotted hyenas in the early phase of the night (18h00-23h00) and in the early morning (1h00-3h00, and 5h00-6h00), while Chobe spotted hyenas had significantly more tortuous movements than lions during the late morning (6h00-10h00, Watson's test statistic 0.269, $p < 0.05$).

Additionally, during nocturnal periods, the travelling speed of Etosha lions differed across various lunar phases ($F = 16.36$, $p < 0.0001$; Table S2.5.2), while lions from Botswana travelled further on new moon nights (mean ± SE: new moon 242.81 ± 146.57 m, full moon 222.71 ± 139.56 m, $F = 7.34$, $p < 0.05$; Table S2.5.2) and in the dry season (mean ± SE: new moon 286.42 ± 154.61 m, full moon 223.80 ± 145.39 m, $F = 8.21$, $p < 0.05$; Table S2.5.2). Chobe lions also presented with more tortuous movements during full moon nights (mean ± SE: full moon 0.442 ± 0.91, new moon -0.272 ± 0.80), and in the wet season (mean ± SE: full moon 0.674 ± 0.88, new moon -0.128 ± 0.77; Watson's test statistic in both cases: 0.168 and $0.5 < p < 0.10$; Table S2.5.2). Furthermore, variations in the path tortuosity according to the different phases of the lunar cycle were observed for Etosha lions and Chobe spotted hyenas during nocturnal periods of the dry season (Etosha lion: $F = 34.10$, $p < 0.0001$; Chobe hyena: $F = 4.19$, $p < 0.05$; Table S2.5.2), with Etosha lions having more tortuous movements on new moon nights (mean ± SE: full moon 0.013 ± 0.84, new moon 0.351 ± 0.86, $F = 22.99$, $p < 0.05$; Table S2.5.2). Etosha male lions were observed to have more directional movements during periods of low light conditions (waning and waxing crescents; Appendix S2.3.11). Conversely, the path tortuosity of both Chobe lions and Etosha hyenas differed across lunar phases in the wet season during dusk/dawn and nocturnal periods, respectively (Chobe lion: $F = 2.51$, $p < 0.05$; Etosha hyena: $F = 2.32$, $p < 0.05$; Table S2.5.2).

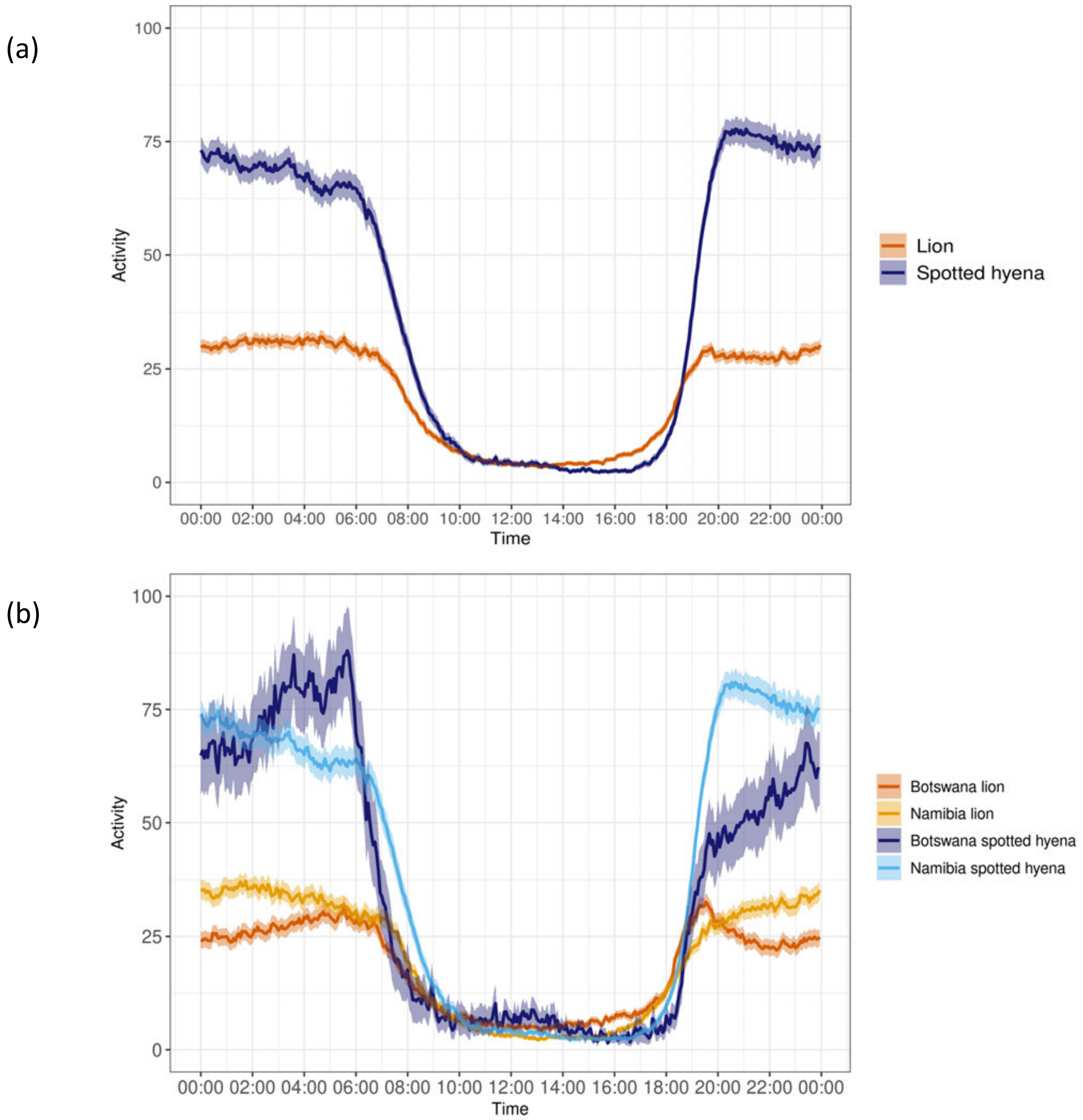

Figure 2.5. Activity rates over the 24 h cycle of (a) lions and spotted hyenas, and (b) lions and spotted hyenas from the Etosha National Park, Namibia and the Chobe National Park, Linyanti Conservancy, and the Okavango Delta[†], Botswana. Means are represented by solid lines with 95% confidence intervals the shaded bars.

[†] *No spotted hyenas were collared from the Okavango Delta, Botswana.*

2.4.3. Species activity patterns

Analyses of lion and spotted hyena activity in relation to the lunar cycle reveals both a seasonal effect and regional differences on the temporal activity patterns during the nocturnal period. Lions and hyenas generally exhibited significantly higher proportion of activity during the periods of the night from dusk to dawn in both ecosystems (Night mean ± SE: lion 0.531 ± 0.014 AMVs, hyena 0.591 ± 0.009 AMVs; Dusk/dawn mean ± SE: lion 0.356 ± 0.010 AMVs, hyena 0.350 ± 0.007 AMVs; t = -16.25, df = 23.1, $p < 0.0001$; Fig. 2.6), regardless of moon phase. However, lions in Botswana had increased activity during new moon periods, and also in the dry season (F = 19.39 and 20.30 respectively, $p < 0.05$; Fig. 2.6; Table S2.5.2). In addition, the nocturnal activity of both lions and spotted hyenas in Etosha differed according to the various moon phases in the dry season (lion, F = 11.33, $p < 0.0001$; hyena, F = 20.13, p < 0.0001; Table S2.5.2).

During both new and full moon nights in Etosha, spotted hyenas exhibit heightened proportions of activity in the initial phase of the night (dusk-night mean ± SE: lion 0.159 ± 0.008 AMVs, hyena 0.193 ± 0.009 AMVs, t = -2.77, df = 14, $p < 0.05$; Fig. 2.6; Table S2.5.3) However, the opposite is true for Chobe with lions having heightened proportions of activity in the initial phase (dusk-night mean ± SE: lion 0.177 ± 0.013 AMVs, hyena 0.129 ± 0.012 AMVs, t = -2.81, df = 13.9, $p < 0.05$; Fig. 2.6; Table S2.5.3), and hyenas during the latter phase (night end-dawn mean ± SE: lion 0.177 ± 0.010 AMVs, hyena 0.241 ± 0.008 AMVs, t = -5.03, df = 13.7, $p < 0.001$; Fig. 2.6; Table S2.5.3). Despite the differences in whether lions or hyenas were exhibiting heightened proportions of activity during specific time periods, there remains a temporal shift in activity between lions and hyenas in which periods of heightened proportions of activity is dominated by one species during different time periods of the night. Thus, these distinctive differences in the activity patterns between the two species during the night suggests a temporal partitioning strategy in areas where both species co-exist.

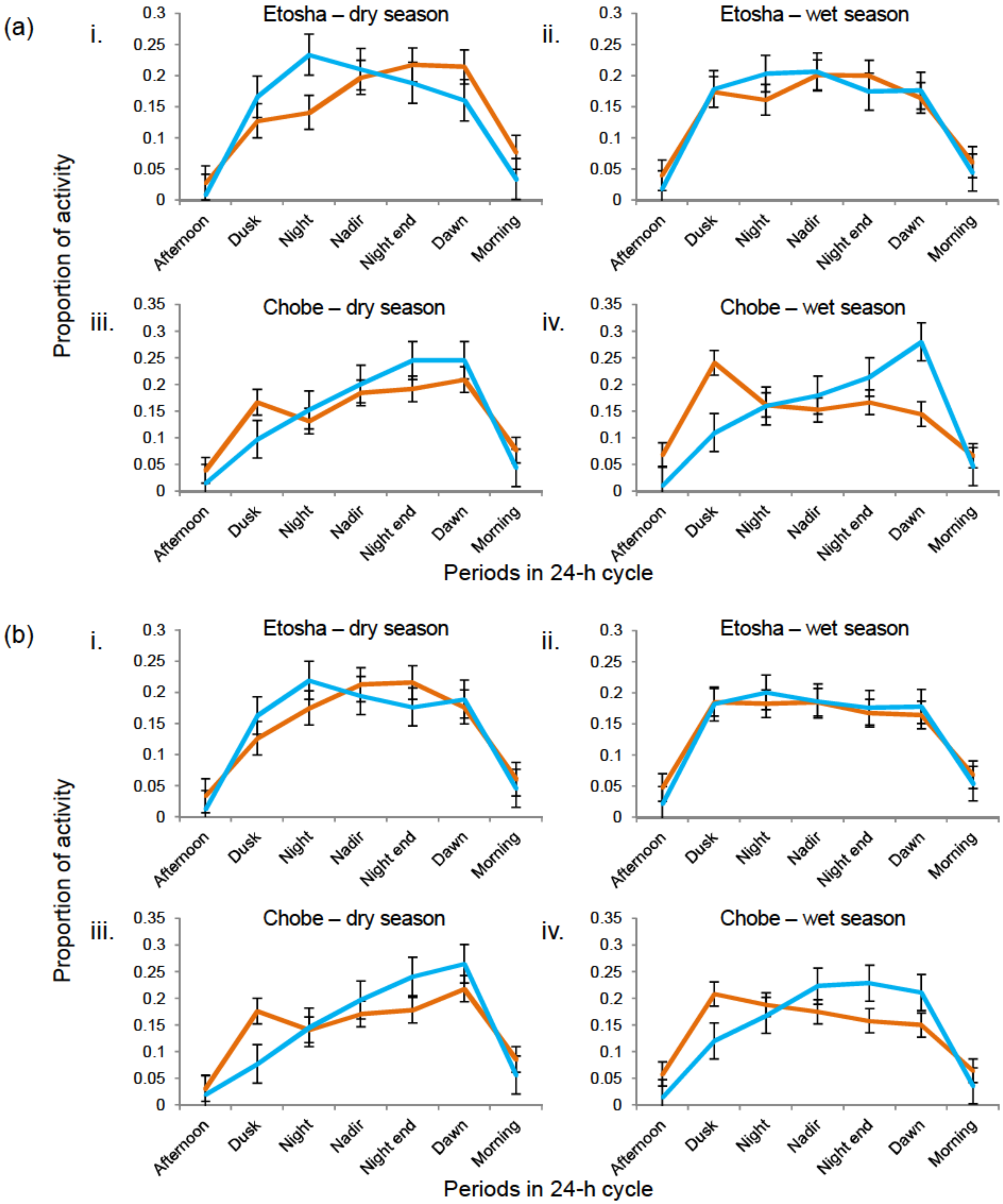

Figure 2.6. Proportion of activity of lions (orange lines) and spotted hyenas (blue lines) during full moon (a) and new moon (b) phases for each of the dry and wet seasons in Etosha and Chobe/Linyanti study areas. The 24 h cycle was subdivided into seven different periods (see *Methods: Species activity patterns* for details). Points represent the mean and error bars the standard error (SE). Connecting lines have been drawn through the means for visualization purposes.

2.4.4. Species variations

Due to our small sample sizes, lions from all areas were grouped together (n = 19) as were spotted hyenas (n = 13). For both species, the size of the home ranges and core areas did not differ significantly with age, despite older animals being weakly correlated with larger home ranges and core areas for lions and smaller home ranges and core areas for hyenas (Spearman's correlation lion home range: 0.46, and core areas: 0.37; spotted hyena home range: -0.08, and core areas: -0.08). However, the relationship between age and the sizes of home ranges and core areas was not significant (lion home range adjusted R^2: 0.01, lion core areas adjusted R^2: 0.12; hyena home range adjusted R^2: -0.05, hyena core areas adjusted R^2: -0.08; all p-values > 0.05). Female hyenas had larger home ranges and core areas in the wet season than male hyenas (mean ± SE home ranges: females 394.2 ± 111.8, males 118.7 ± 12.5, t = 2.45, df = 9.2, $p < 0.05$; core areas: females 101.8 ± 28.0, males 34.5 ± 8.7, t = 2.30, df = 10.0, $p < 0.05$), while there were no differences in the home ranges and core areas between male and female lions.

In addition, we found no significant effects of group size on the space use patterns of lions or spotted hyenas. Although lions of larger pride sizes were weakly correlated with smaller home ranges (Spearman's correlation: -0.11), this was not a significant relationship (adjusted R^2: -0.05, $p > 0.05$). Conversely, while spotted hyenas from larger clans were weakly correlated with larger core areas (Spearman's correlation: 0.19), the relationship was not significant (adjusted R^2: -0.09, $p > 0.05$).

Furthermore, higher body condition scores appeared to be weakly correlated with smaller home ranges (Spearman's correlation: -0.14 for each of lions and hyenas), although the relationship was again insignificant (lion adjusted R^2: -0.06, hyena adjusted R^2: -0.07, all p-values > 0.05). However, there was a significant two-way interaction between sex and body condition scores on the traveling speed and path tortuosity of lions. Although lions of lower body condition scores ($n = 3$) tended to move at faster speeds during nocturnal periods ($F = 42.36$, $p < 0.05$; Table S2.5.4), male lions of low ($n = 1$) to medium ($n = 2$) body condition scores travelled at higher speeds than females of similar body condition scores ($n = 9$), whereas females with high ($n = 3$) body condition scores moved at faster speeds than male lions with high ($n = 3$) body condition scores (F = 81.89, $p < 0.05$; Table S2.5.4). In spite of female lions having more tortuous movements than male lions during dusk/dawn periods (mean ± SE: females 0.117 ± 0.67, males -0.104 ± 0.76; $F = 729.79$, $p < 0.05$), the sex-specific tortuosity of lions differed across the categories of low, medium, and high body condition scores ($F = 50.06$, $p < 0.05$; Table S2.5.4). Male lions of low body condition had mostly directional movements which increased to more tortuous movements with increasing body condition. Alternatively, female lions of high body condition had mostly directional movements, but had consistently more tortuous movements than males ($F = 51.38$, $p < 0.05$; Table S2.5.4). Moreover, spotted hyenas with lower ($n = 9$) body condition scores also presented with more tortuous movements during nocturnal periods than hyenas of higher ($n = 4$) body condition scores which had more directional movements ($F = 29.46$, $p < 0.05$; Table S2.5.4).

Additional investigations revealed no significant differences in the travelling speed of Etosha lions ($n = 11$) and spotted hyenas ($n = 8$) among the various bins of site-attracted foraging ungulate probabilities. However, the tortuosity of Etosha spotted hyenas during dusk/dawn periods differed significantly among the five bins of site-attracted foraging ungulate probabilities. Hyenas exhibited the most tortuous movements within areas of higher probabilities of site-attracted foraging ungulates (mean ± SE: -0.043 ± 0.66), and were relatively more directional in their movements within the regions of lowest probabilities (mean ± SE: 0.015 ± 0.60; $F = 3.83$, $p < 0.05$; Table S2.5.5).

2.4.5. Inter- and intraspecific effects

The activity recorded from the accelerometers of Chobe lions and spotted hyenas were significantly higher when inside the core use area of the competitor species (Fig. 2.7), although the activity of Etosha lions and hyenas also increased when inside competitor core areas. Chobe lions had higher activity inside competitor core areas during the dusk/dawn period (mean ± SE: inside 34.29 ± 29.38 AMVs, outside 30.66 ± 25.08 AMVs; $F = 51.31$, $p < 0.05$; Table S2.5.6), while a hyena from Chobe had higher activity both inside the competitor, and outside the conspecific core areas (competitor mean ± SE: inside 84.32 ± 1.59 AMVs, outside 65.34 ± 0.68 AMVs; conspecific mean ± SE: inside 50.97 ± 0.90 AMVs, outside 77.58 ± 0.81 AMVs; F = 111.7 and 433.1, respectively, all p-values < 0.0001; Table S2.5.6).

Additionally, lions in both ecosystems had increased activity when at closer distances to conspecifics than to competitors (Etosha mean ± SE: 100-200 m to conspecifics 56.86 ± 20.30 AMVs, to competitors 25.70 ± 20.50 AMVs, $t = -3.77$, df = 8.9, $p < 0.01$; Chobe mean ± SE: 500-600 m to conspecifics 45.39 ± 36.94 AMVs, to competitors 29.50 ± 0.01 AMVs, $t = -80.71$, df = 1, $p < 0.01$; Table S2.5.6), with Etosha lions travelling faster (calculated from GPS locations) at closer distances to conspecifics than to competitors during dusk/dawn periods (mean ± SE: 100-200 m to conspecifics 0.412 ± 0.14 m/s, to competitors 0.082 ± 0.10 m/s, $t = -6.78$, df = 6.7; 200-300 m to conspecifics 0.337 ± 0.14 m/s, to competitors 0.155 ± 0.12 m/s, $t = -3.78$, df = 6.7; 300-400 m to conspecifics 0.302 ± 0.16 m/s, to competitors 0.085 ± 0.08 m/s, $t = -4.96$, df = 5.9; 400-500 m to conspecifics 0.396 ± 0.15 m/s, to competitors 0.135 ± 0.10 m/s, $t = -$

3.25, df = 10.4; all p-values < 0.01; Table S2.5.6). Similarly, hyenas from Etosha demonstrated increased activity at closer distances to conspecifics than to competitors during nocturnal periods (mean ± SE: 100-200 m to conspecifics 127.18 ± 22.53 AMVs, to competitors 47.33 ± 25.13 AMVs, $t = 2.74$, df = 5.0, $p < 0.05$), whereas they travelled at faster speeds when closer to competitors than to conspecifics during dusk/dawn periods (mean ± SE: 0-100 m to competitors 0.135 ± 0.06 m/s, to conspecifics 0.010 ± 0.004 m/s, $t = 2.77$, df = 5.1, $p < 0.05$; Table S2.5.6). Contrarily, the dusk/dawn activity of the Chobe hyena was significantly higher at closer distances to competitors than to conspecifics (mean ± SE: 200-300 m to competitors 92.50 ± 11.59 AMVs, to conspecifics 53.06 ± 7.32 AMVs, $t = 2.88$, df = 3.9; 600-700 m to competitors 106.17 ± 11.28 AMVs, to conspecifics 59.17 ± 10.30 AMVs, $t = 3.08$, df = 15.0; all p-values < 0.05; Table S2.5.6).

During dusk/dawn periods, spotted hyenas from both Etosha and Chobe travelled at faster speeds inside of competitor core areas relative to outside of competitor core areas (Etosha mean ± SE: inside 0.470 ± 0.14 m/s, outside 0.422 ± 0.14 m/s, F = 12.96, $p < 0.05$; Chobe mean ± SE: inside 0.527 ± 0.22 m/s, outside 0.363 ± 0.21 m/s, F = 8.33, $p < 0.05$; Table S2.5.6). Similarly, hyenas from Chobe also travelled at faster speeds inside of competitor core areas during nocturnal periods (mean ± SE: inside 0.438 ± 0.13 m/s, outside 0.297 ± 0.13 m/s, F = 18.93, $p < 0.05$; Table S2.5.6). Conversely, Chobe hyenas travelled at slower speeds when inside of conspecific core areas relative to outside of conspecific core areas during nocturnal periods (mean ± SE: inside 0.233 ± 0.23 m/s, outside 0.334 ± 0.17 m/s, $F = 1515.36$, $p < 0.05$; Table S.2.4.6). Additionally, Chobe hyenas moved at faster speeds inside competitor core areas in comparison to when they were inside conspecific core areas during nocturnal and dusk/dawn periods (nocturnal mean ± SE: competitor 0.425 ± 0.16 m/s, conspecific 0.233 ± 0.23 m/s, $t =$

6.04, df = 4.2; dusk/dawn mean ± SE: competitor 0.527 ± 0.22 m/s, conspecific 0.268 ± 0.29 m/s, t = 4.88, df = 4.9, all p-values < 0.01; Table S2.5.6).

The tortuosity of lion movements differed when they were inside of competitor core areas in relation to when they were outside of it (Fig. 2.8). During nocturnal periods, lions from Chobe had more directional movements inside competitor core areas (mean ± SE: inside 0.032 ± 1.08, outside -0.222 ± 0.99, Watson's test statistic: 0.242, $p < 0.05$; Table S2.5.6), and were also more directional inside competitor core areas than they were inside of conspecific core areas (mean ± SE: 0.113 ± 1.71; Watson's test statistic: 0.153, $0.05 < p < 0.10$; Table S2.5.6). In addition, Chobe lions were less tortuous inside competitor core areas than Etosha lions were (mean ± SE: Etosha 0.055 ± 0.64, Chobe 0.032 ± 1.08, Watson's test statistic 0.204, $p < 0.05$; Table S2.5.6). Contrarily, Etosha lions had more tortuous movements inside competitor core areas than outside of them during dusk/dawn periods (mean ± SE: inside 0.073 ± 0.79, outside 0.029 ± 0.79, Watson's test statistic: 0.171, 0.05 < p < 0.10; Table S2.5.6). Chobe lions were also more directional inside of competitor core areas (0.032 ± 2.41) than they were inside of conspecific core areas (0.113 ± 2.88; Watson's test statistic: 0.153, $0.05 < p < 0.10$; Table S2.5.6).

In addition, lions from Chobe demonstrated sex-specific differences in path tortuosity with regards to conspecific core areas during the nocturnal period. Although Chobe male lions had more tortuous paths than female lions (mean ± SE: males -0.512 ± 1.74, females 0.078 ± 0.80; F = 7.81, $p < 0.05$), both sexes demonstrated less tortuous paths inside conspecific core areas than they did outside of them (F = 10.98, $p < 0.05$; Table S2.5.6). Conversely, spotted hyenas from Etosha had more tortuous paths inside conspecific core areas with more directional movements outside conspecific core areas during nocturnal periods (mean ± SE: inside -0.079 ±

0.65, outside 0.018 ± 0.62, F = 8.65, $p < 0.05$; Fig. 2.8; Table S2.5.6). Furthermore, lions from Etosha had more tortuous movements when at close distances to competitors (up to 500 m) during nocturnal and dusk/dawn periods, relative to when at close distances to conspecifics (nocturnal mean ± SE: 0-100 m to competitors -2.912 ± 0.74, to conspecifics 0.169 ± 0.85, Watson’s test statistic 0.242; 100-200 m to competitors 2.775 ± 0.60, to conspecifics 0.170 ± 0.46, Watson’s test statistic 0.227; 400-500 m to competitors 2.305 ± 0.48, to conspecifics -0.001 ± 0.50, Watson’s test statistic 0.227; dusk/dawn: 100-200 m to competitors 3.130 ± 0.71, to conspecifics 0.076 ± 0.46, Watson’s test statistic 0.264; 400-500 m to competitors -2.666 ± 0.71, to conspecifics 0.058 ± 0.60, Watson’s test statistic 0.191; all p-values < 0.05; Appendix S2.3.12; Table S2.5.6).

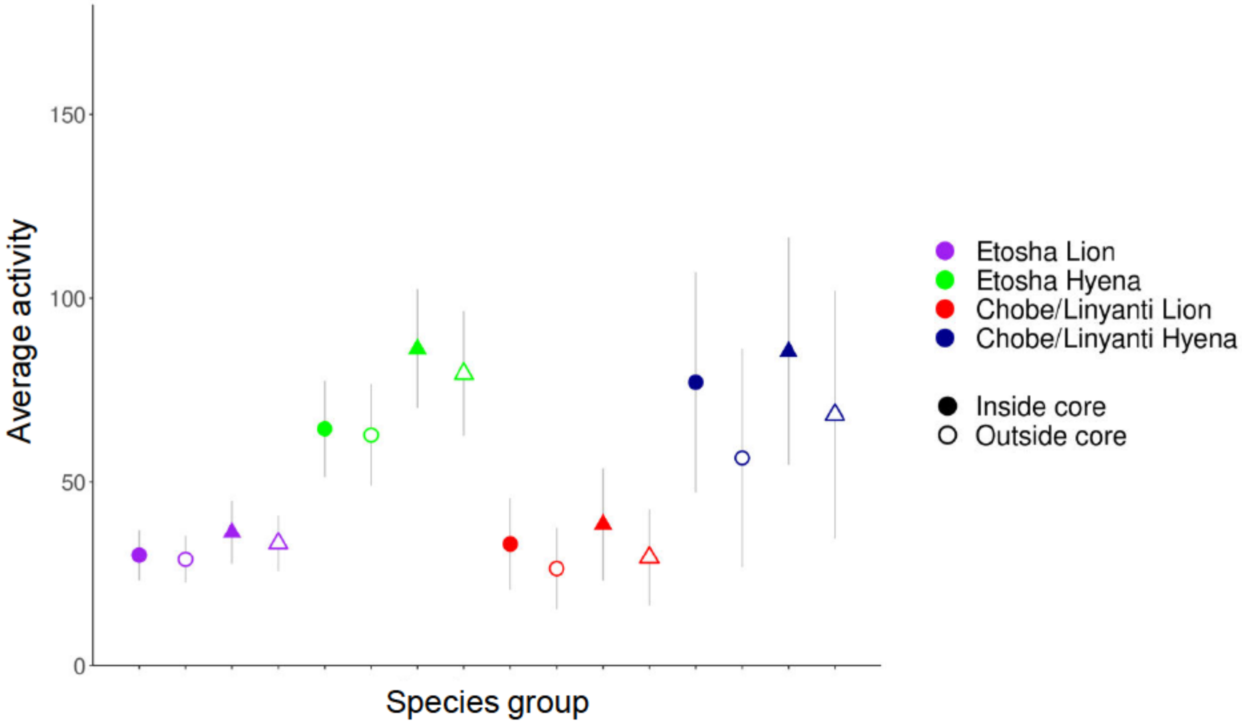

Figure 2.7. Average activity of lions and spotted hyenas with respect to competitor core use areas. Inside competitor core areas are represented by solid shapes, and outside competitor core areas are represented by open shapes. Shapes represent the mean activity and error bars the standard error (SE). Activity was measured simultaneously on each axis as the difference in acceleration between two consecutive measurements and given a relative range between 0 and 255 (activity monitor values [AMVs]), characterizing the mean activity/acceleration. Activity X (circles) = forward/backward motion. Activity Y (triangles) = rotary/sideways motion.

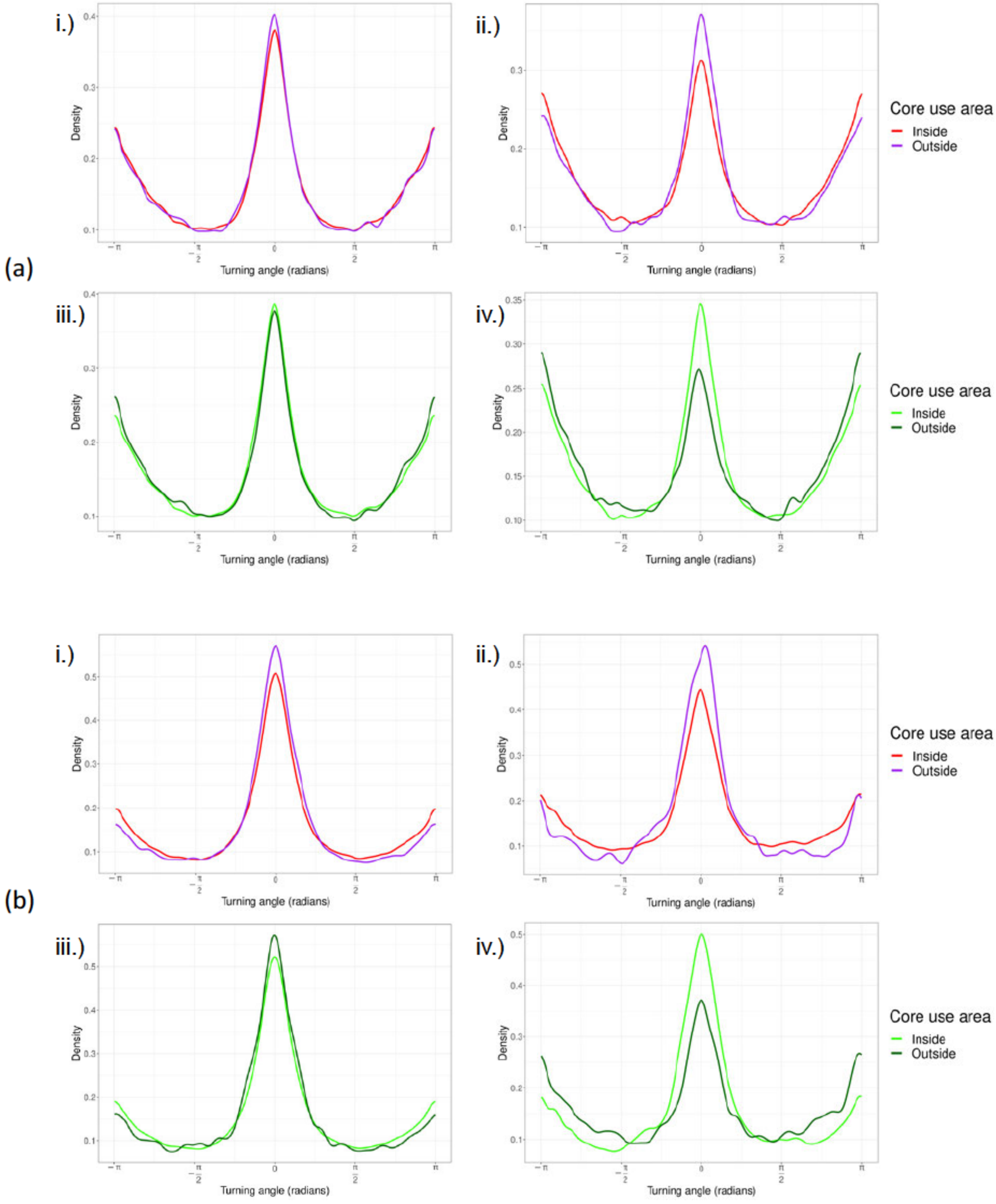

Figure 2.8. Tortuosity of (a) lions and (b) spotted hyenas from the Etosha National Park, Namibia (i & iii) and the Chobe National Park and Linyanti Conservancy, Botswana (ii & iv). Path tortuosity is shown from inside and outside of competitor core areas (i & ii), and conspecific core areas (iii & iv).

2.4.6. Time-use metrics

Revisitation and Duration (RD) space plots that indicate areas of high revisitation rates and locations of long visit durations for each individual are presented in Appendix S2.4 (Supplementary materials). The distribution of the selected variables for each of the clusters are presented alongside a map of the individual's relocations, colour-coded according to the identified clusters within the RD space in Appendix S2.5 (Supplementary materials). For all individuals, the factor analysis of mixed data (FAMD) method consistently selected land cover categories and time of day as high-scoring variables among the principal dimensions explaining the patterns of recursions and extended stays for each lion and spotted hyena individual. The next most consistently selected ecogeographical variables as important factors explaining the patterns of recursions and extended stays for lions were variables related to interspecific and intraspecific interactions (probability of, distance to, and whether inside of core), chosen 75% and 68.8% of the time, respectively (Table 2.3). However for hyenas, the most consistently selected factors among the principal dimensions were variables related to interspecific interactions (probability of, distance to, and whether inside of core), chosen 61.5% of the time. Other variables selected with equal consistency as variables of interspecific interactions for Etosha hyenas included probability of site-attracted foragers and moon illumination, while distance to permanent water was selected with equal frequency for Chobe hyenas (Table 2.3).

Focusing our time-use observations on variables associated with interspecific competition, we observed that lions tended to demonstrate longer durations in locations of low competitor probabilities, at far distances to competitors, and when outside competitor core use areas (see a.3 and a.8 in Appendix S2.5.1). Lions also had increased recursions in areas of high competitor probabilities, at close distances to competitors and inside competitor core use areas (all chi-square p-values < 0.001; Table 2.4). However, male lions and females of mating pairs exhibited longer durations in localities of high competitor probabilities; while single female lions had shorter durations with increased revisitations (see a.5 and c.3 versus a.4 and b.2 in Appendix S2.5.1). Similarly, spotted hyenas also tended to have longer durations in locations of low competitor probabilities, and they had higher recursions with short durations in locales of high competitor probabilities (see a.1 and b.3 in Appendix S2.5.2). Furthermore, hyenas exhibited longer durations at further distances from competitors with shorter durations and increased revisitations at shorter distances to competitors (all chi-square p-values < 0.001; Table 2.4; see a.6 and c.2 in Appendix S2.5.2).

However, with regards to intraspecific competition, our observations revealed no differences in the time-use duration and revisitation of lions in locations of low and high conspecific probabilities (Table 2.4). Conversely, hyenas had twice the frequency of extended durations than they did shorter durations in locations of higher conspecific probabilities (chi-square p-value < 0.05; Table 2.4; see a.2 and a.3 in Appendix S2.5.2). In addition, hyenas also had higher recursions in localities of lower conspecific probabilities, at far distance to conspecifics, and outside conspecific core use areas (chi-square p-value < 0.001; Table 2.4).

Table 2.3. Frequency percentage occurrence of highest-scoring variables among the principal dimensions as important factors to explain >80% of the cumulative variation for each of Etosha, Chobe/Linyanti and overall lions and spotted hyenas, as selected by the FAMD (factor analysis of mixed data) method.

Ecogeographical Variables		**Lion**			**Spotted hyena**		
		Etosha	**Chobe/ Linyanti**	**Overall**	**Etosha**	**Chobe/ Linyanti**	**Overall**
		n = 10	**n = 6**	**n = 16**	**n = 8**	**n = 5**	**n = 13**
Bioclimatic variables	Time of day	100	100	100	100	100	100
	Temperature	40	33.3	37.5	50	20	38.5
	Season	20	33.3	25	12.5	40	23.1
	Moon Illumination	20	16.7	18.8	62.5	20	46.2
	Precipitation amounts	40	0	25	25	0	15.4
Landscape features	Slope	50	16.7	37.5	50	40	46.2
	Land cover category	100	100	100	100	100	100
	NDVI	20	16.7	18.8	12.5	20	15.4
	Probability of site-attracted foragers	40	-	-	62.5	-	-
	Distance to carcasses	30	-	-	37.5	-	-
	Distance to permanent water	-	50	-	-	60	-
	Distance to seasonal water	30	16.7	25	37.5	20	30.8
	Distance to roads	0	0	0	12.5	0	7.7
Human disturbances	Distance to anthropogenic features	40	0	25	0	40	15.4
Competitive effects	Interspecific interactions	80	66.7	75	62.5	60	61.5
	Intraspecific interactions	70	66.7	68.8	37.5	40	38.5

Table 2.4. Percent frequency occurrence of revisitation (nsv, number of separate visits) and duration (mnlv, mean number of locations per visit) obtained from the *k*-prototype clustering of interaction covariates in RD space of each individual. Significance from chi-square analyses is denoted with an asterisk at the alpha level of < 0.05, and with a triple asterisk at < 0.001. Numbers in brackets indicate short durations.

Species	Cases	Interaction variables	Revisitation	Duration	Significance
Lion	n = 11	- high competitor probability - close distance to competitor(s) - inside competitor core use area	73%	27%	***
		- low competitor probability - far distance to competitor(s) - outside competitor core use area	27%	73%	***
	n = 10	- high conspecific probability - close distance to conspecific(s) - inside conspecific core use area	50%	50%	
		- low conspecific probability - far distance to conspecific(s) - outside conspecific core use area	50%	50%	
Spotted hyena	n = 6	- high competitor probability - close distance to competitor(s) - inside competitor core use area	83%	(17%)	***
		- low competitor probability - far distance to competitor(s) - outside competitor core use area	0%	100%	***
	n = 5	- high conspecific probability - close distance to conspecific(s) - inside conspecific core use area	40%	40% (20%)	*
		- low conspecific probability - far distance to conspecific(s) - outside conspecific core use area	60%	20% (20%)	***

2.5. Discussion

Combining patterns of space use, temporal activity, fine-scale habitat use differentiation, and localized reactive avoidance behaviours in response to the potential risk of competition, has revealed the complex dynamics among lions and spotted hyenas within an apex predator system. Our findings are consistent with other studies in which lions and hyenas are often positively associated with one another (Hayward et al. 2007, Périquet et al. 2015b, 2016, Kittle et al. 2016), and they appear to behaviourally mediate the potential for competition by active avoidance or fine-scale behavioural mechanisms, as exhibited by other carnivores in response to the direct risk of encountering other predators (Broekhuis et al. 2013, Swanson et al. 2016).

Environmental spatial complexity, which allows for the selection of different habitats, may promote coexistence between species (Rosenzweig 1981), and has been recorded for several sympatric carnivores (Di Bitetti et al. 2010, Pereira et al. 2012, Lovari et al. 2013, 2015, Kamler et al. 2015, Soto & Palomares 2015, Bianchi et al. 2016, Chetri et al. 2017, Tsunoda et al. 2018, Hearn et al. 2018), including lions and spotted hyenas (Swanson et al. 2016, Sogbohossou et al. 2018). However, fine-scale habitat use differentiation likely occurs as the key mechanism allowing for the coexistence of species within homogeneous landscapes (Soto & Palomares 2015, Manlick et al. 2017). Therefore, while the heterogeneous landscapes of the Chobe riverfront may facilitate coexistence of species of the same trophic level (Dominguez-Rodrigo 2001), subtle patterns of habitat use partitioning reflected in the movement decisions of lions and spotted hyenas may further explain the persistence of the two predators across arid and mesic extremes of their environment. Our results indicate differences between lion and spotted hyena movements, which can be attributed to differences in the hunting strategies of the two species

(Preisser et al. 2007), potentially resulting in fine scale habitat separation rather than complete segregation (Milleret et al. 2018).

Mainly cursorial predators, spotted hyenas are generally more active, travel faster and further than lions (Kruuk 1972, Périquet et al. 2015a). As sit-and-wait predators, lions typically have lower activity, move at slower speeds, and cover shorter distances than spotted hyenas (Schaller 1972, Funston et al. 2001). Corresponding to the findings of Durant et al. (2010), lions and spotted hyenas in this study utilized similar habitats, both mainly occurring within grassland habitats in Etosha and shrubland habitats in Botswana (Trinkel & Kastberger 2005, Cozzi et al. 2013, Winterbach et al. 2014). Despite utilizing similar habitats, how the two species exploit these habitats differs, and reflects the differences in habitat characteristics between ambush and cursorial predators (Eisenberg 1986, Creel 2001). Lions typically use areas in which stalking cover is available (Van Orsdol 1984, Patterson et al. 2004), whereas hyenas prefer to use open areas, and are generally more dispersed across the landscape (Mills & Hofer 1998, Holekamp & Dloniak 2010). Likewise, Bender et al. (2017) reported fine-scale habitat segregation among pumas (*Puma concolor*), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) in the San Andres Mountains as a result of preferences for habitat characteristics that facilitate movements, despite being positively associated with one another. Thus, our results lends support to a growing body of evidence that demonstrates coexistence among carnivores is facilitated by behavioural mechanisms, in addition to spatial and temporal partitioning (Dröge et al. 2017, Bender et al. 2017, Kushata et al. 2018, Hilborn et al. 2018, Engebretsen et al. 2021).

Although the movement decisions and behavioural responses of lions and spotted hyenas is adaptable across different systems, we found that lions and spotted hyenas do not respond to inter- and intraspecific interactions equally among heterogeneous and homogeneous environments. Hyena clans in Etosha were observed to participate in more territorial clashes than they did in Chobe (unpublished data). As heterogeneous environments, or habitats of increased complexity, permit coexistence among carnivore species (Scognamillo et al. 2003, Monterroso et al. 2016, Davies et al. 2021), presumably the potential for competition (both inter- and intraspecific) is mitigated in Chobe (Pereira et al. 2012), an environment of increased complexity (Sianga & Fynn 2017).

Previous studies have demonstrated lion movements to be inextricably tied to the location of water-holes across the landscape due to concentrated search efforts for prey (Valeix et al. 2010, de Boer et al. 2010). In Etosha during the dry season, water is primarily supplied at developed locations from a system of pumped boreholes that are routinely serviced and maintained by park personnel. Conversely, perennial water from the Chobe River and the Okavango Delta provides a permanent water source at the Botswana sites (Fox et al. 2017). In this study, lion core use areas either encompassed, or were anchored, by such water sources, while only half or fewer of hyena core use areas were. Our results indicate that hyenas in Chobe spent more time in areas that were closer to permanent water and had increased recursion to locations further from water. Spotted hyenas have been found to use locations far from water for den sites and resting (Périquet et al. 2016, Kushata et al. 2018), thus we suggest that hyenas are potentially choosing to remain in areas with landscape characteristics that minimizes detection (Beier 2010) while increasing prey vulnerability (Sunquist & Sunquist 1989). Although spotted hyenas require access to drinking water, they can survive on very little of it (Mills 1990). Presumably, hyenas in Chobe spend more time in riverine habitats which consist of relatively dense vegetative cover and greater topographic heterogeneity to increase the potential of obtaining food resources when prey aggregate at water sources (Hopcraft et al. 2005, Balme et al. 2007). In areas where lions are the dominant predator, spotted hyenas may be relegated to suboptimal areas away from readily-available and prime resources, similar to coyotes and wolves (*Canis lupus*) (Klauder et al. 2021). In this way, spotted hyenas are potentially equivalent to naïve or subordinate lions that have been forced into peripheral habitats (Loveridge et al. 2017). Thus, the behavioural plasticity and opportunistic behaviour in foraging and habitat use of spotted hyenas may facilitate coexistence with lions in areas where they overlap.

Interestingly, hyenas in Etosha had higher recursions to locations with higher probabilities of encountering site-attracted foragers, thus increasing their chances of coming across foraging ungulates or potentially new carcasses (Berger-Tal & Bar-David 2015). However, hyenas that shifted their ranges in the wet season to include the anthrax endemic areas had longer durations at these locations; presumably because they had to travel further (±60 km) to access these localities. The ability to leave their home range and traverse across territories of other clans to benefit from an abundance of resources (i.e. surplus carcasses from anthrax outbreaks), is reminiscent of the commuting behaviour exhibited by spotted hyenas as they follow to exploit migratory prey during the wet season in the Serengeti (Frank 1986, Hofer & East 1993). We suggest this behavioural plasticity is an ecological strategy that spotted hyenas appear to exploit as necessary to increase the potential appropriation of resources, thus conferring a fitness advantage.

Furthermore, recursion and duration were synonymous with travelling movements for Etosha hyenas during new moon and full moon periods. Hyena movements were more localized at higher durations during the periods between new and full moons as they spent more time foraging or searching for prey. Similar to wolves, which were documented to be nearly twice as successful when hunting on moonlit nights (Theuerkauf et al. 2003), hyenas likely require sufficient visibility to increase their hunting success (Hayward & Slotow 2009). During this study, hyenas were observed to undertake cursorial hunts during moonlit nights, and switched to an ambush strategy coupled with opportunistic chases during darker periods. Comparably, lions typically experience higher hunting success during dark nights, although they were less successful at appropriating prey during moonlit nights (Packer et al. 2011). In addition, hyenas were observed (during night follows in this study) to rest when the moon was at its brightest during full moon nights, and would only resume foraging activities after the moon had lowered in the sky (pers. obs.). This suggests that hyenas are likely to focus on directed movements (traversing between patches) during dark periods, and resting when it is too bright to avoid detection by prey (Pratas-Santiago et al. 2017). Accordingly, hyenas focus their foraging and hunting efforts during periods of sufficient light conditions between the time of new and full moon nights, allowing for avoidance of the potential risk of interspecific encounters with lions (Broekhuis et al. 2014, Haswell et al. 2020).

Temporal heterogeneity in conjunction with spatial heterogeneity likely occurs as a mitigation strategy in response to interference competition, and facilitates coexistence among carnivores (Di Bitetti et al. 2010, Santos et al. 2019). Our findings indicate lions and spotted hyenas were both nocturnal, with the lion more diurnal than the hyena. Similarly, Sogbohossou et al. (2018) found the activity of lions and spotted hyenas to be spread over the night with no real peaks. However, we found evidence of temporal partitioning on a finer scale than nocturnal and crepuscular patterns, as has been recorded in other studies (Hayward & Slotow 2009, Cozzi et al. 2012, Dröge et al. 2017, Massara et al. 2018). Thus, our results correspond with studies in which temporal partitioning occurred as a result of differences in activity periods between predator species, and was presumed to be the main driver for coexistence in sympatric carnivores (Edwards et al. 2015, Herrera et al. 2018, Hearn et al. 2018).

2.5.1. Intraspecific and interspecific interactions

Since lions tend to exhibit a high degree of coordinated movements among lion pairs (Benhamou et al. 2014), intraspecific interactions were also selected as important factors accounting for the time-use patterns among lions. However, as we did not differentiate between competitive or mutually beneficial intraspecific interactions, it is plausible that our mating pairs may have exaggerated or confounded this result. Although we assumed that conspecifics for the purpose of this study were unfamiliar and, thus, served as a proxy of intraspecific competition, a caveat should be noted that some conspecifics may have actually been familiar to some individuals, as in the case of mating pairs. Nonetheless, interspecific interactions were important influences on the time-use metrics that drives both lion and spotted hyena space-use patterns. Surprisingly, although female lions had shorter durations in locations with high competitor probabilities, we found that male lions (and their mating partners) had longer durations in these areas. As dominant predators, male lions are either unaffected by being in locations of higher competitor probabilities, or it is likely that they spend more time within these areas to increase the likelihood of encountering hyenas, because they appear to derive benefits from hyenas through kleptoparasitism (Cooper 1991, Honer et al. 2002, Höner et al. 2005, Watts & Holekamp 2008, 2009). During this study, male lions were often observed to be attracted to spotted hyena calls: they would immediately perk up their ears, turn to face the direction of the calls, and often walked towards the direction of the hyena sounds. Observations of direct interactions between lions and spotted hyenas during this study almost always involved hyenas actively avoiding male lions by retreating and moving away, as was also observed in other studies (Cooper 1991, Honer et al. 2002). At encounters with male lions at fresh kills, hyenas often lost their kills to lions or aggregated into large groups (>20 individuals) before attempting to initiate mobbing behaviour, similar to the findings of previous studies (Trinkel & Kastberger 2005, Lehmann et al. 2017).

In addition, our results demonstrated patterns of recursions and locations of extended stays within the home ranges of apex predators to be influenced by the probability of, and proximity to, competitor and conspecifics. We suggest this to be the result of a perceived risk of competition, in which carnivores behaviourally mediate the potential for competition by altering their space use, or movement patterns (Vanak et al. 2013). Furthermore, other studies have documented the behavioural response of carnivore species to the potential risk of either encountering competitors or competitive interactions with increased vigilance and movements, either in preparation for potential interactions, or to move through/exit the area as quickly as possible (Durant 1998, 2000b, Swanson et al. 2016). Pangle and Holekamp (2010) attributed the vigilance levels of spotted hyenas to be more influenced by interspecific than intraspecific threats. Likewise, Valeix et al. (2012) documented lions moving at quicker speeds, and with relatively straighter trajectories, in response to the risk of conflict when close to human settlements. Specifically, we found spotted hyenas to behaviourally reduce the risk of potential interaction with lions by remaining longer in areas of low competitor probabilities and at far distances to competitors. This type of behaviour is mirrored in the behaviour-specific habitat selection of lions' in response to mitigating the potential risk of conflict with humans (Suraci et al. 2019). Thus, the behavioural responses of lions and spotted hyenas towards the perceived risk of competition appears to be similar, regardless of whether it stems from inter- or intraspecific interactions.

2.6. Conclusions

Our results have implications for the conservation of large carnivores in substantiating the potential effects of interference competition on lion and spotted hyena spatial patterns and movements. These findings supplement the growing body of evidence that demonstrates coexistence among carnivores is facilitated by fine-scale behavioural mechanisms in addition to spatial and temporal partitioning. While the patterns of spatial and temporal overlap observed among lions and hyenas do not differ from earlier studies; combining patterns of space use, temporal activity, fine-scale habitat use differentiation, and localized reactive avoidance behaviours in response to the potential risk of competition, has revealed the complex dynamics among lions and spotted hyenas within an apex predator system. Additionally, patterns of recursion and locations of extended stays within the home ranges of apex predators are influenced by the probability of and proximity to competitors and conspecifics, and can be used to inform management strategies for the maintenance of carnivore communities.

As large carnivores are becoming increasingly constrained to protected areas, it is important to note that lions and spotted hyenas do not respond to inter- and intraspecific interactions equally among heterogeneous and homogeneous environments. Specifically, the movement decisions and behavioural responses of lions and spotted hyenas exhibit behavioural plasticity across different systems, and are likely a result of several factors, including habitat complexity, hunting strategies, and the active avoidance of intraspecific and heterospecific competitors. Consequently, we encourage conservation practitioners to recognize the importance of the potential effects of inter- and intraspecific interactions among apex predators in managing diverse, ecological communities.

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2.8. SUPPLEMENTARY MATERIALS

Supplementary materials to Chapter 2 Methods:

Etosha National Park

Etosha National Park, a 22,270km^2 fenced reserve in northern Namibia (Fig. 2.1), is classified as semi-arid savanna (Huntley & Walker 1982), with perennial water available only natural artesian springs or from pumped boreholes (Auer 1997). The 9000km^2 Etosha site occupied the central regions of Okaukeujo and Halali, and included an area outside the southeastern boundary of the park that a collared individual had dispersed to. Seasonal rainfall occurs mainly between November and April, with the highest monthly rainfall in January and February (Engert 1997). The area is interspersed with dolomite inselberge and sandy bushveld, and is comprised mainly of grasslands, short-grass plains, shrub-land, dwarf-shrub and mixed tree savanna, including Mopani (*Colophospermum mopane*) (le Roux et al. 1988).

Chobe/Linyanti River system

The Chobe National Park, a 11,700km^2 unfenced reserve in northeastern Botswana, and the Linyanti Conservancy, a 1660km^2 community managed wildlife area within the Chobe Enclave surrounded by the Chobe National Park (Fig. 2.1) form part of the core component of the Kavango-Zambezi (KAZA) Transfrontier Conservation Area. The 7500km^2 Botswana site occupies the floodplains of the northern Kalahari bounded by the waters of the Chobe and Linyanti Rivers, complete with papyrus swamps, lagoons and marshes. The Linyanti-Chobe Rivers, fed by the Kwando and Zambezi rivers, and the Cubango River that feeds into the Okavango Delta are the main sources of permanent water for this ecosystem (Fox et al. 2017).

Seasonal rainfall occurs mainly between November and March with a mainly dry season from April to October. The vegetation of the area is highly varied with riparian and mopane woodlands, Baikiaea forests (*Baikiaea plurijuga*), open grasslands and mixed Acacia savanna (*Vachellia spp.*), with *Terminalia sericea* and *Philenoptera nelsii* in sandveld communities (Murray-Hudson et al. 2011, Sianga & Fynn 2017).

NG32 concession, Okavango Delta

The NG32 concession, a 1000km^2 site in the southeastern section of the Okavango Delta, borders the Moremi Game Reserve, and includes the private concession of Sanctuary Retreats and adjoining Wildlife Management Areas (Fig. 2.1). The area is characterized by seasonal flooding and rainfall, with rising floodwaters occurring between April to July, and typically highest in August (Bennitt et al. 2019). Rainfall occurs mainly between December and March, with a cool dry season from May to August and a hot dry season from September to November. Comprised of floodplains with a network of waterways, islands, lagoons, reed banks, and pans (Beehner et al. 2005), the area consists mainly of riparian tree species (*Croton megalobotrys, Hyphaene petersiana, Philenoptera violacea, and Diospyros mespiliformis*), dryland tree species of acacia (*Vachellia*) and mopane (*Colophospermum*) woodland, and grasslands (Tsheboeng et al. 2017).

Data collection

A total of 19 lions (13 females and 6 males) and 14 spotted hyenas (10 females and 4 males) were fitted with GPS satellite telemetry collars (IridiumTrackM, Lotek Wireless Inc., Newmarket, Ontario, Canada) programmed to record GPS fixes every 30 minutes during nocturnal periods (18h00 – 6h00 or 17h00 – 8h00) and every 5 minutes for two hours after sunset (19h00 – 21h00) and before sunrise (4h00 – 6h00). All collars recorded diurnal fixes at 10h00 and 14h00 to aid in locating individuals prior to night follows. Collars were also outfitted with dual-axis accelerometers, which measure acceleration on the *x*-axis (representing forward-backward movement), and on the *y*-axis (representing the sideways or rotary movement) continuously in 8 second bursts, and averaged over 240 seconds. Activity was measured four times per second simultaneously on each axis as the difference in acceleration between two consecutive measurements and given a relative range between 0 and 255 (activity monitor values [AMVs]), characterizing the mean activity/acceleration. The activity data were downloaded from all retrieved collars, and any activity from more than 7 consecutive tracking days were used for subsequent analysis. Collared animals were located in the field from daily uploads of GPS locations via satellite uplink, and, when necessary, radio-tracked from a vehicle with a handheld 3-element yagi antenna (Lotek), and a custom built vehicular-mounted 5-element antenna with a SRX 600 telemetry receiver. Lions and spotted hyenas were monitored on a daily basis via satellite to ensure no mortality events occurred. Individuals whose locations were accessible by the road network prior to sundown were selected for night follows for the maintenance of demographic records and observations of social dynamics. All collared individuals were monitored each day from daily satellite uploads of relocations and up to two or three individuals were selected each day according to their proximity to accessible roads for continuous follows during the night for the ground-truthing of acceleration data and to record any predated events or competitive interactions that occurred.

In the Etosha National Park, 17 collars were deployed on 9 lions and 8 spotted hyenas in the late dry season of 2013 (Appendix 2.1, Supplementary materials). Two collars (1 lion and 1 hyena) suffered structural failures during the dry season and were retrieved. A collar was also recovered from a lioness that had been shot outside the park. Subsequently, an additional two lions and one hyena were collared in the wet season of 2014. During the wet season, five additional collars (4 lions and 1 hyena) suffered structural failures and four lion collars were recovered. All but two hyena collars were retrieved at the end of the study in Etosha, including a collar from a hyena killed by a lion, and a collar from a hyena that had dispersed 120 km outside of the park.

In Botswana, 13 collars were deployed on 6 lions and 5 spotted hyenas along the Chobe/Linyanti (hereafter “Chobe”) riverfront in the dry season of 2015, and on 2 lions in the NG32 concession of the Okavango Delta in the late dry/early wet season of 2015 (Appendix 2.1, Supplementary materials). All hyena collars included remote drop-off features, eliminating the need to immobilize hyenas for collar retrieval. The drop-off units were programmed to release in the dry season of 2016, but failed to release. Two collars were recovered via wildlife authorities from a hyena shot by a local farmer, and a lioness that had been lured across the river and poached by a Namibian wildlife official. At the end of the study, four collars were recovered from the remaining eleven collars whose batteries had depleted. Collars unable to be removed would eventually fall off due to the deterioration of the collar material.

Prior to collaring, we determined the individuals of lion prides and hyena clans within the study areas over a period of 8 months in Etosha and 5 months in Chobe. We identified lion individuals using whisker/scarring patterns, and used spot patterns/pelage colouration for hyenas. We placed a collar on each of the known groups within the study areas, and data therefore represent the movements and behaviour of the species groups within these areas.

Capture and sample collection

All immobilizations were undertaken by registered wildlife veterinarians or under supervision of a veterinarian by persons who successfully passed the Zimbabwe wildlife capture and handling course. All animals were darted with a cartridge-fired projector system (Pneu-Dart, Inc.) from a range of 10-50m. Most of the animals were darted at night using red-filtered spotlights from vehicles for deployment, with 2 lions darted from a helicopter during the late afternoon for retrievals. In the case of a collared spotted hyena that had dispersed outside of Etosha onto privately owned ranchland, this individual was tracked and darted on foot with permission from the landowner. Initial drug combinations consisted of 3.81 ± 2.17 mg/kg Ketamine hydrochloride, 2.55 ± 1.20 mg/kg Xylazine, 1.48 ± 0.51 mg/kg Tiletamine/Zolazepam hydrochloride (Zoletil), and 0.07 ± 0.02 mg/kg Medetomidine reversed with 0.20 ± 0.07 mg/kg Atipamazole and 0.43 ± 0.19 mg/kg Yohimbine. Later drug combinations consisted of 0.31 ± 0.11 mg/kg Butorphanol with 0.05 ± 0.01 mg/kg Medetomidine and 0.15 ± 0.03 mg/kg Midazolam, reversed with 0.58 ± 0.19 mg/kg Naltrexone and 0.27 ± 0.05 mg/kg Atipamazole, or 1.12 ± 0.65 mg/kg Zoletil and 0.07 ± 0.04 mg/kg Medetomidine, with 1.05 ± 0.87 mg/kg Ketamine as required, reversed with 0.24 ± 0.20 mg/kg Atipamazole and 0.22 ± 0.13 mg/kg Yohimbine.

Recumbency in animals occurred 9 ± 4 mins after darting and immobilizations lasted for 80 ± 65 mins. Eyes were covered with a blindfold to reduce stress and stimuli during handling. Specimens were collected from all animals and included blood, tissue, and feces, with anal gland excretions collected from spotted hyenas only and stored in vials with ethanol. External parasites were noted and visually estimated, with a subset extracted and placed into vials filled with ethanol or methylated spirits. Morphometric measurements were undertaken on all animals after de Waal et al. (de Waal et al. 2004), and included the length of the mane of male lions at four points (B. Stapelkamp, pers. comm). Morphometric measures and spinal palpations were used to assign a body condition score to each individual (for lions, Dikeman, unpub.; Treiber & Mann, unpub.; for spotted hyenas, Watts & Holekamp, 2008). Once assigned, the animal's body condition was monitored visually throughout the tracking period and was confirmed during collar retrieval when the animal was immobilized again. In cases where the animal's condition deteriorated or improved, the score was taken as an average between the two values. All animals collared were fully mature, and age estimates of lions from Etosha were compared against a database of branded lions of known ages. Lion ages were estimated from visual scoring of body size and pelage colouration, facial scarring, mane development, nose darkness, and based on teeth wear after Smuts et al. (Smuts et al. 1978). Spotted hyena ages were estimated from visual scoring of body size and pelage colouration, facial scarring, and based on teeth wear after van Horn et al. (Van Horn et al. 2003).

Collar accuracy

We tested collar accuracy by placing all collars out at known GPS locations under a variety of canopy cover ranging from low cover (grassland/shrubs) to very dense cover (heavily vegetated wooded areas) at different times. The location fixes collected by the collars (*n* = 5159) was used to measure the distances between each consecutive fix. This information was then averaged to give a fix accuracy error rate of 3.49 ± 3.80m, and is representative of the accuracy of collars deployed on the animals.

Etosha carcass data

As carcasses provide lions and spotted hyenas with an essential resource, we assessed how distances to available carcasses in the Etosha National Park influenced lion and spotted hyena recursion rates and the duration of stays throughout their ranges. Carcasses were found while following collared individuals or during cluster investigations and were recorded with the ENP's Mortality database (*n*=30). The relative homogeneous and open plains of Etosha lends itself to the detection of carcasses, vultures circling above carrion, or to conspicuous groups of feeding vultures (Bellan et al. 2013). Carcasses sighted during road transects and management or (other) research activities were recorded by park personnel and researchers. Carcasses are identified to species, noted as either adults or juveniles, and sexed when possible. Cause of death was investigated to determine whether a predation event or anthrax death had occurred (other proximate causes of death in the Etosha plain's ungulates are negligible, Gasaway et al. 1996). If a carcass was determined to be predated, the suspected predator was identified or confirmed when possible due to tracks, spoor and field signs. The remains were scored as whether to be fresh, partially consumed or completely consumed leaving only skins, bones and horns. Evidence of anthrax death typically includes bloated, unopened carcasses with bloody discharges at body orifices. Carcasses of suspected anthrax incidences were swabbed with standard cotton swabs, which were submitted to the Central Veterinary Laboratory (Windhoek, Namibia) for confirmation of the presence of anthrax spores. GPS locations were obtained at carcass sites or coordinates were later assigned to specified locations.

ENP's mortality records for the period of the study in Etosha (September 2013 – March 2015, *n*=304) was used to include carcasses as an available resource on the landscape. Records of carnivore mortalities (*n*=49) were removed, as they were expected not to pose as an attractant to predators as an available food resource. Animals that were shot to be used for feeding captured carnivores awaiting transport to Cuba were removed, as were old and desiccated carcasses as these were assumed to have no effects on predator movement. The remaining carcass locations were assigned a starting and ending time based on the weight of the species, the estimated date of death and according to the detection and consumption times for carrion (Moleón et al. 2015) or the mean persistence times for predated carcasses (Benbow et al. 2016). We then measured the minimum Euclidean distances of the locations of collared individuals to these carcass locations only during those times that the carcasses were deemed to have existed on the landscape for.

While we acknowledge that our carcass data do not fully include all the available carcasses that occurred during the study period, and likely excludes many smaller sized carcasses which are likely to have been completely consumed prior to detection by observers, we assume the survey area to be a random (i.e. unbiased) sample of the larger study area, and the distance of carcasses to the nearest road is assumed to be uniform and an unbiased sample of live animal locations (Bellan et al. 2013). Although the collective effort in detecting carcasses by park personnel and researchers alike while undertaking other work results in a highly variable surveillance effort, communication amongst researchers ensures that carcasses were reported only once, which safeguards against double sampling. As anthrax carcass sites from previous years pose an attractant to ungulates in subsequent years as a result of the enriched nutrients found in the soil (Turner et al. 2013), these sites now possess an inherent risk of infection for foraging ungulates as anthrax spores were found to persist in these locations one and two years following initial deposition of the carcass (Turner et al. 2014, Dougherty et al. 2020). Anthrax carcass records from a recent period of an anthrax outbreak (2009-2010) was used to create a GIS layer of anthrax risk sites, which we defined as the probability of encountering site-attracted foraging ungulates (Turner et al. 2014, 2016). We included carcasses that were identified as anthrax positive from blood swabs that were tested for *B. anthracis* through culture with PCR confirmation (Beyer et al. 2012). The area representing high incidences of anthrax carcasses (3405.7 km^2) was constructed using the 95% kernel density estimator from the locations of confirmed anthrax positive carcasses. We converted this into a volume UD to obtain probability of presence values for each cell. We subtracted volume UD values from 100 as described above for the combined UD layers.

Statistical analysis

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018), and all GIS applications were conducted in ArcGIS (ESRI ArcMap v.10.0, Redlands, CA, USA). The *t*-test was used to examine for differences among lion and spotted hyena movement metrics, as well as for differences in the sizes of home ranges and core use areas according to lion and hyena ages, body condition scores, and group sizes. We examined with the *t*-test whether lions and hyenas moved faster and in straighter paths when at closer distances to competitors compared to conspecifics. In addition to the *t*-test, we used a mixed model ANOVA to compare the speed and tortuosity of lions and spotted hyenas between reserves, and to determine whether lion and hyena activity and movement metrics differed according to the lunar cycle (i.e. new moon versus full moon), and when they were within competitor core areas compared to when they were outside of competitor core areas.

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Table S2.1. Percent frequency of lion and spotted hyena relocations by land cover type from the Etosha National Park, Namibia, and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana.

Region	Land cover type	% Available Cover	Percent frequency	
			Lion	Spotted hyena
Etosha	Forest	4.16	-	1.68
	Woodland	12.08	17.20	17.62
	Shrubland	33.15	16.02	26.88
	Grassland	40.65	58.75	48.18
	Pan	8.21	5.58	3.74
	Cropland	0.56	0.02	0.10
	Settlement	0.01	0.05	0.01
	Other	1.18	2.38	1.79
Botswana	Forest	9.97	11.75	28.12
	Woodland	9.03	0.16	-
	Shrubland	41.94	43.21	59.15
	Grassland	16.84	27.52	4.81
	Pan	0.84	-	0.04
	Wetland	18.45	13.10	6.55
	Cropland	0.73	-	0.03
	Settlement	0.08	0.01	-
	Other	2.12	4.25	1.29

Table S2.2. Kernel density (a, c) and *a*-LoCoH (b, d) area measures for home ranges and core use areas (km^2) of lion (a, b) and spotted hyena (c, d) individuals. CS = combined seasons, DS = dry season, WS = wet season. Upper panels consist of individuals from the Etosha National Park, Namibia, and lower panels consist of individuals from the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana.

(a)

	HOME RANGE (95%)									**CORE AREA (50%)**								
						DRY SEASON		**WET SEASON**							**DRY SEASON**		**WET SEASON**	
INDIVIDUAL	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**
OK-33863	456	284	457	604	586	326	308	604	586	129	62	128	170	168	73	69	170	168
RE-33864	538	117	539	691	674	120	119	691	674	106	23.7	107	137	134	24.8	27.1	137	134
NU-33865	841	614	653	1067	1051	837	825	842	834	198	172	158	252	245	230	227	215	208
MO-33866	1192	1111	871	1440	1433	1497	1487	1130	1128	277	188	242	370	367	296	290	307	308
OJ-33867	787	415	765	937	979	443	474	937	979	168	87	160	224	221	97	103	224	224
SU-33868	667	495	646	915	872	810	726	897	868	112	74	114	159	147	159	141	162	149
OM-34308	369	131	375	487	490	131	144	487	490	87	24.2	90	116	117	25.1	28.2	116	117
LU-34308	214	185	129	241	254	212	220	195	191	29.3	27.5	33.5	36.3	34.6	34.5	32.4	49.7	48.6
OF-34309	375	436	361	418	424	433	472	418	424	87	56	87	125	119	62	67	125	119
G2-35678	329	329	127	439	424	439	424	-	-	62	62	27.7	83	83	83	83	-	-
Mean	***577***	***411***	***435***	***724***	***719***	***525***	***520***	***688***	***686***	***125***	***135***	***115***	***167***	***163***	***109***	***107***	***167***	***164***
SD	***297***	***294***	***276***	***364***	***361***	***422***	***411***	***293***	***296***	***72***	***189***	***63***	***95***	***94***	***92***	***88***	***74***	***75***
SW-33950	255	208	272	314	331	278	290	341	356	56	45.5	63	69	72	62	64	79	82
AF-34308	210	40.0	236	284	297	61	58	326	341	36.8	10.7	43.8	56	54	17.4	16.1	69	68
BE-35678	727	38.5	720	1196	1096	-	-	1196	1099	213	11.4	211	335	316	-	-	335	317
BO-35947	296	304	216	399	399	451	461	270	265	67	79	46.6	84	85	120	124	56	56
AM-36714	1032	710	1171	1378	1386	901	971	1693	1612	132	71	214	258	226	154	137	381	337
BA-36715	47.0	49.8	38.1	48.9	48.1	42.8	40.0	50	50	8.0	7.7	7.5	8.0	8.1	7.5	7.3	8.5	8.8
KW-36716	244	125	304	283	304	147	161	388	404	39.5	29.6	59	48.5	53	34.4	37.8	81	88
KB-36717	97	72	113	126	137	75	74	164	190	11.3	9.3	14.6	15.6	17.5	11.1	11.3	23.7	28.5
Mean	***363***	***193***	***384***	***504***	***500***	***279***	***294***	***554***	***540***	***70***	***33.0***	***82***	***109***	***104***	***58***	***57***	***129***	***123***
SD	***339***	***229***	***377***	***498***	***477***	***311***	***335***	***576***	***533***	***69***	***29.0***	***83***	***120***	***109***	***58***	***54***	***144***	***129***

(b)

	HOME RANGE (95%)									CORE AREA (50%)								
						DRY SEASON		WET SEASON							DRY SEASON		WET SEASON	
INDIVIDUAL	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**
OK-33863	295	54	283	209	269	39.8	69	209	269	144	16.1	123	84	134	6.5	17.3	84	134
RE-33864	345	41.8	335	309	362	0.2	38.6	309	362	92	12.2	85	96	91	0.1	14.9	96	91
NU-33865	580	362	358	553	609	326	371	384	449	174	120	131	177	212	167	185	169	189
MO-33866	622	370	294	734	829	446	554	454	507	178	103	77	232	298	99	114	176	208
OJ-33867	348	105	273	265	393	41.7	101	265	393	165	33.3	98	92	160	33.8	21.6	92	160
SU-33868	484	162	375	537	503	161	228	412	423	101	46.9	99	97	106	23.1	25.1	99	106
OM-34308	221	66	233	189	244	29.5	69	189	244	91	14.4	74	68	90	11.4	18.3	68	90
LU-34308	170	150	43.8	149	210	129	167	39.0	44.7	31.1	28.6	18.5	33.9	44.2	43.3	33.7	18.6	21.5
OF-34309	327	141	254	201	256	15.1	200	201	256	104	16.1	71	91	63	5.5	27.1	91	63
G2-35678	229	229	-	220	258	220	258	-	-	55	54.5	-	78	81	78	81	-	-
Mean	***362***	***168***	***272***	***337***	***394***	***141***	***206***	***273***	***328***	***113***	***44.5***	***86***	***105***	***128***	***46.8***	***54***	***99***	***118***
SD	***153***	***118***	***98***	***199***	***200***	***150***	***160***	***131***	***140***	***50***	***38.2***	***33.1***	***57***	***77***	***53***	***57***	***48.2***	***60***
SW-33950	171	113	171	163	194	134	106	134	181	43.2	25.9	40.2	61	51	64	32.2	64	73
AF-34308	87	16.0	89	117	120	14.3	17.2	117	125	30.5	5.8	27.8	35.0	28.3	5.3	6.6	40.0	25
BE-35678	282	1.5	275	241	314	-	-	241	310	59	0.8	57	79	144	-	-	79	140
BO-35947	271	230	180	243	316	191	274	166	185	70	73	46.1	82	83	82	99	56	50
AM-36714	934	604	849	751	692	161	-	729	651	195	168	182	353	125	43.3	49	418	358
BA-36715	52	49	47.4	44.8	43	30.2	29.6	39.0	38.2	9.8	8.8	10.9	11.6	11.5	7.6	6.6	11.0	10.7
KW-36716	174	89	167	183	208	79	85	192	225	36.5	21.5	37.5	34.2	44.7	29.5	27.7	42.7	67
KB-36717	88	59	83	74	78	42.1	32.1	75	68	11.6	7.1	10.9	19.2	16.5	18.7	11.6	22.6	18.2
Mean	***257***	***145***	***233***	***227***	***246***	***93***	***91***	***212***	***223***	***57***	***38.9***	***52***	***84***	***63***	***35.7***	***33.2***	***92***	***93***
SD	***286***	***199***	***259***	***223***	***206***	***69***	***97***	***219***	***193***	***60***	***57***	***55***	***112***	***49.6***	***28.8***	***32.9***	***134***	***115***

(c)

	HOME RANGE (95%)									CORE AREA (50%)								
						DRY SEASON		WET SEASON							DRY SEASON		WET SEASON	
INDIVIDUAL	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**
GO-33869	235	185	265	273	283	205	210	315	332	57	42.6	66	62	67	55	50.8	67.6	80.6
TJ-33870	290	307	289	326	362	-	-	326	362	42.1	70	42	40.6	60	-	-	40.6	60.4
NE-33871	284	215	309	249	315	168	238	292	360	46.1	25.6	60	36.3	63	15.1	35.0	65.5	87.8
SA-33872	1355	201	1465	2013	1973	258	251	2117	2056	210	49.0	325	365	358	70	63.8	495.0	495.9
AU-33873	2808	136	4128	4126	4124	148	185	6007	6025	383	10.8	869	639	635	13.5	17.8	1357.5	1355.2
OM-33874	299	256	311	283	341	245	295	290	362	43.1	36.7	43.7	39.8	52	38.0	46.1	42.3	56.7
SU-33951	169	298	168	264	267	-	-	264	267	27.6	69	27.1	39.7	41	-	-	39.7	41.3
WO-34310	309	309	-	354	353	354	353	-	-	69	69	-	74	84	74	84	-	-
Mean	***719***	***239***	***991***	***986***	***1002***	***230***	***255***	***1373***	***1395***	***110***	***46.6***	***205***	***162***	***170***	***44.2***	***49.7***	***301***	***311***
SD	***927***	***64***	***1454***	***1405***	***1388***	***75***	***61***	***2153***	***2140***	***125***	***22.1***	***311***	***223***	***215***	***26.3***	***23.0***	***494***	***488***
AR-33869	142	-	142	137	162	-	-	137	162	19.6	-	19.6	25.9	31.9	-	-	25.9	31.9
IH-33870	136	119	147	108	156	101	144	103	152	20.4	20.1	13.9	20.0	29.4	19.2	29.4	13.5	24.9
KW-33871	82	83	60	45.9	95	48.2	99	13.7	60	10.1	10.9	5.4	7.1	14.5	7.5	16.0	2.3	9.2
RV-33873	136	96	137	140	149	-	-	140	149	29.1	16.6	29.5	30.4	41.4	-	-	29.8	41.4
SR-34310	1898	173	3655	2932	3025	154	211	5553	5599	164	24.8	463	271	287	28.8	38.7	840	866
Mean	***479***	***118***	***828***	***673***	***717***	***101***	***151***	***1189***	***1224***	***48.7***	***18.1***	***106***	***71***	***81***	***18.5***	***28.0***	***182***	***194***
SD	***794***	***39.6***	***1581***	***1264***	***1290***	***53***	***56***	***2440***	***2446***	***65***	***5.9***	***200***	***112***	***116***	***10.7***	***11.4***	***368***	***376***

(d)

	HOME RANGE (95%)									CORE AREA (50%)								
						DRY SEASON		WET SEASON							DRY SEASON		WET SEASON	
INDIVIDUAL	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**
GO-33869	232	175	242	216	258	129	166	213	280	75	51	91	110	83	58	55	88	101
TJ-33870	249	9.6	246	132	259	-	-	132	259	44.8	4.6	44.8	19.6	44.3	-	-	19.6	44
NE-33871	282	217	282	205	285	125	198	195	284	79	39.2	93	35.1	56	5.2	35.4	63	95
SA-33872	786	171	831	714	876	147	168	762	939	118	54	220	123	138	57	73	234	422
AU-33873	1057	112	1148	853	1075	29.8	110	969	1239	168	8.4	281	106	224	2.6	12.8	169	293
OM-33874	292	225	299	246	309	148	183	230	303	76	55	87	90	90	34.6	77	81	91
SU-33951	135	5.7	134	43.0	62	-	-	43.0	62	55	0.4	55	10.7	18.3	-	-	10.7	18.3
WO-34310	275	275	-	239	289	239	289	-	-	67	67	-	68	88	68	88	-	-
Mean	***414***	***149***	***455***	***331***	***427***	***136***	***186***	***363***	***481***	***85***	***35.0***	***124***	***70***	***93***	***37.6***	***57***	***95***	***152***
SD	***326***	***99***	***380***	***289***	***352***	***67***	***59***	***354***	***432***	***39.6***	***26.4***	***90***	***43.7***	***64***	***28.3***	***28.5***	***80***	***148***
AR-33869	106	-	106	38.7	54	-	-	38.7	54	25.8	-	25.8	14.5	29.1	-	-	14.5	29.1
IH-33870	128	114	133	70	117	61	90	61	84	45.8	24.6	11.5	16.8	42.4	15.5	30.6	4.0	34.9
KW-33871	79	77	38.7	12.5	53	11.9	52	-	9.0	9.5	9.5	2.7	2.4	19.8	1.5	27.3	-	7.5
RV-33873	135	37.8	131	65	80	-	-	65	80	43.1	5.2	43.1	27.0	40.0	-	-	27.0	40.0
SR-34310	523	156	587	514	594	84	134	515	1016	67	43.7	133	85	97	34.2	33.2	98	148
Mean	***194***	***96***	***199***	***140***	***179***	***52***	***92***	***170***	***249***	***38.1***	***20.8***	***43.2***	***29.1***	***45.7***	***17.1***	***30.4***	***36.0***	***52***
SD	***185***	***50***	***220***	***210***	***233***	***37***	***41***	***230***	***430***	***21.6***	***17.4***	***52***	***32.4***	***30.3***	***16.4***	***3.0***	***42.6***	***55***

Table S2.3. Total overlapped areas in km^2 between lions' (vertical column) and spotted hyenas' (horizontal column) home ranges and core areas in the (a) Etosha National Park, Namibia; (b) Chobe National Park and Linyanti Conservancy, Botswana. Utilization distributions were generated with the home range (95%) and core use area (50%) kernel density estimator (i) and *a*-LoCoH (ii) isopleths. Males are underlined. An asterisk denotes mortality.

(a)(i)

HOME RANGE (95%)

		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				210				199				-
	RE-33864		85		94	0		64			116		399	67		167	-
	NU-33865	181	130		6.1					231	108		0				-
	MO-33866	90	301		161			179		53	134		12			2.5	-
	OJ-33867			167	0		36.8		93			193	375		31.6		-
	SU-33868		122		171			198			195		482			168	-
	OM-34308*			0	0	0	102					62	109	47.9	173		-
	LU-34308			70	0.5		76		0.4			12	129		50		-
	OF-34309*				0	0							68	361			-
	G2-35678				0	0	1.7			-	-	-	-	-	-	-	-

CORE AREA (50%)

		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				24.5				0				-
	RE-33864		0		5.2	0		0.8			3.0		20.6	0		20.4	-
	NU-33865	33.2	12.3		0					19.9	0		0				-
	MO-33866	0	65		4.8			3.4		0	16.0		0			0	-
	OJ-33867			6.5	0		0		0			0.01	13.2		0		-
	SU-33868		0		7.2			11.3			3.0		41.5			18.5	-
	OM-34308*			0	0	0	0					0	0	0	10.7		-
	LU-34308			0	0		0		0			0	31.6		1.9		-
	OF-34309*				0	0							0	51			-
	G2-35678				0	0	0			-	-	-	-	-	-	-	-

(a)(ii)

HOME RANGE (95%)

		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				48.7				43.8				-
	RE-33864		0.6		38.8	0		0			76		236	0		124	-
	NU-33865	126	4.9		0.1					172	60		0				-
	MO-33866	22.8	6.8		62			0		17	23.2		0			0	-
	OJ-33867			56	0		0		27.1			69	98		4.4		-
	SU-33868		0.7		72			0.9			131		260			124	-
	OM-34308*			0	0	0	57					35.8	0.2	0	100		-
	LU-34308			53	0		58		0			1.3	43.8		25.2		-
	OF-34309*				0	0							0.7	102			-
	G2-35678				0	0	0			-	-	-	-	-	-	-	-

CORE AREA (50%)

		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				4.2				0				-
	RE-33864		0		0.2	0		0			0		56	0		26.4	-
	NU-33865	32.3	1.1		0					34.8	0		0				-
	MO-33866	0	3.3		0			0		0	14.7		0			0	-
	OJ-33867			1.3	0		0		0			0	4.6		0		-
	SU-33868		0		21.5			0			1.7		69			40.7	-
	OM-34308*			0	0	0	0.2					0	0	0	16.0		-
	LU-34308			0	0		0.1		0			0	9.7		0.3		-
	OF-34309*				0	0							0	28.8			-
	G2-35678				0	0	0			-	-	-	-	-	-	-	-

(b)(i)

HOME RANGE (95%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	67			96		104			272
	AF-34308	-			0					78	
	BE-35678*	-			0		93			15.4	
	BO-35947	-									
	AM-36714	-			65		84			131	
	BA-36715	-									
	KW-36716*	-	4.1	40.1		25.0		26.1	47.0		198
	KB-36717*	-	29.8	0.9		47.1		42.6	2.8		106

CORE AREA (50%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	2.0			2.9		0			56
	AF-34308	-			0					0	
	BE-35678*	-			0		0			0	
	BO-35947	-									
	AM-36714	-			0		0			22.0	
	BA-36715	-									
	KW-36716*	-	0	0		0		0	0		7.8
	KB-36717*	-	0	0		0		0	0		13.7

(b)(ii)

HOME RANGE (95%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	52			65		75			130
	AF-34308	-			0					23.7	
	BE-35678*	-			0		32.8			0	
	BO-35947	-									
	AM-36714	-			17.7		64			97	
	BA-36715	-									
	KW-36716*	-	3.2	23.7		15.5		10.0	13.1		13.2
	KB-36717*	-	27.7	0		40.7		30.3	0.3		39.1

CORE AREA (50%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	0.6			4.6		0			0.4
	AF-34308	-			0					0	
	BE-35678*	-			0		0.1			0	
	BO-35947	-									
	AM-36714	-			0		0			0	
	BA-36715	-									
	KW-36716*	-	0	0		0		0	0		0
	KB-36717*	-	0	0		1.5		0	0		0.7

Table S2.4.1. Total proportion of lion (vertical column) home ranges and core areas overlapped by spotted hyena individuals (horizontal column) in the (a) Etosha National Park, Namibia; (b) Chobe National Park and Linyanti Conservancy, Botswana. Utilization distributions were generated with the home range (95%) and core use area (50%) kernel density estimator (i) and *a*-LoCoH (ii) isopleths. Males are underlined. An asterisk denotes mortality.

(a)(i)

		HOME RANGE (95%)															
		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				0.740				0.436				-
	RE-33864		0.730		0.806	0		0.549			0.214		0.741	0.125		0.309	-
	NU-33865	0.294	0.211		0.0099					0.354	0.165		0				-
	MO-33866	0.081	0.271		0.145			0.161		0.061	0.154		0.014			0.0029	-
	OJ-33867			0.402	0		0.089		0.224			0.252	0.490		0.041		-
	SU-33868		0.246		0.345			0.401			0.302		0.746			0.260	-
	OM-34308*			0	0	0	0.776					0.166	0.290	0.128	0.461		-
	LU-34308			0.376	0.0027		0.409		0.002			0.091	1.0		0.389		-
	OF-34309*				0	0							0.187	1.0			-
	G2-35678				0	0	0.005			-	-	-	-	-	-	-	-

		CORE AREA (50%)															
		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				0.395				0				-
	RE-33864		0		0.219	0		0.034			0.028		0.193	0		0.192	-
	NU-33865	0.193	0.071		0					0.126	0		0				-
	MO-33866	0	0.343		0.025			0.018		0	0.066		0			0	-
	OJ-33867			0.073	0		0		0			0	0.082		0		-
	SU-33868		0		0.097			0.152			0.026		0.365			0.163	-
	OM-34308*			0	0	0	0					0	0	0	0.119		-
	LU-34308			0	0		0		0			0	0.943		0.057		-
	OF-34309*				0	0							0	0.594			-
	G2-35678				0	0	0			-	-	-	-	-	-	-	-

(a)(ii)

		HOME RANGE (95%)															
		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				0.895				0.155				-
	RE-33864		0.014		0.928	0		0			0.225		0.703	0		0.369	-
	NU-33865	0.349	0.014		0.00028					0.481	0.167		0				-
	MO-33866	0.062	0.018		0.167			0		0.059	0.079		0			0	-
	OJ-33867			0.536	0		0		0.257			0.253	0.360		0.016		-
	SU-33868		0.0043		0.444			0.0056			0.348		0.695			0.330	-
	OM-34308*			0	0	0	0.871					0.154	0.00086	0	0.430		-
	LU-34308			0.354	0		0.385		0			0.030	1.0		0.575		-
	OF-34309*				0	0							0.0028	0.402			-
	G2-35678				0	0	0			-	-	-	-	-	-	-	-

		CORE AREA (50%)															
		DRY SEASON								WET SEASON							
		SPOTTED HYENA															
		GO-33869	TJ-33870	NE-33871	SA-33872	AU-33873	OM-33874	SU-33951	WO-34310	GO-33869	TJ-33870*	NE-33871	SA-33872	AU-33873*	OM-33874	SU-33951*	WO-34310
LION	OK-33863				0				0.261				0				-
	RE-33864		0		0.016	0		0			0		0.651	0		0.309	-
	NU-33865	0.269	0.0092		0					0.265	0		0				-
	MO-33866	0	0.032		0			0		0	0.191		0			0	-
	OJ-33867			0.039	0		0		0			0	0.047		0		-
	SU-33868		0		0.458			0			0.017		0.699			0.411	-
	OM-34308*			0	0	0	0.014					0	0	0	0.217		-
	LU-34308			0	0		0.0035		0			0	0.524		0.016		-
	OF-34309*				0	0							0	0.403			-
	G2-35678				0	0	0			-	-	-	-	-	-	-	-

(b)(i)

HOME RANGE (95%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	0.324			0.462		0.382			1.0
	AF-34308	-			0					0.331	
	BE-35678*	-			0		0.129			0.021	
	BO-35947	-									
	AM-36714	-			0.092		0.072			0.111	
	BA-36715	-									
	KW-36716*	-	0.033	0.320		0.200		0.086	0.155		0.651
	KB-36717*	-	0.413	0.012		0.653		0.378	0.025		0.945

CORE AREA (50%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	0.044			0.064		0			0.895
	AF-34308	-			0					0	
	BE-35678*	-			0		0			0	
	BO-35947	-									
	AM-36714	-			0		0			0.103	
	BA-36715	-									
	KW-36716*	-	0	0		0		0	0		0.133
	KB-36717*	-	0	0		0		0	0		0.938

(b)(ii)

HOME RANGE (95%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	0.466			0.575		0.437			0.763
	AF-34308	-			0					0.266	
	BE-35678*	-			0		0.119			0	
	BO-35947	-									
	AM-36714	-			0.029		0.075			0.114	
	BA-36715	-									
	KW-36716*	-	0.036	0.267		0.174		0.060	0.078		0.079
	KB-36717*	-	0.470	0		0.691		0.364	0.0036		0.470

CORE AREA (50%)

		DRY SEASON					WET SEASON				
		SPOTTED HYENA									
		AR-33869	IH-33870	KW-33871	RV-33873*	SR-34310	AR-33869*	IH-33870	KW-33871*	RV-33873	SR-34310*
LION	SW-33950	-	0.023			0.178		0			0.015
	AF-34308	-			0					0	
	BE-35678*	-			0		0.125			0	
	BO-35947	-									
	AM-36714	-			0		0			0	
	BA-36715	-									
	KW-36716*	-	0	0		0		0	0		0
	KB-36717*	-	0	0		0.211		0	0		0.064

Table S2.4.2. Total proportion of spotted hyena (vertical column) home ranges and core areas overlapped by lion individuals (horizontal column) in the (a) Etosha National Park, Namibia; (b) Chobe National Park and Linyanti Conservancy, Botswana. Utilization distributions were generated with the home range (95%) and core use area (50%) kernel density estimator (i) and *a*-LoCoH (ii) isopleths. Males are underlined. An asterisk denotes mortality.

(a)(i)

HOME RANGE (95%)

		DRY SEASON										WET SEASON									
		LION																			
		OK	**RE**	**NU**	**MO**	**OJ**	**SU**	**OM***	**LU**	**OF***	**G2**	**OK**	**RE**	**NU**	**MO**	**OJ**	**SU**	**OM***	**LU**	**OF***	**G2**
SPOTTED HYENA	**GO-33869**			0.974	0.487									0.873	0.201						-
	TJ-33870		0.277	0.423	0.983		0.397						0.400	0.372	0.464		0.676				-
	NE-33871					0.776		0	0.324							0.622		0.201	0.038		-
	SA-33872	0	0.466	0.030	0.801	0	0.849	0	0.0025	0	0	0.136	0.273	0	0.008	0.256	0.329	0.074	0.088	0.046	-
	AU-33873		0					0		0	0		0.016					0.012		0.087	-
	OM-33874					0.144		0.397	0.296		0.007					0.102		0.556	0.161		-
	SU-33951		0.215		0.601		0.665						0.993		0.015		1.0				-
	WO-34310	0.678				0.301			0.001			-	-	-	-	-	-	-	-	-	-

CORE AREA (50%)

		DRY SEASON										WET SEASON									
		LION																			
		OK	**RE**	**NU**	**MO**	**OJ**	**SU**	**OM***	**LU**	**OF***	**G2**	**OK**	**RE**	**NU**	**MO**	**OJ**	**SU**	**OM***	**LU**	**OF***	**G2**
SPOTTED HYENA	**GO-33869**			0.779	0									0.302	0						-
	TJ-33870		0	0.175	0.919		0						0.071	0	0.381		0.071				-
	NE-33871					0.254		0	0							0		0	0		-
	SA-33872	0	0.106	0	0.098	0	0.147	0	0	0	0	0	0.063	0	0	0.041	0.128	0	0.097	0	-
	AU-33873		0					0		0	0		0					0		0.059	-
	OM-33874					0		0	0		0					0		0.245	0.043		-
	SU-33951		0.012		0.049		0.164						0.753		0		0.683				-
	WO-34310	0.355				0			0			-	-	-	-	-	-	-	-	-	-

(a)(ii)

HOME RANGE (95%)

		DRY SEASON										WET SEASON									
		LION																			
		OK	RE	NU	MO	OJ	SU	OM*	LU	OF*	G2	OK	RE	NU	MO	OJ	SU	OM*	LU	OF*	G2
SPOTTED HYENA	**GO-33869**			0.723	0.131									0.713	0.071						-
	TJ-33870		0.063	0.51	0.708		0.073						0.307	0.243	0.094		0.53				-
	NE-33871					0.26		0	0.244							0.244		0.127	0.005		-
	SA-33872	0	0.227	0.001	0.362	0	0.42	0	0	0	0	0.053	0.284	0	0	0.12	0.313	0.0002	0.053	0.001	-
	AU-33873		0					0		0	0		0					0		0.089	-
	OM-33874					0		0.255	0.256		0					0.015		0.335	0.084		-
	SU-33951		0		0		0.158						0.922		0		0.920				-
	WO-34310	0.177				0.098			0			-	-	-	-	-	-	-	-	-	-

CORE AREA (50%)

		DRY SEASON										WET SEASON									
		LION																			
		OK	RE	NU	MO	OJ	SU	OM*	LU	OF*	G2	OK	RE	NU	MO	OJ	SU	OM*	LU	OF*	G2
SPOTTED HYENA	**GO-33869**			0.632	0									0.382	0						-
	TJ-33870		0	0.239	0.717		0						0	0	0.328		0.038				-
	NE-33871					0.033		0	0							0		0	0		-
	SA-33872	0	0.004	0	0	0	0.40	0	0	0	0	0	0.253	0	0	0.021	0.315	0	0.044	0	-
	AU-33873		0					0		0	0		0					0		0.103	-
	OM-33874					0		0.004	0.002		0					0		0.183	0.003		-
	SU-33951		0		0		0						0.481		0		0.741				-
	WO-34310	0.063				0			0			-	-	-	-	-	-	-	-	-	-

(b)(i)

HOME RANGE (95%)

		DRY SEASON						WET SEASON					
		LION											
		SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*	SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*
SPOTTED HYENA	AR-33869*	-	-	-	-	-	-			0.656	0.594		
	IH-33870	0.566				0.034	0.250	0.707				0.178	0.291
	KW-33871*					0.432	0.011					0.782	0.047
	RV-33873*		0	0	0.681				0.572	0.113	0.955		
	SR-34310*	0.556				0.145	0.273	0.074				0.054	0.029

CORE AREA (50%)

		DRY SEASON						WET SEASON					
		LION											
		SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*	SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*
SPOTTED HYENA	AR-33869*	-	-	-	-	-	-			0	0		
	IH-33870	0.100				0	0	0				0	0
	KW-33871*					0	0					0	0
	RV-33873*		0	0	0				0	0	0.746		
	SR-34310*	0.117				0	0	0.122				0.017	0.030

(b)(ii)

HOME RANGE (95%)

		DRY SEASON						WET SEASON					
		LION											
		SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*	SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*
SPOTTED HYENA	AR-33869*	-	-	-	-	-	-			0.309	0.598		
	IH-33870	0.461				0.028	0.244	0.561				0.075	0.228
	KW-33871*					0.307	0					0.339	0.007
	RV-33873*		0	0	0.468				0.181	0	0.736		
	SR-34310*	0.416				0.100	0.262	0.222				0.022	0.067

CORE AREA (50%)

		DRY SEASON						WET SEASON					
		LION											
		SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*	SW-33950	AF-34308	BE-35678*	AM-36714	KW-36716*	KB-36717*
SPOTTED HYENA	AR-33869*	-	-	-	-	-	-			0.0039	0		
	IH-33870	0.024				0	0	0				0	0
	KW-33871*					0	0					0	0
	RV-33873*		0	0	0				0	0	0		
	SR-34310*	0.105				0	0.034	0.003				0	0.0053

Table S2.5.1. Movement metrics of (a) all lions and spotted hyenas, and (b) lions and spotted hyenas from the Etosha National Park, Namibia (ENP) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (CNP). Movement metrics consist of the means ± standard deviations for activity (activity monitor values [AMVs]), step length (m), speed (m/s), net-squared displacement (NSD, km^2), and path tortuosity (radian).

(a)

Metric	Lion	Spotted hyena
Activity (AMVs in 24 h period)	21.88 ± 41.2	40.20 ± 68
Nocturnal step length from 30 min fixes (m)	289 ± 424	618 ± 685
Dusk/dawn step length from 5 min fixes (m)	51 ± 82	122 ± 147

(b)

Metric		ENP		CNP	
		Lion	Spotted Hyena	Lion	Spotted Hyena
Speed (m/s)		0.187 ± 0.25	0.364 ± 0.39	0.128 ± 0.23	0.310 ± 0.35
24 h step length from 4 h fixes (m)		1257 ± 1535	2009 ± 2156	898 ± 1159	1744 ± 1857
Nocturnal step length from 30 min fixes (m)		308 ± 462	649 ± 685	208 ± 340	529 ± 570
Dusk/dawn step length from 5 min fixes (m)		55 ± 99	130 ± 148	44 ± 78	119 ± 153
12 h nocturnal NSD from 4 h fixes (km^2)		8.3 ± 19.1	17.9 ± 43.1	2.9 ± 9.1	6.2 ± 19.9
12 h diurnal NSD from 4 h fixes (km^2)		2.6 ± 6.8	5.2 ± 21.7	1.1 ± 3.9	0.97 ± 3.7
12 h nocturnal dry season NSD from 30 min fixes (km^2)		12.4 ± 0.59	27.4 ± 0.78	5.2 ± 0.70	12.6 ± 0.53
12 h nocturnal wet season NSD from 30 min fixes (km^2)		12.8 ± 0.58	32.6 ± 1.2	6.9 ± 0.26	17.2 ± 0.58
24 h path tortuosity (4 h fixes)		0.080 ± 2.07	-0.077 ± 2.39	0.432 ± 2.41	2.963 ± 2.18
	Dry season	0.070 ± 2.07	-1.377 ± 2.24	0.296 ± 2.33	2.660 ± 2.03
	Wet season	-0.022 ± 2.07	0.991 ± 2.60	0.209 ± 2.35	-2.942 ± 2.01
	Male	0.194 ± 1.98	-1.255 ± 2.50	-0.044 ± 2.63	-3.09 ± 1.87
	Female	0.029 ± 2.09	0.806 ± 2.39	0.612 ± 2.05	2.800 ± 2.27
Nocturnal path tortuosity (30 min fixes)		0.135 ± 1.90	0.012 ± 1.73	0.052 ± 2.48	0.034 ± 1.87
	Dry season	0.018 ± 1.89	0.027 ± 1.84	-0.068 ± 2.44	-0.018 ± 1.87
	Wet season	0.151 ± 1.93	0.025 ± 1.68	0.003 ± 2.49	0.035 ± 1.87
	Male	0.046 ± 1.78	-0.053 ± 1.58	0.095 ± 2.46	0.069 ± 1.95
	Female	0.172 ± 1.92	0.021 ± 1.74	0.026 ± 2.52	0.011 ± 1.83
Dusk/dawn path tortuosity (5 min fixes)		0.053 ± 2.43	0.013 ± 1.59	0.847 ± 1.92	0.001 ± 1.31
	Dry season	-0.012 ± 2.40	0.036 ± 1.68	0.024 ± 2.01	0.019 ± 1.42
	Wet season	0.097 ± 2.42	0.012 ± 1.54	1.062 ± 1.85	0.004 ± 1.25
	Male	-0.094 ± 2.33	-0.011 ± 1.43	3.067 ± 1.82	-0.026 ± 1.07
	Female	0.123 ± 2.45	0.017 ± 1.60	0.448 ± 2.19	0.019 ± 1.43

Table S2.5.2. Activity (AMVs), step length (m), and path tortuosity (radian) of lions and spotted hyenas from the Etosha National Park, Namibia (ENP), and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (CNP). Values are means ± standard deviations during the nocturnal (30 min fixes from 18h00-6h00 and 17h00-8h00) and dusk/dawn (5 min fixes from 19h00-21h00 and 4h00-6h00) periods for the different phases of the lunar cycle.

Period	**Lunar phase**	**Activity**				**Step length (m)**				**Tortuosity**			
		Lion		**Spotted Hyena**		**Lion**		**Spotted Hyena**		**Lion**		**Spotted Hyena**	
		ENP	**CNP**	**ENP**	**CNP**	**ENP**	**CNP**	**ENP**	**CNP**	**ENP**	**CNP**	**ENP**	**CNP**
Nocturnal combined seasons	**New moon**	32.67 ± 49.27	29.34 ± 45.53	76.37 ± 74.82	70.18 ± 65.65	305.29 ± 430.55	242.81 ± 414.56	622.07 ± 702.96	576.63 ± 645.44	0.367 ± 2.21	-0.272 ± 2.26	-0.049 ± 1.79	-0.015 ± 1.88
	Full moon	33.39 ± 48.98	27.16 ± 44.46	79.65 ± 75.11	64.40 ± 64.83	333.58 ± 442.03	222.71 ± 394.73	680.66 ± 715.93	565.66 ± 626.43	-0.011 ± 1.81	0.442 ± 2.58	0.001 ± 1.70	0.041 ± 1.92
Nocturnal dry season	**New moon**	38.46 ± 52.31	30.28 ± 45.85	78.11 ± 77.72	59.39 ± 65.62	304.10 ± 453.23	286.42 ± 409.05	659.76 ± 697.12	543.53 ± 634.24	0.351 ± 1.93	-0.162 ± 2.29	-0.075 ± 1.94	0.139 ± 1.88
	Waxing crescent	45.35 ± 53.94	31.19 ± 47.54	73.21 ± 77.41	49.03 ± 59.45	400.64 ± 472.46	275.59 ± 425.23	635.33 ± 713.10	505.70 ± 617.45	0.014 ± 1.82	-0.030 ± 2.24	0.066 ± 1.83	-0.029 ± 1.82
	First quarter	27.17 ± 48.32	27.73 ± 44.82	65.85 ± 76.68	55.17 ± 59.19	288.77 ± 437.63	263.57 ± 414.39	676.00 ± 716.69	490.43 ± 624.94	-0.170 ± 2.03	0.077 ± 2.32	0.139 ± 1.78	-0.057 ± 1.77
	Waxing gibbous	23.75 ± 45.48	30.39 ± 49.22	86.40 ± 80.02	72.68 ± 71.36	243.85 ± 400.09	289.05 ± 458.72	739.00 ± 742.85	534.73 ± 667.53	-0.245 ± 2.05	-0.243 ± 2.29	-0.194 ± 1.72	-0.046 ± 1.85
	Full moon	33.23 ± 50.35	26.42 ± 44.38	85.07 ± 80.38	68.51 ± 69.09	327.22 ± 456.94	223.80 ± 384.66	724.96 ± 766.69	540.41 ± 643.28	0.013 ± 1.88	-0.024 ± 2.49	0.101 ± 1.83	0.020 ± 1.92
	Waning gibbous	36.16 ± 50.15	27.85 ± 47.76	66.01 ± 79.53	54.22 ± 64.02	330.55 ± 430.07	242.42 ± 409.72	662.18 ± 739.07	532.14 ± 668.52	0.164 ± 1.82	-0.057 ± 2.36	0.089 ± 1.81	0.026 ± 1.89
	Last quarter	37.39 ± 52.07	32.60 ± 46.91	75.38 ± 77.10	57.26 ± 62.45	334.28 ± 449.32	277.93 ± 397.18	677.94 ± 728.41	464.26 ± 585.57	-0.223 ± 1.80	-0.135 ± 2.56	-0.017 ± 1.77	0.075 ± 1.93
	Waning crescent	37.22 ± 53.67	29.47 ± 49.82	73.23 ± 75.08	65.82 ± 70.23	389.16 ± 479.82	253.94 ± 438.29	642.67 ± 709.89	465.94 ± 633.93	-0.009 ± 2.00	0.259 ± 2.30	0.023 ± 1.92	0.021 ± 1.94
Nocturnal wet season	**New moon**	29.41 ± 46.60	27.87 ± 45.19	73.84 ± 71.91	80.92 ± 63.90	280.48 ± 405.82	229.89 ± 414.66	612.65 ± 701.19	610.08 ± 642.25	0.279 ± 2.40	-0.128 ± 2.18	-0.089 ± 1.77	-0.035 ± 1.92
	Waxing crescent	34.29 ± 49.79	27.51 ± 44.07	77.15 ± 71.30	76.06 ± 59.17	333.92 ± 443.52	221.28 ± 408.04	676.41 ± 700.03	595.96 ± 631.11	0.094 ± 1.90	-0.182 ± 2.38	-0.043 ± 1.60	-0.009 ± 1.80
	First quarter	34.05 ± 48.81	24.31 ± 41.38	79.06 ± 71.52	80.88 ± 70.23	337.00 ± 455.68	210.67 ± 385.91	693.34 ± 690.07	531.91 ± 618.95	-0.085 ± 1.87	-0.024 ± 2.53	0.084 ± 1.61	0.432 ± 1.85
	Waxing gibbous	36.90 ± 50.21	25.59 ± 44.34	74.46 ± 71.45	67.54 ± 64.49	380.32 ± 461.24	213.71 ± 414.33	678.80 ± 691.21	544.71 ± 598.91	0.200 ± 1.91	0.377 ± 2.41	0.009 ± 1.71	-0.008 ± 1.86
	Full moon	32.68 ± 47.55	27.30 ± 43.68	75.49 ± 69.68	59.11 ± 58.48	318.44 ± 428.26	221.29 ± 397.06	663.43 ± 671.91	566.62 ± 622.22	0.017 ± 1.76	0.674 ± 2.49	0.010 ± 1.65	-0.142 ± 1.92
	Waning	36.53 ±	23.79 ±	75.74 ±	59.16 ±	342.38 ±	201.83 ±	679.31 ±	572.46 ±	0.139 ±	0.519 ±	0.028 ±	-0.005 ±

	gibbous	51.71	41.63	70.51	61.74	458.54	387.32	670.25	639.97	1.78	2.60	1.67	1.79
	Last quarter	36.05 ± 51.51	28.79 ± 44.52	74.79 ± 71.14	70.74 ± 70.15	333.92 ± 473.36	219.99 ± 397.79	641.18 ± 674.57	597.52 ± 642.67	-0.110 ± 1.92	0.230 ± 2.35	0.137 ± 1.74	0.049 ± 1.81
	Waning crescent	34.63 ± 49.27	28.29 ± 44.71	70.94 ± 72.39	74.34 ± 58.46	301.41 ± 429.88	216.85 ± 393.75	616.88 ± 679.42	590.43 ± 633.41	0.072 ± 2.10	0.127 ± 2.33	0.059 ± 1.74	-0.198 ± 1.93
Dusk/dawn combined seasons	**New moon**	32.25 ± 48.36	31.44 ± 47.38	74.68 ± 73.48	66.61 ± 64.09	54.69 ± 87.62	41.51 ± 78.48	117.07 ± 151.05	116.64 ± 138.92	-1.173 ± 2.38	0.844 ± 1.91	0.011 ± 1.66	-0.023 ± 1.36
	Full moon	34.49 ± 47.63	28.53 ± 44.50	79.25 ± 73.26	66.91 ± 63.48	61.84 ± 87.42	38.73 ± 75.12	130.90 ± 154.58	117.80 ± 140.95	-0.033 ± 2.44	1.506 ± 1.74	0.011 ± 1.57	-0.008 ± 1.31
Dusk/dawn dry season	**New moon**	40.25 ± 52.00	33.80 ± 46.61	76.43 ± 76.73	54.56 ± 60.78	55.26 ± 94.10	42.43 ± 77.68	123.08 ± 152.44	96.66 ± 128.23	-0.654 ± 2.47	-0.023 ± 1.94	0.074 ± 1.90	-0.111 ± 1.51
	Waxing crescent	44.32 ± 53.96	32.81 ± 47.82	77.99 ± 75.64	54.85 ± 61.29	77.17 ± 104.41	44.64 ± 83.82	128.91 ± 151.58	94.87 ± 135.97	0.038 ± 2.19	-0.356 ± 1.92	0.133 ± 1.65	0.060 ± 1.47
	First quarter	24.61 ± 48.13	32.81 ± 45.07	72.86 ± 75.03	62.01 ± 63.02	50.38 ± 94.18	46.39 ± 82.31	134.27 ± 152.94	97.98 ± 128.66	-3.045 ± 2.43	-0.539 ± 1.87	0.024 ± 1.58	0.047 ± 1.36
	Waxing gibbous	24.67 ± 44.71	32.34 ± 49.42	84.84 ± 78.97	68.70 ± 73.40	45.27 ± 84.72	45.78 ± 85.88	139.50 ± 166.50	109.04 ± 143.66	-0.106 ± 2.26	-0.038 ± 2.07	-0.007 ± 1.74	0.034 ± 1.33
	Full moon	34.56 ± 48.77	29.13 ± 44.30	86.23 ± 79.98	65.82 ± 66.37	52.43 ± 89.88	39.62 ± 75.64	139.76 ± 169.42	99.97 ± 136.05	-0.054 ± 2.45	2.994 ± 1.75	-0.068 ± 1.74	-0.013 ± 1.38
	Waning gibbous	34.39 ± 49.85	35.13 ± 50.05	70.62 ± 77.86	59.98 ± 62.19	58.02 ± 93.94	42.26 ± 80.11	134.31 ± 157.50	104.37 ± 138.26	0.141 ± 2.27	1.068 ± 1.94	0.023 ± 1.58	0.014 ± 1.40
	Last quarter	34.85 ± 50.04	34.75 ± 48.97	79.34 ± 75.24	55.45 ± 62.82	59.50 ± 96.01	41.92 ± 75.98	139.84 ± 153.21	89.95 ± 123.05	0.147 ± 2.22	-0.013 ± 1.77	-0.028 ± 1.57	-0.161 ± 1.60
	Waning crescent	35.05 ± 52.38	33.54 ± 51.74	78.63 ± 74.78	64.19 ± 69.48	64.30 ± 100.82	39.75 ± 84.56	123.89 ± 146.00	89.77 ± 126.34	-0.011 ± 2.31	0.354 ± 2.03	0.008 ± 1.72	0.099 ± 1.44
Dusk/dawn wet season	**New moon**	30.13 ± 45.49	30.71 ± 47.94	71.65 ± 70.10	79.33 ± 65.06	53.28 ± 82.14	42.73 ± 78.83	115.69 ± 148.34	123.85 ± 144.87	-2.659 ± 2.25	0.785 ± 1.92	0.012 ± 1.58	0.001 ± 1.29
	Waxing crescent	35.09 ± 48.60	31.83 ± 44.60	75.58 ± 68.15	79.60 ± 61.14	62.14 ± 89.65	39.92 ± 74.88	128.85 ± 138.92	123.54 ± 147.11	-0.163 ± 2.35	0.862 ± 1.85	0.008 ± 1.51	0.015 ± 1.22
	First quarter	36.24 ± 49.59	29.70 ± 43.85	77.79 ± 69.73	93.75 ± 69.60	68.19 ± 94.63	38.14 ± 74.58	125.10 ± 142.73	116.65 ± 151.16	-0.107 ± 2.29	1.818 ± 1.93	0.030 ± 1.53	0.069 ± 1.22
	Waxing gibbous	39.36 ± 51.94	31.46 ± 48.08	73.85 ± 69.95	71.06 ± 62.73	75.70 ± 99.99	39.58 ± 80.33	129.37 ± 148.14	105.13 ± 138.76	-0.195 ± 2.20	0.145 ± 1.76	-0.010 ± 1.54	-0.041 ± 1.24
	Full moon	34.21 ± 46.13	29.44 ± 44.54	72.38 ± 66.30	68.25 ± 59.75	58.39 ± 84.40	38.16 ± 74.63	124.89 ± 137.49	102.68 ± 145.11	-0.228 ± 2.11	1.232 ± 1.73	0.031 ± 1.50	-0.089 ± 1.25
	Waning gibbous	34.27 ± 50.36	28.11 ± 43.15	73.51 ± 69.59	65.92 ± 67.60	59.76 ± 93.85	35.84 ± 73.21	121.07 ± 139.68	124.33 ± 155.93	0.180 ± 2.30	-1.526 ± 1.77	0.040 ± 1.53	0.021 ± 1.30
	Last quarter	33.68 ± 48.72	32.28 ± 46.56	71.73 ± 68.01	78.36 ± 69.36	57.81 ± 93.29	38.61 ± 73.96	113.50 ± 131.89	125.62 ± 146.76	-0.282 ± 2.42	0.988 ± 1.81	-0.018 ± 1.54	-0.009 ± 1.23
	Waning crescent	30.61 ± 44.76	33.68 ± 46.29	70.30 ± 70.49	76.18 ± 58.79	49.69 ± 83.14	43.17 ± 76.29	118.35 ± 145.10	128.95 ± 146.78	0.037 ± 2.41	-1.314 ± 1.78	-0.010 ± 1.59	-0.017 ± 1.26

Table S2.5.3. Activity (AMVs) of lions and spotted hyenas from the Etosha National Park, Namibia (ENP), and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (CNP). The 24 h cycle was subdivided into seven different periods. Night/nadir/night end consists of the end of evening twilight to the beginning of morning twilight divided into three equal intervals. Afternoon = noon to sundown; dusk = sundown to twilight end; dawn = beginning of morning twilight to sunrise; morning = sunrise to noon. Values indicate the means ± standard deviations of the seven different periods of the 24 h cycle during new and full moon phases of the dry and wet seasons.

Season	**24 h period cycle**	**New Moon**				**Full Moon**			
		Lion		**Spotted Hyena**		**Lion**		**Spotted Hyena**	
		ENP	**CNP**	**ENP**	**CNP**	**ENP**	**CNP**	**ENP**	**CNP**
Dry season	**Afternoon**	6.49 ± 11.93	5.47 ± 10.30	4.95 ± 10.68	6.01 ± 4.03	4.97 ± 9.87	6.10 ± 11.53	3.64 ± 8.67	5.39 ± 3.20
	Dusk	24.35 ± 40.59	31.30 ± 48.54	68.12 ± 61.88	24.05 ± 15.10	23.20 ± 43.14	25.90 ± 44.05	74.17 ± 65.99	34.81 ± 17.41
	Night	33.72 ± 34.28	25.07 ± 30.98	91.80 ± 42.73	45.43 ± 12.77	25.67 ± 32.85	20.35 ± 28.26	104.43 ± 48.12	54.49 ± 16.13
	Nadir	41.01 ± 38.98	30.31 ± 32.03	81.54 ± 47.29	61.49 ± 17.05	35.95 ± 38.61	28.52 ± 32.80	94.11 ± 48.88	71.81 ± 17.24
	Night end	41.64 ± 39.22	31.60 ± 33.84	73.92 ± 46.38	75.15 ± 15.45	39.63 ± 38.25	29.77 ± 33.69	84.27 ± 44.80	87.56 ± 16.65
	Dawn	34.07 ± 51.66	38.74 ± 51.01	79.21 ± 59.44	82.73 ± 25.09	39.02 ± 55.81	32.40 ± 47.98	71.70 ± 62.64	87.65 ± 23.31
	Morning	11.67 ± 17.31	15.20 ± 19.70	19.10 ± 24.28	17.55 ± 8.41	13.98 ± 20.63	11.98 ± 18.01	15.05 ± 23.77	15.61 ± 8.75
Wet season	**Afternoon**	8.12 ± 13.99	9.48 ± 14.32	9.20 ± 16.40	6.23 ± 3.87	6.93 ± 13.03	10.54 ± 14.25	7.46 ± 14.97	3.66 ± 2.84
	Dusk	31.48 ± 55.97	34.01 ± 48.31	76.52 ± 64.24	53.71 ± 18.24	30.42 ± 44.76	37.52 ± 48.07	76.06 ± 60.70	37.23 ± 15.23
	Night	31.14 ± 43.57	30.69 ± 31.50	84.21 ± 49.53	75.03 ± 13.06	28.17 ± 34.34	25.15 ± 33.04	86.71 ± 42.02	54.44 ± 11.13
	Nadir	31.52 ± 44.39	28.56 ± 33.30	78.38 ± 52.26	99.62 ± 16.77	35.06 ± 40.30	23.73 ± 30.56	88.13 ± 48.66	61.12 ± 12.63
	Night end	28.51 ± 40.47	25.82 ± 34.28	73.89 ± 46.56	102.01 ± 17.15	34.91 ± 39.89	25.91 ± 32.34	74.29 ± 44.51	72.71 ± 13.08
	Dawn	28.02 ± 50.06	24.47 ± 43.64	74.66 ± 54.77	94.28 ± 21.70	28.73 ± 48.65	22.54 ± 36.63	74.97 ± 62.14	95.17 ± 14.82
	Morning	11.70 ± 20.30	10.50 ± 15.62	22.74 ± 28.79	15.90 ± 7.77	10.61 ± 17.86	10.31 ± 14.98	18.80 ± 26.16	15.67 ± 8.22

Table S2.5.4. Speed (m/s) and path tortuosity (radian) of lions and spotted hyenas during nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods according to low, medium, and high body condition scores. Values are indicated in means ± standard deviations. Body conditions of individuals were scored from spinal palpations of immobilized individuals during capture events.

Period	**BCS**	**Speed (m/s)**				**Tortuosity**			
		Lion	**Male lion**	**Female lion**	**Spotted Hyena**	**Lion**	**Male lion**	**Female lion**	**Spotted Hyena**
Nocturnal periods	**Low BCS**	0.195 ± 0.26	0.221 ± 0.31	0.181 ± 0.25	-	-0.016 ± 1.86	0.052 ± 1.66	-0.050 ± 1.89	-
	Medium BCS	0.153 ± 0.23	0.195 ± 0.28	0.136 ± 0.22	0.328 ± 0.36	0.044 ± 2.28	0.042 ± 1.81	0.044 ± 2.34	0.043 ± 1.83
	High BCS	0.145 ± 0.22	0.108 ± 0.20	0.169 ± 0.24	0.377 ± 0.45	0.081 ± 2.37	0.095 ± 2.46	0.068 ± 2.02	-0.031 ± 1.60
Dusk/dawn periods	**Low BCS**	0.217 ± 0.35	0.253 ± 0.39	0.200 ± 0.34	-	-0.023 ± 2.29	0.008 ± 1.91	-0.038 ± 2.34	-
	Medium BCS	0.153 ± 0.25	0.220 ± 0.35	0.134 ± 0.24	0.393 ± 0.46	0.141 ± 2.34	-0.145 ± 2.41	0.284 ± 2.33	0.015 ± 1.50
	High BCS	0.173 ± 0.28	0.142 ± 0.27	0.205 ± 0.32	0.433 ± 0.57	0.037 ± 1.87	3.067 ± 1.82	-0.000 ± 2.30	-0.007 ± 1.44

Table S2.5.5. Speed (m/s) and path tortuosity (radian) of lions and spotted hyenas during nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods according to the probability of site-attracted foragers (i.e., ungulates) in sites that consisted of anthrax positive carcasses from previous years.

Period	Probability of site-attracted foragers	Speed (m/s)		Tortuosity	
		Lion	Spotted Hyena	Lion	Spotted Hyena
Nocturnal periods	**0-20%**	0.181 ± 0.24	0.410 ± 0.37	0.088 ± 1.91	0.012 ± 1.77
	20-40%	0.198 ± 0.27	0.456 ± 0.46	0.088 ± 1.78	-0.216 ± 1.85
	40-60%	0.230 ± 0.28	0.417 ± 0.46	0.089 ± 1.74	0.039 ± 1.77
	60-80%	0.167 ± 0.26	0.460 ± 0.47	-0.225 ± 1.93	-0.037 ± 1.54
	80-100%	0.226 ± 0.28	0.470 ± 0.43	0.079 ± 2.18	-0.113 ± 1.49
Dusk/dawn periods	**0-20%**	0.220 ± 0.29	0.484 ± 0.46	-0.021 ± 2.50	0.015 ± 1.70
	20-40%	0.213 ± 0.35	0.556 ± 0.60	0.011 ± 2.17	0.004 ± 1.36
	40-60%	0.241 ± 0.33	0.447 ± 0.56	0.008 ± 2.22	0.020 ± 1.69
	60-80%	0.187 ± 0.33	0.528 ± 0.62	0.014 ± 2.51	-0.007 ± 1.33
	80-100%	0.214 ± 0.40	0.536 ± 0.58	-0.034 ± 2.45	-0.043 ± 1.32

Table S2.5.6. Nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods of lion and spotted hyena activity (AMVs), speed (m/s), and path tortuosity (radian) from (a) inside and outside of competitor and conspecific core use areas, and (b) at distance intervals in metres to the nearest competitor and conspecific.

(a)

			Competitor						Conspecific					
			Activity		Speed (m/s)		Tortuosity		Activity		Speed (m/s)		Tortuosity	
			Lion	Hyena	Lion	Hyena	Lion	Hyena	Lion	Hyena	Lion	Hyena	Lion	Hyena
Nocturnal	ENP	**Inside**	36.60 ± 42.69	82.95 ± 61.26	0.183 ± 0.26	0.417 ± 0.39	0.055 ± 1.91	-0.016 ± 1.57	36.73 ± 40.62	93.43 ± 67.68	0.205 ± 0.25	0.435 ± 0.40	-0.056 ± 1.99	-0.079 ± 1.59
		Outside	34.41 ± 40.46	73.75 ± 68.48	0.186 ± 0.25	0.385 ± 0.41	0.059 ± 1.90	0.027 ± 1.80	35.78 ± 41.07	74.25 ± 66.84	0.192 ± 0.25	0.367 ± 0.41	0.138 ± 1.87	0.018 ± 1.74
	CNP	**Inside**	28.52 ± 39.35	78.76 ± 53.32	0.152 ± 0.22	0.438 ± 0.36	0.032 ± 2.41	0.049 ± 1.68	41.08 ± 32.77	43.99 ± 44.83	0.178 ± 0.21	0.233 ± 0.32	0.113 ± 2.88	0.131 ± 2.03
		Outside	27.55 ± 34.61	61.11 ± 56.42	0.141 ± 0.22	0.297 ± 0.36	-0.222 ± 2.43	0.041 ± 1.94	31.50 ± 36.45	74.89 ± 59.10	0.146 ± 0.23	0.334 ± 0.38	-0.123 ± 2.33	0.027 ± 1.80
Dusk/dawn	ENP	**Inside**	37.89 ± 50.69	85.40 ± 68.64	0.217 ± 0.33	0.470 ± 0.49	0.073 ± 2.37	-0.015 ± 1.40	37.21 ± 47.90	95.73 ± 76.36	0.226 ± 0.32	0.478 ± 0.53	-0.369 ± 2.63	-0.048 ± 1.27
		Outside	33.80 ± 47.92	78.17 ± 75.01	0.204 ± 0.31	0.422 ± 0.52	0.029 ± 2.51	0.022 ± 1.65	34.45 ± 48.82	78.05 ± 73.44	0.200 ± 0.31	0.415 ± 0.51	0.088 ± 2.34	0.017 ± 1.62
	CNP	**Inside**	34.29 ± 50.88	84.32 ± 61.43	0.165 ± 0.28	0.527 ± 0.49	0.282 ± 1.79	0.002 ± 1.11	33.52 ± 41.75	50.97 ± 56.15	0.155 ± 0.25	0.268 ± 0.41	0.203 ± 1.39	0.091 ± 1.59
		Outside	30.66 ± 43.43	65.34 ± 64.85	0.157 ± 0.28	0.363 ± 0.47	0.263 ± 1.62	0.006 ± 1.38	37.16 ± 46.29	77.58 ± 67.21	0.173 ± 0.30	0.407 ± 0.50	0.097 ± 1.66	-0.004 ± 1.21

(b)

Nocturnal	ENP	**0-100**	22.33 ± 30.74	72.87 ± 41.51	0.100 ± 0.22	0.136 ± 0.17	-2.912 ± 1.66	-2.176 ± 1.56	26.26 ± 33.29	113.48 ± 26.97	0.127 ± 0.19	0.375 ± 0.38	0.169 ± 2.07	3.102 ± 1.52
		100-200	23.00 ± 30.16	79.20 ± 56.20	0.044 ± 0.11	0.124 ± 0.21	2.775 ± 1.58	-0.119 ± 2.20	53.78 40.41	127.18 ± 31.86	0.313 ± 0.26	0.179 ± 0.09	0.170 ± 1.12	1.254 ± 1.74
		200-300	29.52 45.83	81.61 ± 60.14	0.139 ± 0.25	0.291 ± 0.28	1.047 ± 1.65	-1.823 ± 1.38	41.75 ± 41.82	111.72 ± 102.84	0.245 ± 0.26	0.109 ± 0.10	-0.155 ± 1.52	-1.110 ± 1.23
		300-400	31.41 ± 35.05	70.41 ± 60.52	0.080 ± 0.15	0.266 ± 0.33	-2.159 ± 1.73	1.608 ± 1.70	34.01 ± 39.56	67.92 ± 59.42	0.212 ± 0.29	0.340 ± 0.56	0.014 ± 1.46	-0.412 ± 1.52
		400-500	18.67 ± 28.12	80.84 ± 49.37	0.059 ± 0.12	0.267 ± 0.24	2.305 ± 1.27	0.708 ± 1.38	51.92 ± 44.42	66.87 ± 1.00	0.289 ± 0.27	0.139 ± 0.13	-0.001 ± 1.21	1.268 ± 1.48
		500-600	40.03 ± 45.91	68.73 ± 77.49	0.094 ± 0.15	0.255 ± 0.25	0.055 ± 1.12	0.636 ± 1.56	26.49 ± 31.14	135.17 ± 35.09	0.105 ± 0.19	0.234 ± 0.30	0.897 ± 1.56	-0.660 ± 0.98
		600-700	31.88 ± 37.33	93.37 ± 49.59	0.151 ± 0.23	0.345 ± 0.28	0.626 ± 1.65	-0.773 ± 1.62	53.74 ± 47.67	178.92 ± 23.74	0.224 ± 0.28	0.680 ± 0.77	-0.011 ± 1.34	-1.060 ± 1.41
		700-800	36.89 ± 40.20	68.23 ± 60.23	0.135 ± 0.23	0.335 ± 0.36	0.401 ± 1.71	0.481 ± 1.22	48.83 ± 50.73	80.93 ± 88.70	0.226 ± 0.26	0.363 ± 0.37	0.293 ± 1.51	0.831 ± 1.05
		800-900	29.80 ± 33.87	68.39 ± 65.28	0.185 ± 0.28	0.344 ± 0.34	1.147 ± 1.65	-0.020 ± 1.64	40.74 ± 38.65	-	0.271 ± 0.25	-	0.093 ± 1.57	2.407 ± 2.32
		900-1000	34.28 ± 42.46	80.51 ± 56.58	0.150 ± 0.23	0.292 ± 0.30	-0.223 ± 1.89	0.439 ± 1.73	35.72 ± 45.01	117.53 ± 92.47	0.168 ± 0.24	0.326 ± 0.43	1.761 ± 1.59	-0.008 ± 0.89
	CNP	**0-100**	9.71 ± 4.73	-	0.041 ± 0.03	0.088 ± 0.09	2.799 ± 1.58	-2.147 ± 1.30	-	72.09 ± 53.20	0.024 ± 0.09	0.120 ± 0.18	-2.162 ± 2.16	0.036 ± 2.12
		100-200	28.57 ± 36.33	116.35 ± 58.80	0.014 ± 0.02	0.407 ± 0.23	-2.134 ± 1.50	1.204 ± 1.43	46.86 ± 28.76	49.40 ± 41.43	0.128 ± 0.02	0.221 ± 0.32	-2.342 ± 1.71	-1.825 ± 2.57
		200-300	37.47 ± 48.78	75.89 ± 89.11	0.082 ± 0.20	0.288 ± 0.46	0.380 ± 1.25	0.323 ± 1.47	51.45 ± 48.20	39.26 ± 45.29	0.069 ± 0.05	0.114 ± 0.16	1.911 ± 1.45	1.526 ± 2.41
		300-400	14.20 ± 15.97	33.23 ± 33.74	0.022 ± 0.02	0.285 ± 0.60	-0.762 ± 1.46	-0.185 ± 1.41	11.42 ± 24.22	73.31 ± 56.89	0.101 ± 0.34	0.137 ± 0.19	-2.775 ± 2.46	1.033 ± 2.75
		400-500	37.89 ± 57.70	131.33 ± 56.82	0.128 ± 0.25	0.163 ± 0.19	1.460 ± 1.67	-0.080 ± 1.34	51.54 ± 42.14	53.33 ± 56.82	0.073 ± 0.07	0.108 ± 0.30	-0.739 ± 2.30	1.125 ± 2.15
		500-600	26.63 ± 47.72	66.80 ± 47.18	0.115 ± 0.25	0.535 ± 0.34	-1.710 ± 1.62	-0.887 ± 1.43	-	29.50 ± 23.29	0.057 ± 0.11	0.141 ± 0.24	-0.340 ± 2.08	-1.412 ± 1.80
		600-700	2.08 ± 2.92	127.08 ± 102.00	0.079 ± 0.11	0.267 ± 0.40	-0.844 ± 2.36	-0.259 ± 1.30	-	47.18 ± 52.83	0.031 ± 0.04	0.124 ± 0.19	2.567 ± 1.82	-1.847 ± 1.91
		700-800	12.64 ± 23.05	49.68 ± 57.51	0.041 ± 0.10	0.245 ± 0.29	-1.433 ± 2.15	-0.696 ± 1.71	-	63.15 ± 51.95	0.126 ± 0.19	0.267 ± 0.33	-0.078 ± 1.86	0.744 ± 1.94
		800-900	32.19 ± 58.03	71.89 ± 48.63	0.076 ± 0.19	0.282 ± 0.35	2.083 ± 2.08	0.826 ± 1.90	21.33 ± 35.93	41.41 ± 37.79	0.053 ± 0.13	0.111 ± 0.28	0.739 ± 1.60	-1.765 ± 1.72
		900-1000	19.45 ± 24.51	77.99 ± 35.51	0.207 ± 0.38	0.185 ± 0.17	0.120 ± 1.87	0.289 ± 1.61	-	28.13 ± 38.93	0.024 ± 0.04	0.127 ± 0.26	0.929 ± 1.76	2.164 ± 2.10

Dusk/dawn	ENP	**0-100**	32.26 ± 43.67	54.04 ± 48.55	0.063 ± 0.14	0.135 ± 0.15	-3.037 ± 2.03	-0.485 ± 2.02	26.84 ± 37.69	-	0.108 ± 0.21	0.010 ± 0.01	-1.533 ± 2.39	-0.658 ± 1.46
		100-200	23.32 ± 50.22	44.29 ± 57.19	0.082 ± 0.24	0.171 ± 0.22	3.130 ± 1.73	1.038 ± 1.87	53.66 ± 49.73	-	0.412 ± 0.34	0.139 ± 0.01	0.076 ± 1.14	-0.754 ± 1.17
		200-300	35.13 ± 52.09	88.49 ± 73.61	0.155 ± 0.26	0.318 ± 0.30	1.620 ± 1.79	0.002 ± 1.64	46.28 ± 50.56	137.00 ± 110.31	0.337 ± 0.34	0.239 ± 0.17	0.145 ± 1.43	0.350 ± 0.94
		300-400	31.35 ± 42.61	68.58 ± 64.74	0.085 ± 0.21	0.294 ± 0.42	-2.571 ± 1.94	-0.647 ± 1.72	50.00 ± 51.91	164.00 ± 128.69	0.302 ± 0.39	0.508 ± 0.11	0.102 ± 1.92	-0.028 ± 0.82
		400-500	33.79 ± 44.56	81.96 ± 59.40	0.135 ± 0.26	0.282 ± 0.29	-2.666 ± 1.88	0.047 ± 1.50	79.47 ± 47.28	-	0.396 ± 0.37	0.070 ± 0.06	0.058 ± 1.48	-0.264 ± 0.93
		500-600	20.41 ± 38.26	84.33 ± 71.13	0.188 ± 0.33	0.406 ± 0.36	2.414 ± 1.77	0.280 ± 1.38	35.86 ± 46.90	104.56 ± 94.04	0.184 ± 0.34	0.328 ± 0.43	-0.131 ± 2.03	0.571 ± 1.10
		600-700	42.27 ± 59.37	61.78 ± 69.45	0.257 ± 0.36	0.390 ± 0.50	0.906 ± 1.37	-0.116 ± 1.61	50.93 ± 58.36	149.38 ± 106.21	0.254 ± 0.43	0.506 ± 0.53	0.624 ± 1.71	-0.522 ± 0.68
		700-800	27.42 ± 41.12	57.03 ± 66.58	0.162 ± 0.33	0.339 ± 0.44	-2.842 ± 1.70	0.105 ± 2.02	49.20 ± 57.70	-	0.319 ± 0.40	0.168 ± 0.06	-0.057 ± 1.57	0.265 ± 0.68
		800-900	46.56 ± 56.70	99.41 ± 77.77	0.160 ± 0.27	0.405 ± 0.43	-0.322 ± 1.65	0.188 ± 1.27	70.72 ± 58.96	-	0.325 ± 0.40	0.080 ± 0.16	-0.351 ± 1.47	0.971 ± 0.96
		900-1000	43.79 ± 49.08	69.08 ± 49.65	0.154 ± 0.28	0.319 ± 0.37	-1.089 ± 2.11	0.171 ± 1.62	56.68 ± 50.48	-	0.257 ± 0.35	0.102 ± 0.02	-0.440 ± 1.86	0.090 ± 0.79
	CNP	**0-100**	79.60 ± 26.02	57.60 ± 56.21	0.163 ± 0.03	0.150 ± 0.25	-0.878 ± 2.18	-0.290 ± 1.30	76.71 ± 34.34	69.85 ± 71.64	0.048 ± 0.15	0.157 ± 0.39	0.053 ± 1.32	-0.330 ± 1.74
		100-200	16.46 ± 28.87	34.03 ± 50.63	0.071 ± 0.15	0.312 ± 0.49	0.973 ± 1.47	-1.014 ± 1.32	123.84 ± 35.98	63.42 ± 60.98	0.118 ± 0.22	0.209 ± 0.30	0.401 ± 1.18	-0.143 ± 1.49
		200-300	39.34 ± 33.27	92.50 ± 20.07	0.121 ± 0.22	0.290 ± 0.25	-0.262 ± 1.35	-0.132 ± 0.91	70.69 ± 57.12	53.06 ± 47.97	0.079 ± 0.15	0.175 ± 0.34	-0.687 ± 1.32	-1.362 ± 1.74
		300-400	13.44 ± 43.89	57.25 ± 80.96	0.133 ± 0.43	0.340 ± 0.67	-0.070 ± 1.09	0.141 ± 1.14	90.79 ± 48.49	58.01 ± 59.28	0.117 ± 0.19	0.169 ± 0.27	-0.402 ± 1.19	-0.104 ± 1.31
		400-500	10.83 ± 39.96	157.00 ± 138.59	0.103 ± 0.18	0.272 ± 0.40	-2.849 ± 1.64	0.112 ± 0.96	125.31 ± 51.26	44.76 ± 51.58	0.169 ± 0.20	0.125 ± 0.23	-1.092 ± 1.09	-0.170 ± 1.42
		500-600	29.50 ± 0.10	90.50 ± 26.87	0.064 ± 0.01	0.521 ± 0.07	-0.280 ± 1.06	-0.230 ± 0.83	45.55 ± 52.24	54.46 ± 52.76	0.073 ± 0.21	0.146 ± 0.26	-0.137 ± 1.10	0.083 ± 1.53
		600-700	22.89 37.56	106.17 ± 27.62	0.054 ± 0.14	0.598 ± 0.28	0.124 ± 1.43	0.124 ± 0.69	22.16 ± 37.07	59.17 ± 56.41	0.075 ± 0.20	0.149 ± 0.27	-0.229 ± 1.21	0.057 ± 1.43
		700-800	31.77 ± 42.21	73.66 ± 52.78	0.150 ± 0.36	0.377 ± 0.35	-0.250 ± 1.91	-0.188 ± 1.12	56.44 ± 49.32	46.21 ± 53.27	0.114 ± 0.18	0.187 ± 0.31	0.307 ± 1.12	-1.366 ± 1.69
		800-900	18.41 ± 10.20	83.09 ± 43.51	0.032 ± 0.05	0.321 ± 0.38	-0.579 ± 1.34	0.221 ± 1.22	46.08 ± 33.59	56.63 ± 58.35	0.080 ± 0.19	0.193 ± 0.31	-0.222 ± 1.25	0.273 ± 1.40
		900-1000	15.39 43.24	90.68 ± 34.54	0.234 ± 0.50	0.266 ± 0.43	1.541 ± 1.87	-0.042 ± 1.24	86.99 ± 41.31	61.38 ± 58.80	0.115 ± 0.19	0.233 ± 0.31	-0.474 ± 1.33	-0.313 ± 1.24

CHAPTER THREE

Competitive interactions as a driver of lion movements within semi-arid and wetland environments

3.1. Summary

1. Apex predators have profound impacts on trophic cascades, and interactions among coexisting guild members has the potential to significantly exacerbate or attenuate such ecological processes. An understanding of how inter- and intraspecific interactions drives predator space use may elucidate the role that interference competition has in shaping the movement responses of apex predators. The African lion (*Panthera leo*) faces interference competition with spotted hyenas (*Crocuta crocuta*), yet studies incorporating the effects of such interactions on lion habitat selection and movement are limited. We compared the spatiotemporal and movement patterns of 19 lions in the semi-arid Etosha National Park and the Chobe National Park, Linyanti Conservancy and Okavango Delta wetlands with GPS satellite collars from 2013-2017. We developed models that incorporated measures of intraspecific interactions, and interspecific interactions with spotted hyena across much of their home ranges. We examined habitat selection and the movement of lions in response to conspecifics, competitors, and environmental factors.

2. Lion ranges and movement patterns differed across seasons and as a function of environmental heterogeneity among protected areas. Lions exhibited longer steps and increased activity in drier environments, but had more tortuous paths in wetland areas. Older lions (> 10 years) travelled further than adults (5-10 years), whereas young males (< 5 years) had more

tortuous movements than young females. Females without cubs from larger prides had greater ranges and traveled further, whereas females with cubs from large prides had more tortuous movements. Individuals also showed increased activity monitor values (AMVs), and moved at faster speeds in human-use areas, and when at closer distances to conspecifics or inside the core use areas of competitors.

3. Etosha lions used habitats with median NDVI values and were also more likely to move <5 km to water and anthropogenic features, and towards anthrax areas with a high probability of site-attracted foragers. Chobe lions used habitats with higher NDVI values, and were also more likely to move <2 km to water and roads, and avoided areas close to (<15 km) anthropogenic features. Lions from the Okavango Delta used habitats with median NDVI values and consistently used areas that were >2 km to seasonal water sources. Inter- and intraspecific interactions consistently impacted lion habitat selection and movements during the dry season, in that lions used areas further from heterospecifics (i.e., hyenas) and avoided moving towards areas most likely to have heterospecifics. Lions, however, avoided areas likely to have conspecifics in Etosha, while they were more likely to move to areas where conspecifics were present in Chobe/Linyanti.

4. *Synthesis and applications*. Our findings of lion space-use patterns across arid and mesic environments reveal the influences of habitat characteristics and competitive interactions with competitors (spotted hyenas) on lion habitat selection and movement. The responses of lions to various landscape features across an environmental gradient, in combination with inter- and intraspecific effects, provides insights in lion movement ecology that will be important to consider when conserving multi-species communities. Knowledge of these processes can help guide the future planning of reserve design for lion conservation, in ensuring that the available area allows for the movement responses of lions to mitigate competitive effects with competing species.

3.2. Introduction

Our understanding of the factors that drive apex predator space use, particularly lions (*Panthera leo*), is of paramount importance for successful conservation efforts (Cozzi et al. 2013, Elliot et al. 2014, Di Fonzo et al. 2016, Macdonald 2016), especially in light of their global population declines (Packer et al. 2013, Ripple et al. 2014b). Large carnivores are known to be crucial for the maintenance of ecosystem structure and function (Ripple & Beschta 2004, Elmhagen et al. 2010). The distribution and density of apex predators on the landscape has profound effects for trophic cascades (Estes et al. 2011, Ripple & Beschta 2012, Ripple et al. 2014a). Thus, knowledge of predator habitat selection and movement choices are essential for informed conservation and wildlife management strategies. An animal's space-use pattern is a complex amalgamation of many factors which depend not only on the individual's specific differences but also on resource availability, inter- and intraspecific interactions, population demographics, social status and structure, life history traits, as well as landscape features and climatic and environmental effects (Spong 2002, Watts & Holekamp 2009, Valeix et al. 2010, Tuqa et al. 2014). Individuals alter their ranging behaviour in response to heterogeneous environments by varying the frequency and duration of visits to different locations throughout their home range to maximize their survival and fitness (Benhamou & Riotte-Lambert 2012, Van Moorter et al. 2016). Additionally, the characteristics of an animal's movement path can provide insight into where the animal was, for how long, and also potentially what the animal was doing (Morales et al. 2004, Gurarie et al. 2009, 2016, Edelhoff et al. 2016). Thus, measures of movement parameters may reveal changes in an animal's behaviour in response to resource availability and acquisition, landscape characteristics, and interference competition, as well as intragroup influences among gregarious species, including social behaviour and territoriality (Spong & Creel 2004, Mosser & Packer 2009, Valeix et al. 2010, Kittle et al. 2016, Bryce et al. 2017, Kirk & Wascher 2018).

Optimal foraging theory predicts that predators maximize fitness by concentrating foraging efforts in areas with the highest prey densities to minimize the time searching for prey (Charnov 1976, Pyke et al. 1977). However, because of the high energetic costs of hunting, (Carbone et al. 2007), scavenging predators benefit from an opportunistic food acquisition strategy by scavenging carcasses (Pereira et al. 2014, Moleón et al. 2014) or kleptoparasitism (Honer et al. 2002). Anthrax epidemics occur annually in the Etosha National Park with sporadic outbreaks within the Chobe/Linyanti system of the Chobe National Park, and generate a significant subsidy of ungulate carcasses for predators and scavengers (Good et al. 2005, 2008, Getz 2011, Borchering et al. 2017). Ecosystems that are strongly influenced by an embedded herbivore-scavenger-predator trophic food web and supplemented with carcasses from anthrax outbreaks presents a dynamic opportunity to examine the effects of a surplus resource on the movement behaviour of lions and their subsequent space use patterns.

The African lion population is experiencing significant global declines and threatened with extinction across their ranges: only an estimated 23,000 lions are left in Africa (IUCN 2006, Bauer et al. 2015). Lions exist primarily in protected areas, which are often fragmented and subjected to increasing land-use competition in a human-dominated landscape (Woodroffe 2000, Gurd et al. 2001, Riggio et al. 2013). Lions frequently sustain high levels of human-induced mortalities (Funston 2011, Snyman et al. 2018), and have altered their space use patterns in response to these pressures (Valeix et al. 2012, Oriol-Cotterill et al. 2015b).

Lions share their ranges with other carnivore species, particularly the spotted hyena (*Crocuta crocuta*), with whom they potentially compete for the same resources (Linnell & Strand 2000, Caro & Stoner 2003, Hayward & Kerley 2008, Hayward & Slotow 2009, Périquet et al. 2015), and frequently face off in agonistic encounters (Cooper 1991, Honer et al. 2002, Trinkel & Kastberger 2005, Lehmann et al. 2017). Despite these conflicts, lions are positively associated with areas of high hyena utilization (Hayward & Hayward 2007, Kittle et al. 2016), and coexist with spotted hyenas across much of their range (Périquet et al. 2015).

Although resource availability and abundance, and the catchability of prey have been identified as the primary factors influencing the distribution and size of a lion's home range and space-use patterns (Van Orsdol 1984, Funston et al. 2001, Hopcraft et al. 2005, Loveridge et al. 2009, Funston 2011), few studies have incorporated the effects of inter- and intragroup interactions on lion habitat selection and movement (Kittle et al. 2016, Yiu et al. 2019). Lions are a highly gregarious social carnivore (Schaller 1972), they derive benefits from living in groups (Mosser & Packer 2009), and engage in social activities ranging from cooperative hunting (Scheel & Packer 1991) to territory defense (Heinsohn & Packer 1995, Heinsohn et al. 1996). Thus, characterizing the responses of lions to underlying landscape level processes in conjunction to the influences of heterospecific and conspecific interactions may better illuminate the effects of inter- and intraspecific competition on lion habitat use and movement patterns.

Resource selection functions (RSFs) can be used to examine the relationship between species and their habitats in a "use versus availability" assessment (Manly et al. 2002). In contrast, step-selection functions (SSFs), relate the local movement of individuals to fine scale habitat heterogeneity (Fortin et al. 2005). Both RSFs and SSFs are particularly useful in evaluating the relative importance of different variables and landscape features on species space use, and species movements across the landscape. In addition, these approaches quantify species responses to particular factors while controlling for the influence of selected habitat variables (Roever et al. 2010). Thus, using RSFs and SSFs to ascertain patterns of lion habitat use and movement in response to the effects of inter- and intragroup interactions across a gradient of environmental characteristics provides an effective basis by which to analyze the response of lions to the potential impacts of interference competition.

In this study, we address the effects of key seasonally driven environmental factors, intraspecific interactions, and interspecific competition with spotted hyena on lion range use and movement behaviour, by comparing these in a water-restricted, semi-arid landscape in the Etosha National Park, Namibia, and wetland regions in northern Botswana that have abundant permanent water sources. Here we investigated the range utilization and fine-scale movement metrics of global positioning system (GPS) satellite telemetry collared lions from both fenced and unfenced protected areas (PAs) and free-roaming areas, to explore the drivers of lion seasonal space use in a multi-prey system infused with seasonal surplus resources. Specifically, we compared seasonal differences and temporal patterns in the size and shape of lion utilization distributions (UDs) in habitats ranging across a semi-arid to a wetland environmental gradient, and subject to different landscape characteristics. We further compared and contrasted the fine-scale movement metrics of lions in response to various landscape attributes, environmental conditions, and to inter- and intragroup dynamics, to delineate the speed, distances, and tortuosity of lion trajectories, and related these metrics to activity data obtained from the collar accelerometers. In addition, we evaluated the broad-scale habitat responses and fine-scale movement responses of lions to underlying landscape level processes in combination with inter- and intragroup effects to characterize the spatial habitat use and movement of lions by fitting RSFs and SSFs to GPS movement data. We expected that lion habitat selection patterns and movement responses would be influenced by environmental features associated with available resources in addition to interference competition from conspecifics and their main competitor, the spotted hyena. We expected lions to preferentially select for areas of high normalized vegetation index (NDVI) correlated with high prey densities, and to move through habitats of increased vegetation that allows concealment for ambush hunting opportunities. We further expected lions to select for areas closer to water, and far from anthropogenic sources. We also expected lions to avoid encounters with hyenas by using areas of lower hyena utilization to protect from kleptoparasitism and scavenging losses to hyenas, and we expected lions to have different seasonal responses during the dry season when competition becomes important, and during the wet season when prey becomes more dispersed and harder to catch.

3.3. Materials and Methods

3.3.1. Ethics statement

This study was conducted with the permission of the Ministry of Environment and Tourism, Namibia and the Department of Wildlife and National Parks, Botswana. Animal handling procedures adhered with the protocols of the Animal Research Ethics Committee of the University of KwaZulu-Natal, South Africa. CITES permits regulated the shipping of collected specimens outside of Namibia.

3.3.2. Study sites

This study was conducted within four locations of the southern African region: the Etosha National Park, the Chobe National Park, the Chobe Enclave, and an area in the southeastern section of the Okavango Delta system in Botswana, and encompassed a total area of 17,500 km^2 (Fig. 3.1). The Etosha National Park in northern Namibia lies between 18°30’S-19°30’S and 14°20’E-17°10’E and is a large, semi-arid savanna. Etosha is surrounded by a predator-proof fence and consists of a salt pan of approximately 4760 km^2 surrounded by grasslands and dwarf shrub savannas. The Chobe National park is an unfenced protected area in northeastern Botswana and lies between 17°47’S-19°0’S and 23°52’E-25°10’E. To the west of the Chobe National Park’s riverfront is the Chobe Enclave, a community owned conservation area which acts as a wildlife corridor, and is interspersed with human settlements and cattle posts. The Chobe Enclave consists of the Linyanti Conservancy, a riparian wetland ecosystem that lies between 17°57’S-18°22’S and 23°54’E-24°42’E, and is surrounded by the Chobe National Park. The Linyanti Conservancy and the Chobe National Park are bordered by the Kwando-Linyanti-Chobe River to the north and the northern region of the National Park is predominantly a riverine environment with riparian vegetation. These conservation areas and the river that feeds through this system comprises one of the core components of the Kavango-Zambezi (KAZA) Transfrontier Conversation Area, a protected wilderness of approximately 519,912 km^2, that includes parts of Angola, Namibia, Zambia, Botswana, and Zimbabwe.

The NG32 concession, a 1000km^2 site bordering the Moremi Game Reserve in the southeastern section of the Okavango Delta, lies between 19°29’S-19°54’S and 23°4’E-23°35’E, and includes the private concession of Sanctuary Retreats and adjoining Wildlife Management Areas. The topography is comprised of floodplains with a network of waterways, islands, lagoons, reed banks and pans (Beehner et al. 2005). The area is characterized by seasonal flooding and rainfall. Rainfall mainly occurs between December and March, with a cool dry season from May to August with a hot dry season from September to November. Rising floodwaters occurs between April to July and is normally highest in August (Bennitt et al. 2019). The area consists mainly of riparian tree species (*Croton megalobotrys, Hyphaene petersiana, Philenoptera violacea, and Diospyros mespiliformis*), dryland tree species of acacia (*Senegalia spp*. and *Vachellia spp.*) and mopane (*Colophospermum mopane*) woodland, and grasslands (Tsheboeng et al., 2017).

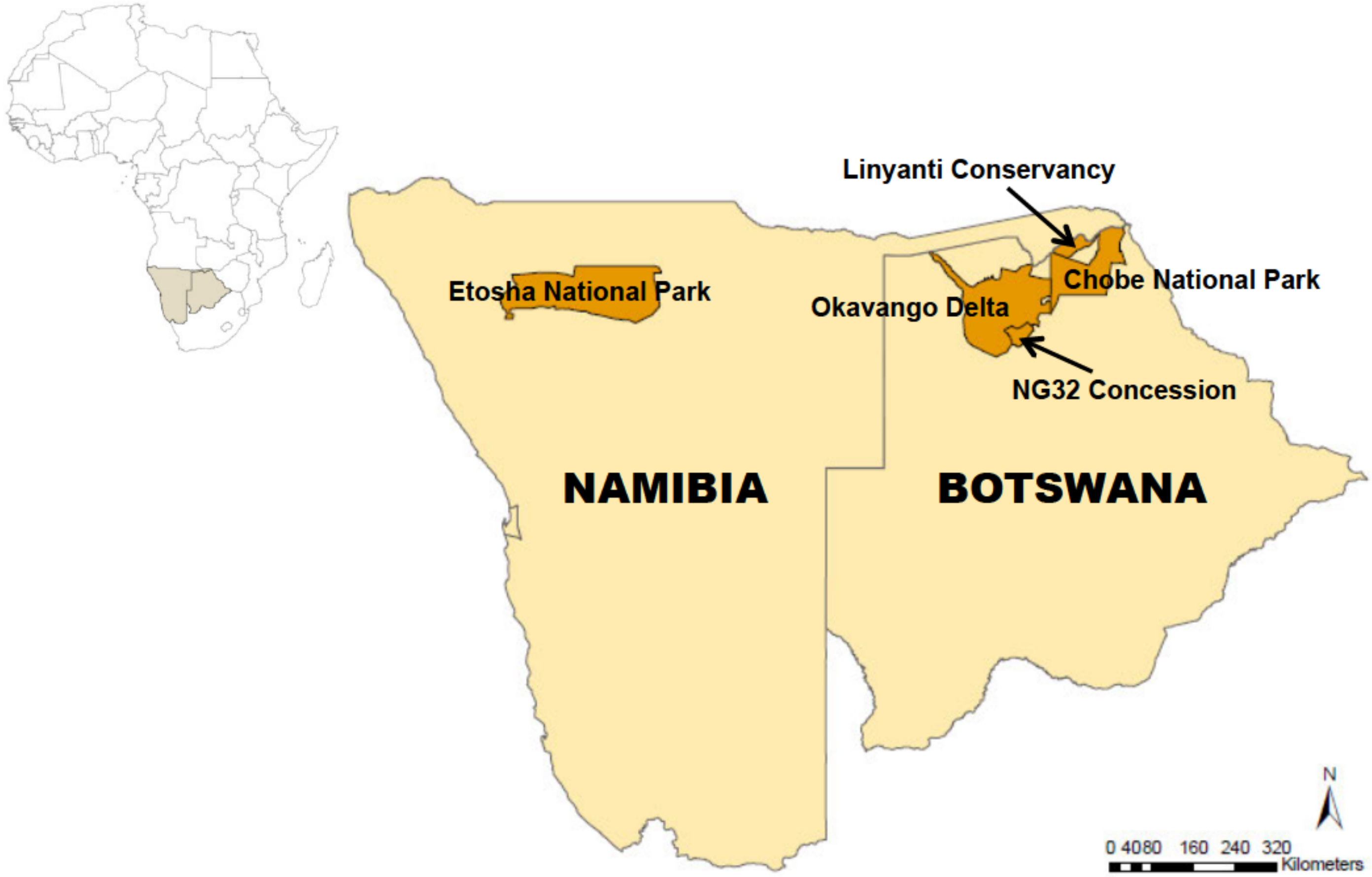

Figure 3.1. Location of the study areas. The map of the African continent shows the countries of Namibia and Botswana shaded, and the protected areas within these countries where the study was conducted. Maps were generated with ArcGIS (ESRI ArcMap v.10.0).

3.3.3. GPS tracking

GPS satellite telemetry collars with dual-axis accelerometers (IridiumTrackM, Lotek Wireless Inc., Newmarket, Ontario, Canada) were deployed on a total of 19 lions: 8 female and 3 male lions in Namibia, and on 5 female and 3 male lions in Botswana (Table 3.1). Collars were programmed to collect location fixes every 30 min from 18h00 – 6h00 for Etosha, or 17h00 – 8h00 for Botswana, with diurnal fixes at 10h00, 14h00, and including 12h00 for some individuals. Sampling schedules of every 5 min corresponded with periods of heightened activity for two hours after sunset (19h00-21h00) and two hours before sunrise (4h00-6h00). Lion activity was recorded by the dual-axis accelerometers continuously in 8 second bursts, and were averaged over 240 seconds (4 minutes) and stored on the collars. Activity was measured four times per second simultaneously on each axis as the difference in acceleration between two consecutive measurements and given a relative range between 0 and 255 (activity monitor values [AMVs]) to indicate the mean activity/acceleration. Data recorded from the two axes were characterized by forward-backward movements on the x-axis and rotary/sideways movements on the y-axis, and were subsequently downloaded from retrieved collars.

All lion collars in Etosha were retrieved at the end of the study (*n* = 11), whereas 5 of 8 lion collars were retrieved from the lions in Botswana after the end of the study. The remaining lion collars were lost after collar batteries had become depleted, or when the animals were killed by the local people after they crossed into Namibia. From these 3 collars, we downloaded the relocations from the Lotek web service (a subset of relocations transmitted during the study period in order to conserve batteries), amounting to 13.5% of sampled locations. The downloaded relocation subset consists of a different sampling interval with a fix every third point, resulting in 15 min and 90 min fixes. Although it was not logistically possible to collar all lion individuals within the study areas, our chosen collared individuals are representative of the lions within these areas, as all known groups included a collared individual and there were minimal gaps between the home ranges of these selected groups. Two collared males in Etosha and one collared male in Linyanti were observed to form mating pairs with collared females for brief periods. Two female lions in Etosha that had been collared separately were observed to sometimes join prides. All other collared lions maintained separate groups throughout the duration of the study.

Table 3.1. Summary of data collection records of the collared lions in this study. Lions of the Etosha National Park (ENP), Namibia are separated from lions of the Chobe National Park (CNP), Linyanti Conservancy (LC), and the NG32 concession in the Okavango Delta (NG32), Botswana between 24 November 2014 and 18 June 2015. Asterisks denote unretrieved collars/missing data.

INDIVIDUAL	REGION	SEX	TRACKING DAYS	GPS LOCATIONS	ACTIVITY RECORDS	TRACKING PERIOD
OK-33863	ENP	F	121	5643	44010	11 Oct 2013 – 9 Feb 2014
RE-33864	ENP	F	166	9875	60116	19 Oct 2013 – 3 April 2014
NU-33865	ENP	F	368	24264	132362	21 Nov 2013 – 24 Nov 2014
MO-33866	ENP	F	342	22966	123335	23 Nov 2013 – 31 Oct 2014
OJ-33867	ENP	M	89	3962	32231	11 Oct 2013 – 8 Jan 2014
SU-33868	ENP	M	234	13971	84276	25 Oct 2013 – 16 June 2014
G1-33950	ENP	F	36	205	14828	5 Oct 2013 – 10 Nov 2013
OM-34308	ENP	F	141	6586	51141	24 Sept 2013 – 12 Feb 2014
LU-34308	ENP	F	212	14169	76401	28 March 2014 – 26 Oct 2014
OF-34309	ENP	M	116	4441	41511	27 Sept 2013 – 21 Jan 2014
G2-35678	ENP	F	178	11893	64089	1 May 2014 – 26 Oct 2014
SW-33950	CNP	F	228	16129	82075	24 July 2015 – 8 March 2016
AF-34308	LC	F	109	10914	39060	10 Oct 2015 – 27 Jan 2016
BE-35678*	LC	F	71	1377	*	29 Oct 2015 – 8 Jan 2016
BO-35947	NG32	M	617	109977	222336	23 Feb 2016 – 1 Nov 2017
AM-36714*	LC	M	638	15410	*	10 Oct 2015 – 9 July 2017
BA-36715	NG32	M	607	116278	218635	11 Dec 2015 – 9 Aug 2017
KW-36716	CNP	F	367	20414	133470	18 June 2015 – 19 June 2016
KB-36717*	CNP	F	355	9128	*	26 June 2015 – 15 June 2016

3.3.4. Lion range use, movement metrics, and activity patterns

All regularly sampled lion trajectories had some degree of missed fixes, and the three un-retrieved collars' uploaded satellite data had a different sampling rate than the 5 min and 30 min schedule (15 min and 90 min instead). In preparation for analysis, we decided not to regularize or interpolate the data as the missing fixes were minimal (mean ± standard deviation: lion 0.57 ± 0.50%), but rather created subsets that were completely regularized at scales corresponded to seasonal and diel types of analysis for range and habitat selection (Thurfjell et al., 2014). We used regularly sampled intervals of every 4 h over a 24 h period and every 30 min from 18h00 – 6h00 or 17h00 – 8h00, and every 5 min for two hours after sunset from 19h00 – 21h00 and for two hours before sunrise from 4h00 – 6h00. We restricted relocations from the three satellite uploaded dataset to include 6 locations per day as equally spaced as possible for 24 h periods, and all relocations between 17h00 – 8h00 which typically ranged between 15 min to 90 min.

To understand how lions use their ranges across seasons, we created two types of utilization distributions for each of the dry and wet seasons for each lion. We used adehabitatHR (Calenge 2006), with the reference bandwidth as the smoothing factor for the kernel density estimator (KDE), and we used the time-local convex hull (*T*-LoCoH, Lyons et al., 2013) package to create seasonal utilization distributions for each lion. To understand how lions use their ranges according to diel cycles, we created adaptive local convex hull (*a*-LoCoH) UDs for each individual's diurnal and nocturnal ranges in each of the dry and wet seasons. We chose the adaptive method (*a*-LoCoH) because of its robustness in areas with a relatively high density of points, such as when an individual makes regularly repeated visits to a particular site, i.e., waterholes (Getz et al. 2007). Our utilization distributions consisted of the 95% isopleth which we defined as the home range, and the 50% isopleth which we defined as the core area.

We used R version 3.5.1 (R Core Team, 2018) to compare the sizes of home ranges and core areas among conspecifics with regards to location (Etosha, Chobe/Linyanti, hereafter Chobe, or Okavango), seasons, and segments of diel cycles. Individual home ranges and core areas that were seen to overlap with one another were included in the analysis for interactions. We measured the areas of home range and core area overlap with the intersect function in R v.3.5.1, and applied the *t*-test to determine for differences between lion individuals across seasons, over diel cycles, and between PAs. We further examined for differences between home ranges and core areas according to variations among individuals and pride factors. We used the mixed effects analysis of variance (ANOVA) to test for significant differences of lion range sizes and habitat selection based on the ages and body condition scores of the collared lion, the size of the pride of the collared lion, and whether prides consisted of cubs or subadults.

We used adehabitatLT (Calenge 2006) to calculate the speed of lion movements, the distance travelled (or step length), the path tortuosity (see Chapter 2 *Methods: Species movement patterns* for details on analyses of turning angles), and displacements over 12 and 24 h (18h00-6h00 and 18h00-18h00, respectively), for each individual. We compared these measures using the *t*-test and the Watson's two sample test for turning angles. We also used measures computed for nocturnal (18h00-6h00 or 17h00-8h00) and crepuscular (19h00-21h00 and 4h00-6h00) time windows to compare factors underlying lion movement behaviour among ecosystems, between the sexes, and at diel, lunar and seasonal time scales, and tested these using ANOVA.

We also examined whether lion activity differed with respect to land cover classes over the lunar cycle. We obtained open-source land cover maps generated from LandSat thematic mapper data for Namibia and Botswana (2010 Scheme II) via the RCMRD GeoPortal (http://geoportal.rcmrd.org), to which we assigned arbitrary values to reflect discrete land cover categories. We identified the land cover classes for all relocations of each individual, and averaged the activity values of each individual according to the various types of land cover. We subsequently plotted the average activity of lions within different land cover classes. In addition, we focused on full moon and new moon nights when available light at night (moon light intensity) occurred between a range of values when ≥ 95% and ≤ 5% of the lunar disc was illuminated. Thus, we defined illumination values at 0.95 to 1.0 as full moon nights and values at 0 to 0.05 as new moon nights. For each of the dry and wet seasons, we subdivided each of these full moon and new moon days into seven periods of a 24 h cycle: afternoon, dusk, night, nadir, night-end, dawn, morning (see Chapter 2 *Methods: Species activity patterns* for details). We averaged lion activity measures that occurred in each period, and calculated the proportion of activity for each period of the 24 h cycle. We applied the t-test to compare lion activity between the semi-arid and wetland environments, and used the ANOVA to test for differences among the activity means according to the lunar cycle.

3.3.5. Inter- and intraspecific interactions

The direct effect of intraspecific interactions was examined from the simultaneous sampling of location records. We included all collared lions that occurred within 5 km of each other throughout the study period. We developed a unique matrix for each individual that overlapped in their temporal collar schedules. We then used this temporally aligned matrix to obtain the minimum Euclidean distance between all collared individuals over all simultaneous sampling records (see Chapter 2 for details). We compared the frequency of distances between collared lions at different distances, and tested whether these differed between PAs. We also assessed whether there was any effect on lion activity when within a conspecific or competitor core area relative to being outside of a conspecific or competitor core area. For each individual, we filtered out all locations that occurred inside and outside a conspecific or competitor core area, and calculated the average activity of both inside and outside conspecific and competitor core areas for each individual. We applied the mixed effects ANOVA to test whether the average activity of lions differed from when they were inside conspecific and competitor core areas, in relation to when they were outside of conspecific and competitor core areas.

To examine the influences of inter- and intraspecific interaction on the habitat selection and movement of lions in the Etosha and Chobe study areas, we included social interaction covariates for model testing. Since we had no collars on spotted hyenas in the Okavango Delta, our social interaction covariates were included in the models only for the Etosha and Chobe populations, which had 9 and 5 collars on spotted hyenas, respectively. Our social interaction covariates consisted of measured distances between competitors and conspecifics at simultaneous times, as well as a representation of the probability of encountering competitors or conspecifics throughout the individual’s range. To achieve this, we included the minimum Euclidean distance for matched points in time among lions for the model predictor “distance to nearest conspecific”. We also measured the minimum Euclidean distance, as above, to the nearest competitor (collared spotted hyenas) to be used for the predictor “distance to nearest competitor”.

In addition, we constructed a geographic information system (GIS) layer for each individual which we defined as the potential conspecific range for each of the dry and wet seasons. This layer was created by overlaying the seasonal UDs of all other lions together (excluding the individual the layer was being created for) and averaging each pixel cell value to create a total combined layer of a potential conspecific range. These UDs were then converted to volume UDs (see Chapter 2 for details) and the cell pixel values were assigned to the individual's relocations as a probability of conspecific use area. We also created a GIS layer of the lion's main competitor, the spotted hyena, to reflect the potential competitor range. We first constructed UDs for all collared spotted hyenas from two of the same areas as this study (see Chapter 2 for capture/tracking details of spotted hyenas, and for construction of spotted hyena UDs). We then combined and overlaid the UDs of all collared spotted hyenas and repeated the process as above to obtain a probability of competitor use area.

3.3.6. Modelling lion habitat selection and movement

We used resource selection functions (RSFs; Manly et al. 2002) and step-selection functions (SSFs; Fortin et al., 2005) to investigate the relationship among lion habitat selection and lion movement to landscape features, bioclimatic factors, and inter- and intra-specific interactions. We fitted RSFs in a use-available design, which provides information on the selection of habitats relative to their availability within the home range as follows. For each observed lion location, we drew 5 random locations from within each individual's 95% kernel UD. We applied mixed effects logistic regression models using frequentist inference with the glmmTMB R package (Jonsen et al. 2019). We used weighted random points and assigned fixed, large intercept variance for our random effects as in Muff et al. (Muff et al. 2019). We also fitted SSFs using a similar case-control design of used and available steps to identify the factors that influenced lion movement (Fortin et al. 2005). Each observed lion step was compared to 5 random steps, created by randomly drawing step lengths and turn angles from lion movement distributions observed within their respective study locations. Sex-specific step length and turn angle distributions were generated for each time period (24-hr periods, nocturnal periods, dusk/dawn periods) for each of the three study areas. We fitted the step-selection function with the mixed conditional Poisson regression model after Muff et al. (2019). As with the RSFs, we used frequentist inference and assigned fixed, large intercept variance for our random effects.

We employed a multi-stage approach to examining lion response to landscape features, bioclimatic factors, and inter- and intra-specific interaction. First, we examined the response of lions to landscape and bioclimatic characteristics in the absence of social interaction covariates to determine broad-scale patterns. We developed a candidate set of ecogeographical variables for model testing to elucidate the factors that influence lion space use and movement across the two types of ecosystems (Table 3.2). We selected variables that have been shown to potentially influence lion distributions, such as distance to water and land cover types (Abade et al. 2014, Oriol-Cotterill et al. 2015a, Kittle et al. 2016). We included information about individual differences because lion age, condition, sex, pride size and the presence of cubs contribute to differences in lion movement behaviours (Funston et al. 1998, 2001, 2003, Mosser & Packer 2009, Elliot et al. 2014).

We incorporated parameters of available resources across the landscape through the use of normalized difference vegetation index (NDVI) as an index of potential prey biomass (Abade et al. 2014, Albon et al. 2017, Ciach & Peksa 2018), and included distances to available carcasses and an anthrax risk probability value layer (defined as the probability of encountering site-attracted foraging ungulates) for the Etosha population (see chapter 2 Supplementary materials for details). In brief, GPS coordinates of recorded carcasses were assigned a starting and ending time based on the species, estimated date of death and according to the detection and consumption times for carrion (Moleón et al. 2015) or the mean persistence times for predated carcasses (Benbow et al. 2016). The minimum Euclidean distance from collared individuals to these carcass sites were measured for the duration of time these carcasses were expected to have lasted. We constructed the anthrax risk probability layer with the 95% kernel density estimator using coordinates of confirmed anthrax positive carcass sites from a recent period of anthrax outbreak (2009-2010). We converted this to a volume utilization distribution to obtain the probability of presence values for each cell, and subtracted volume UD values from 100 to make it more intuitive, as described in Kittle et al. (2016).

We then used correlation analysis to check for multicollinearity among predictor variables and ensured that our selected predictors were minimally correlated ($R \leq 0.70$). Variables that were correlated, such as distances to permanent water and seasonal water, or distances to the nearest carcass and the probability of encountering site-attracted foraging ungulates, were not included in the same model, and instead were substituted for one another within the global model to determine which best fit the data. Prior to building models, we centered and scaled continuous variables to have mean of 0 and SD of 1, to ensure that variables would be comparable.

Models were assessed and ranked based on Akaike's information criterion (AIC; Burnham & Anderson, 2002), and Akaike weights. Models with an Akaike difference of < 2 were categorized as having substantial support, with some support between 2 and 4, less support between 4 and 7, and essentially no support with differences > 10. These models were comprised of landscape and bioclimatic variables but not social interaction variables. Secondly, for both RSFs and SSFs, we developed a set of 6 candidate social interaction models to evaluate the prediction that including inter- and intra-specific covariates would better explain lion range selection and movement than landscape and bioclimatic features alone. These models had an identical structure to the best model based on AIC from above but included social interaction variables. Because the distances to competitors and conspecifics were associated with the probability of competitors and conspecifics respectively, these variables were likely correlated and could not be included in the same model. To test whether lion movements were best described by the distances to competitors and conspecifics, or by the probability of competitors and conspecifics, we examined the change in AIC between the models, interchanging only distances to competitors and conspecifics with the probability of competitors and conspecifics respectively to determine which provided a better fit to the data. We calculated AIC values and AIC weights as above for all models to assess which models had the greater weight of evidence.

Finally, because we wanted to control for other potential factors which may occur when adding additional variables to a model, we selected the social interaction covariates informed from the best AIC-ranked social interaction models, and repeated the RSF and SSF modelling process as above. We utilized the backward stepwise selection procedure towards a globally saturated model based on the AIC to (a) determine the most parsimonious model, and (b) to ascertain whether social interaction covariates were retained in the most parsimonious model. Separate analyses were conducted for each time period (24-hr periods, nocturnal periods, and dusk/dawn periods) for each PA (Etosha, Chobe, and Okavango), and for each of the wet and dry seasons.

Using mixed effects logistic regression, we modelled lion habitat selection and movement as a function of broader landscape and bioclimatic features along with social interaction covariates to assess the influence of inter- and intra-specific interactions on lion habitat selection and movement relative to other landscape and bioclimatic factors. Again, time periods (24-hr, nocturnal and dusk/dawn periods) for each PA for each season were modelled separately, and model building procedures followed the RSF and SSF procedures above to create a full model without correlated variables. All statistical analysis was conducted in R version 3.5.1 (R Core Team, 2018) and all GIS applications were undertaken with ArcGIS (ESRI ArcMap v.10.0, Redlands, CA, USA).

Table 3.2. Variables used for modeling the habitat use and movement of lions, description of variable, and which models the variables were used in: RSF (Resource Selection Function), SSF (Step Selection Function), or both models.

Variables	**Name**	**Description**	**Models**
Individual Variables	*sex*	Sex of individual	RSF
	age	Age of individual	RSF
	bc_score	Body condition score	RSF
	grp_size	Group size	RSF
	cubs_sa	With cubs / subadults	RSF
Bioclimatic Variables	*xhr_day*	Time of day (24 h periods)	RSF
	xhr_night	Time of night (12 h periods)	RSF
	temp	Temperature	SSF
	moon_ill	Moon illumination (probability index, 0-1)	SSF
	precip_mnth/ptd	Precipitation amounts (monthly or 5-day average)	RSF
Landscape features	*elvtn*	Elevation (30m x 30m)	Both
	lndcvr	Land cover categories (30m x 30m)	RSF
	sp_forest†	Binary variable for sparse forest land cover	RSF
	woodland	Binary variable for woodland land cover	RSF
	*grassland**	Binary variable for grassland land cover	RSF
	*savanna_grass**	Binary variable for savanna grass land cover	RSF
	clsd_grass†	Binary variable for closed grass land cover	RSF
	opn_grass†	Binary variable for open grass land cover	RSF
	*shrub**	Binary variable for shrub land cover	RSF
	clsd_shrub†	Binary variable for closed shrub land cover	RSF
	opn_shrub†	Binary variable for open shrub land cover	RSF
	*veget_wet**	Binary variable for vegetated wetland land cover	RSF
	wetland†	Binary variable for wetland land cover	RSF
	floodplain†	Binary variable for floodplain land cover	RSF
	*salt_pan**	Binary variable for salt pan land cover	RSF
	crop	Binary variable for crop land cover	RSF
	settlement	Binary variable for settlement land cover	RSF
	ndvi	NDVI (30m x 30m, seasonal mean)	RSF
	*anthrx_prb**	Anthrax carcass probability (UD value)	Both
	*d_crcs**	Distance to nearest available carcass (m)	Both
	d_prmwtr	Distance to nearest permanent water source (m)	Both
	d_ssnwtr	Distance to nearest seasonal water source (m)	Both
	d_rds	Distance to nearest road (m)	Both
	d_bndry	Distance to reserve boundary (m)	Both
	d_anthr	Distance to nearest anthropogenic feature (m)	Both
Interaction Covariates	*d_cnsp*	Distance to nearest conspecific (m)	Both
	cnsp_prb	Conspecific probability (UD value)	Both
	d_cmp	Distance to nearest competitor (m)	Both
	cmp_prb	Competitor probability (UD value)	Both

** variables included in Etosha models only, †variables included in Botswana models only*

3.4. Results

3.4.1. GPS tracking

Out of 680,526 lion relocations, after cleaning and processing we used 417,602 relocations for analyses. Etosha lion relocations accounted for 28.3% of this dataset with 71.7% of lion relocations from Botswana study areas. Lion relocation records from Etosha were nearly complete (99.6%) compared to lion relocation records from Botswana study areas (53.3%), due to the unretrieved collars from Botswana.

3.4.2. Lion range use, movement metrics and activity patterns

Lion UD measures are presented in Table S3.1 (Supporting Information), with *a*-LoCoH UDs for each individual in Appendix S3.1 (Supporting Information). Kernel density estimates demonstrate overlapping areas in the home ranges among individuals, except for Okavango lions whose home ranges did not overlap (Fig. 3.2). With the inclusion of time scaled distances, lion *a*-LoCoH UDs were significantly smaller than kernel density UDs for both day and night ranges in all seasons in Etosha (mean ± standard error (SE) diurnal: kernel 723.8 ± 115.1 km^2, *a*-LoCoH 336.6 ± 62.9 km^2, $t = 2.95$, df = 13.9, $p < 0.05$; nocturnal: kernel 718.8 ± 114.2 km^2, *a*-LoCoH 393.5 ± 63.1 km^2, $t = 2.49$, df = 14.0, $p < 0.05$), whereas there were no differences in Botswana (mean ± SE diurnal: kernel 503.6 ± 176.2 km^2, *a*-LoCoH 226.9 ± 79.0 km^2; nocturnal: kernel 499.7 ± 168.8 km^2, *a*-LoCoH 245.8 ± 73.0 km^2, all p-values > 0.05; Table S3.1). Concentrating our analyses on lion *a*-LoCoH UDs, although the sizes of the home ranges and core areas of lions did not differ between diurnal and nocturnal periods, they were larger in the wet season for both periods (mean ± SE diurnal home range: dry season 121.2 ± 29.7 km^2, wet season 244.4 ± 42.3 km^2, $t = -2.38$, df = 28.7, $p < 0.05$; nocturnal home range: dry season 162.5 ± 36.9 km^2, wet season 278.4 ± 41.4 km^2, $t = -2.09$, df = 30.8, $p < 0.05$; diurnal core area: dry season 42.2 ± 10.7 km^2, wet season 95.7 ± 23.0 km^2, $t = -2.11$, df = 22.6, $p < 0.05$; nocturnal core area: dry season 45.3 ± 11.7 km^2; wet season 106.1 ± 21.4 km^2, $t = -2.50$, df = 24.7, $p < 0.05$; Table S3.1), whereas the ranges of Okavango lions contracted in the wet season (mean ± SE: Okavango 113.5 ± 66.1 km^2, Chobe/Linyanti 272.5 ± 118.8 km^2, $\varkappa^2 = 65.53$, df = 1.0, $p < 0.0001$; see Appendix S3.1.d, Supporting Information).

The differences in home ranges between seasons were larger for Etosha lions than they were for lions from Botswana (mean ± SE: Etosha 152.0 ± 29.2 km^2, Botswana 100.6 ± 35.9 km^2, $t = 3.14$, df = 11.6, $p < 0.01$). In addition, Etosha lions had larger overall nocturnal core areas than lions in Botswana (mean ± SE: Etosha 127.8 ± 24.4 km^2, Botswana 63.0 ± 17.5 km^2, $t = -2.16$, df = 15.4, $p < 0.05$; Table S3.1). During the wet season in Etosha, 73% of our collared lions exhibited changes in their home ranges. Four lions (OK-33863, OJ-33867, NU-33865, MO-33866) shifted the core areas of their ranges to either encompass new or different regions within the anthrax endemic area, while the ranges of three other lions' previously embedded within the anthrax endemic area were seen to contract (G1-33950, LU-34308, G2-35678). An additional lion (RE-33864) shifted her range from the mostly mopane woodland area to the savanna grasslands along the pan. Conversely, despite the changes in the areas used by lions from Botswana, they remained anchored within their dry season ranges during the wet season.

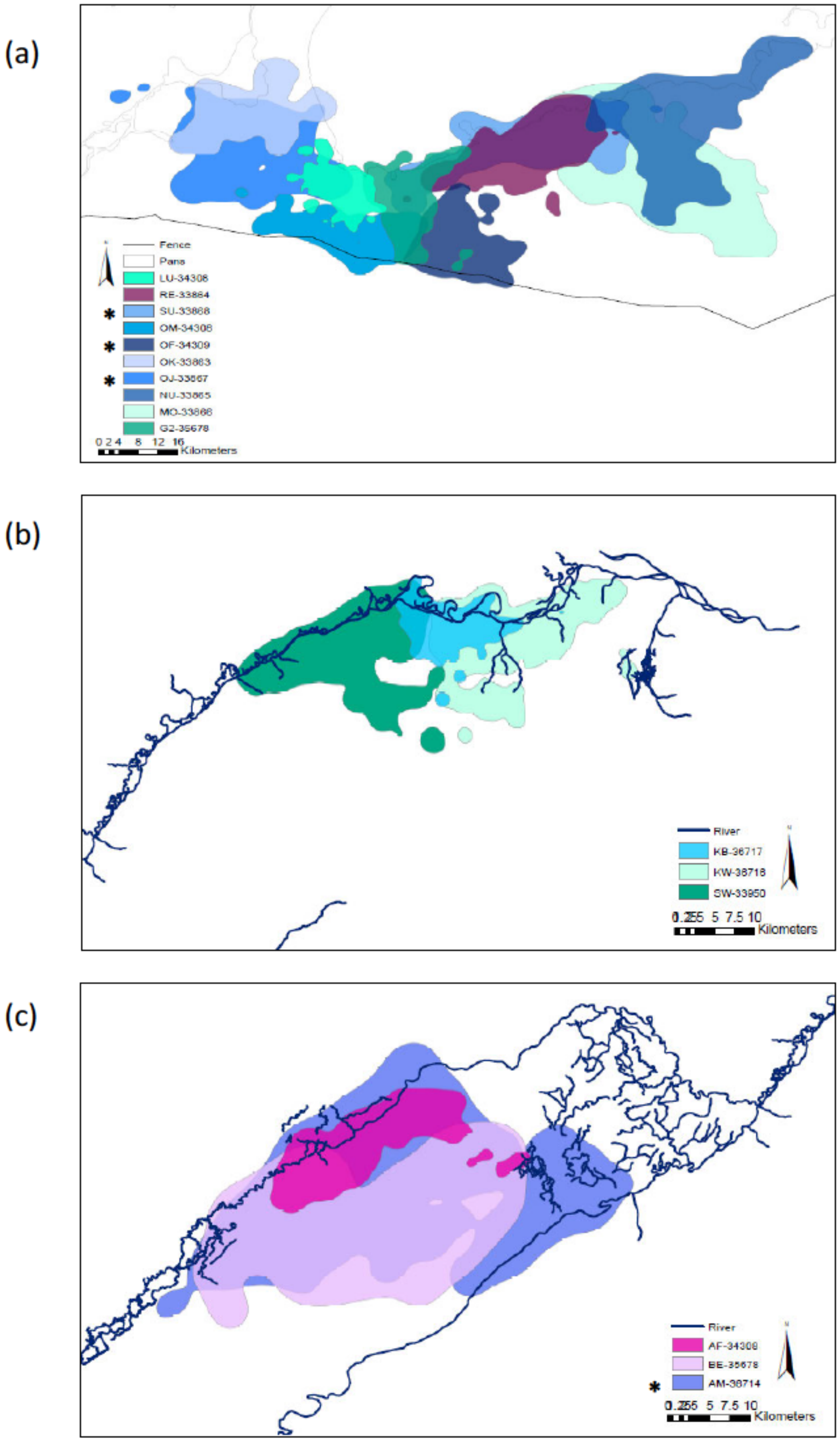

Figure 3.2. Overlapping home ranges of individual lions in the (a) Etosha National Park, Namibia; (b) Chobe National Park, and (c) Linyanti Conservancy, Botswana. Reserve boundaries are indicated by grey lines in Etosha (solid = fence, transparent = pans) and blue lines in Chobe and Linyanti (river). Males are denoted with an asterisk.

Detailed analyses of lion movement parameters revealed information about lion movement behaviour, and are presented in Appendix S3.2 and Table S3.2 (Supporting Information). Lions were predominantly active, and had increased movements, during nocturnal periods between sunset and sunrise, for both seasons (Appendix S3.2.4-5; Table S3.2.1). However, analyses of the movement parameters over specific times of the day provided further insight into the seasonal differences of lion movement behaviours between the two ecosystems. We found lion movement parameters to differ across ecosystems, presumably as a function of the environmental characteristics inherent to each area. Overall, lions from Etosha had consistently larger step lengths and displacements, and higher activity, than Botswana lions did, despite having similar travelling speeds (Appendix S3.2.4-5; Table S3.2.1). This is likely a result of the large spatial difference between the two PAs, with Etosha nearly two times the size of Chobe, and with Okavango lions constrained by the flood waters.

During the nocturnal period, the dry season step lengths of Etosha male lions increased as the night progressed, whereas Etosha female lions had larger step lengths in the dry season during the period of the darkest part of the night to the morning twilight (Appendix S3.2.5.c). Conversely, lions from Botswana exhibited a more crepuscular pattern, with larger step lengths during two periods of the night, from sunset to twilight end (18h00 – 20h00) and from late night to sunrise (3h00 – 7h00; Appendix S3.2.5.c), although there were no significant seasonal differences. Moreover, Etosha lions demonstrated less tortuous movements than Botswana lions during nocturnal periods of the dry season (Watson's test statistic: 0.177, $0.05 < p < 0.10$; see Appendix S3.2.6.a and Table S3.2.1, Supporting Information), while Botswana lions presented with more directional movements only for the early period of the night (19h00 – 20h00, Watson's test statistic: 0.193, $p < 0.05$; Appendix S3.2.6.b).

Although lion activity and movement patterns differ across ecosystems as a result of temporal, seasonal and environmental characteristics, additional discrepancies in lion movement parameters are further explained as a result of variations among individuals (i.e., sex, age, body condition, and pride demographics). Different movement parameters observed among lions in this study were influenced by the sex, age, and condition of the individual, as well as the size of the group, and whether the individual was with cubs. Male lions (n = 3) travelled further than female lions (n = 8) did in Etosha, whereas there were no differences between the sexes in Botswana (see Appendix S3.2.7 and Table S3.2.2a, Supporting Information). However, males from the Okavango Delta (n = 2) had considerably smaller movements than the male from Chobe (Table S3.2.2b, Supporting Information). In addition, Etosha females (n = 8) and Botswana males (n = 2) had more tortuous movements than their male (n = 3) and female (n = 5) counterparts, respectively (see Appendix S3.2.7, and Table S3.2.2a, Supporting Information). Older lions (> 10 years, n = 4) and young lions (< 5 years, n = 5) travelled further than adult lions (5-10 years, n = 10) (all t-tests $p < 0.01$; see Appendix S3.2.8 and Table S3.2.2c, Supporting Information), while young males (n = 2) had more tortuous movements than young females (n = 3) (Watson's test statistic: 0.153, $0.05 < p < 0.10$; Table S3.2.2c). Lions of low condition (n = 3) had higher speeds in Etosha ($F = 25.38$, $p < 0.05$), while lions with high condition (n = 3) had higher speeds in Botswana ($F = 18.57$, $p < 0.05$; Table S3.2.2d). Also in Etosha, lions of low condition (n = 4) had more tortuous movements during the dry season, whereas lions of high condition (n = 2) were more tortuous in the wet season ($F = 19.65$, $p < 0.05$; Table S3.2.2d). Females with cubs (n = 7) tended to have smaller net-squared displacements than females without cubs (n = 6), regardless of pride size (see Appendix S3.2.9, Table S3.2.2e, and supplementary materials to results, Supporting Information). However, females with cubs from larger prides ($n = 4$) had more tortuous movements than females with cubs from smaller prides ($n = 3$) (Table S3.2.2e).

Furthermore, lions exhibited markedly different seasonal responses and temporal differences between the two ecosystems with respect to the lunar cycle. During the dry season, lions exhibited more of a continuous pattern within their movement and activity characteristics during the nocturnal period in Etosha, whereas they had more of a crepuscular pattern with two peaks in the Botswana study areas (Fig. 3.4). Lions had higher mean activity on new moon nights, with Etosha lions having their highest activity during the darker periods of the night, from nadir to night-end for new moon nights, and during night end to dawn on full moon nights (see Table S3.2.3a, Supporting Information). Etosha lions also had more tortuous movements during new moon nights ($F = 22.99$, $p < 0.05$; Table S3.2.3b), while Botswana lions had higher activity and travelled at faster speeds (activity: $F = 20.30$, $p < 0.05$; speed: $F = 8.21$, $p < 0.05$; Table S3.2.3b). However, Botswana lions had more tortuous movements during full moon nights ($F = 2.51$, $p < 0.05$; Table S3.2.3b). Additionally, mean activity was interchangeable between full and new moon nights in the wet season, with Botswana lions peaking at dusk during full moon nights and decreasing to dawn. Etosha lions continued to exhibit their highest activity during nadir to night-end on full moon nights with relatively consistent mean activity throughout the nocturnal period from dusk to dawn for new moon nights (Fig. 3.4; Table S3.2.3a).

Despite environmental heterogeneity among lions from different areas, they were consistent in their responses to anthropogenic influences. Lions had higher activity and moved faster when outside of protected areas than when they were within the boundaries of PAs (Table S3.2.4). This trend was observed among lions in all study areas, despite the different environmental characteristics across the two ecosystems.

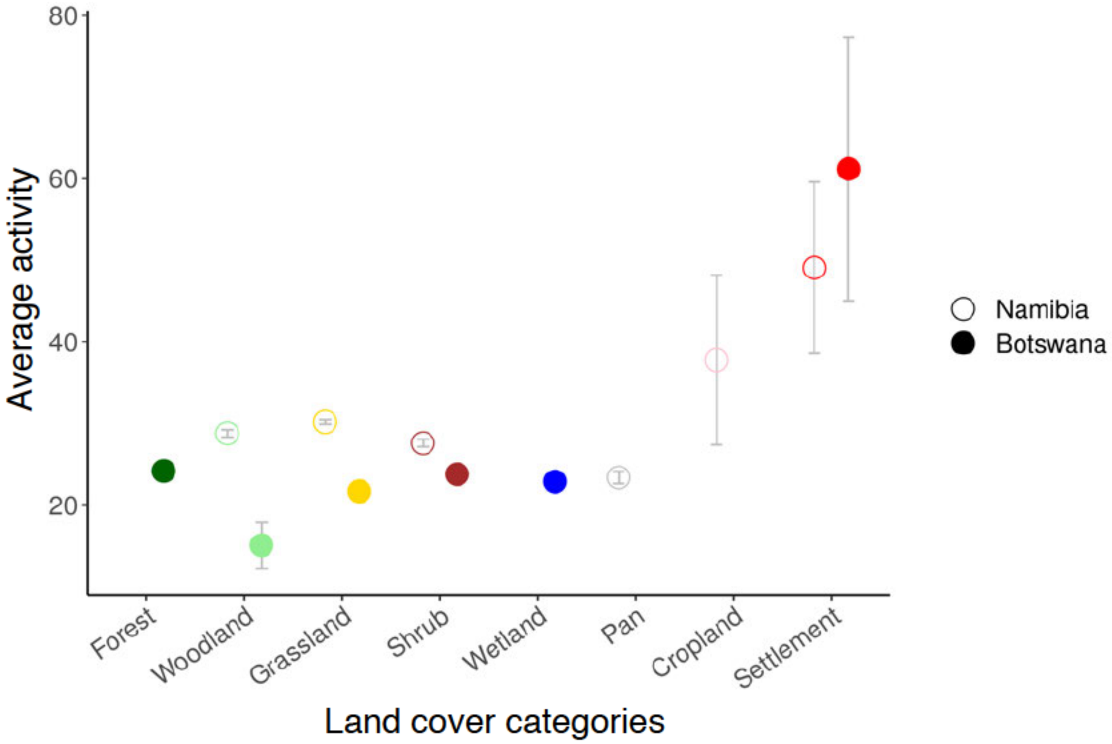

Figure 3.3. Average activity measures of lions (recorded as a relative range between 0 and 255, Activity Monitor Values [AMVs]) in different land cover classes from the Etosha National Park, Namibia (open circles) and the Chobe National Park, Linyanti Conservancy and Okavango Delta, Botswana (solid circles). Points represent the mean and error bars the standard error (SE).

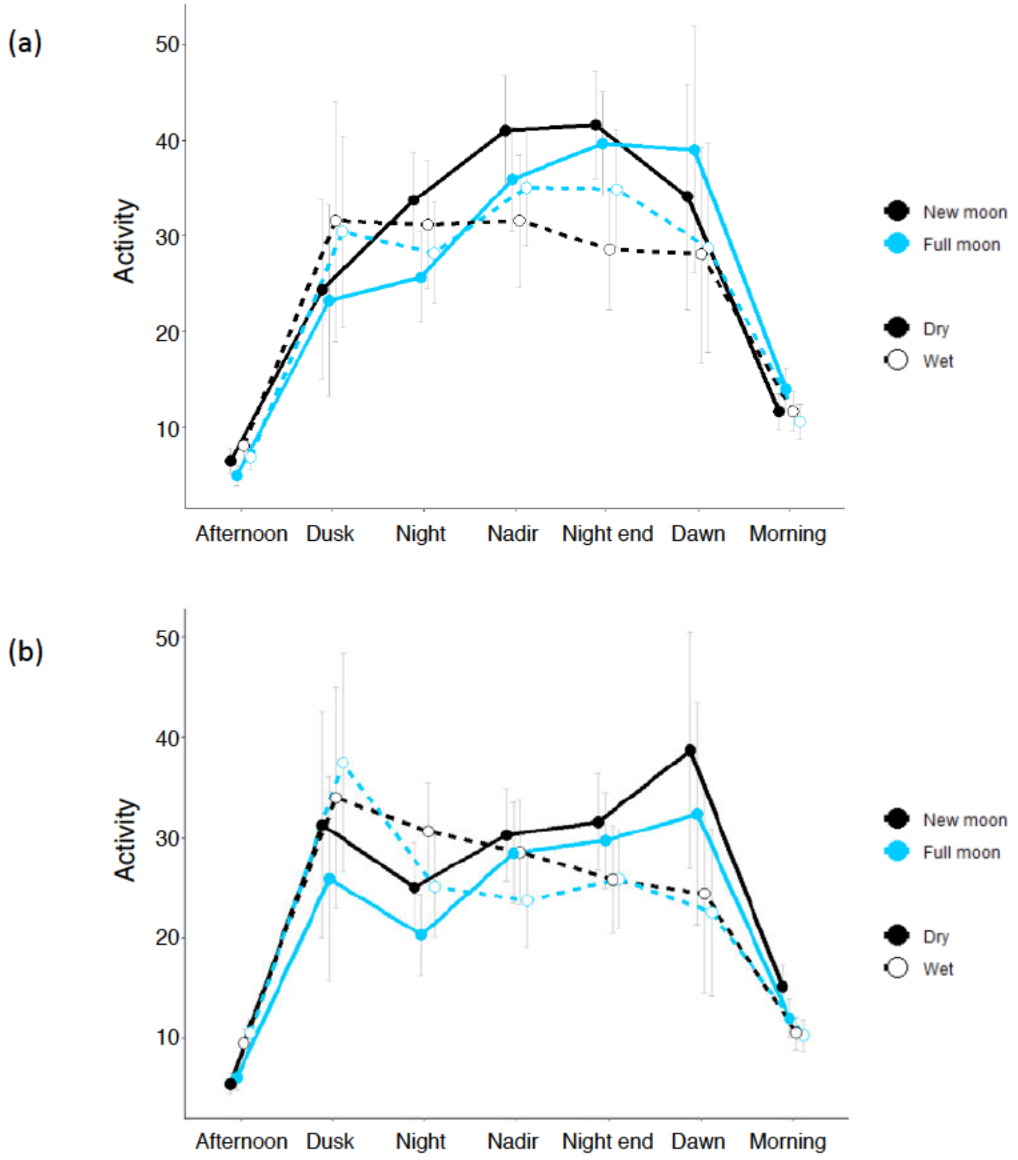

Figure 3.4. Seasonal mean activity of lions during the seven periods of a 24 h cycle for new moon and full moon phases from the (a) Etosha National Park, Namibia and (b) Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana. The 24 h cycle was subdivided into seven different periods. Night/nadir/night end consists of the end of evening twilight to the beginning of morning twilight divided into three equal intervals. Afternoon = noon to sundown; dusk = sundown to twilight end; dawn = beginning of morning twilight to sunrise; morning = sunrise to noon. Points represent the mean and error bars the standard error (SE). Connecting lines were drawn through the means for visualization purposes.

3.4.3. Inter- and intraspecific interactions

Lions did not exhibit any significant differences in the sizes of overlapped areas with conspecifics, in either home ranges or core areas, across seasons and between the two ecosystems (all t-test p-values > 0.05; see Table S3.3.1, Supporting Information). Lions shared significantly more of their home ranges than they did their core areas, in that the proportion of overlaps in the home ranges were significantly larger than the proportion of overlaps in the core areas (mean ± SE: home ranges 0.145 ± 0.027, core areas 0.078 ± 0.020, $t = 2.02$, df = 158.6, $p < 0.05$). Male lions never overlapped in their home ranges or core areas with one another while female lions sometimes did. However, males and females were seen to share some of their areas in that they sometimes overlapped in their home ranges and core areas. In addition, the proportion of lion home ranges that overlapped with conspecifics were significantly larger in Chobe than they were in Etosha (mean ± SE: Etosha 0.101 ± 0.024, Chobe 0.259 ± 0.068, $t = -2.19$, df = 28.9, $p < 0.05$; see Table S3.3.2, Supporting Information).

Out of a total of 917,237 records of measured distances between collared lions that overlapped in time with other collared individuals, a subset of 3.5% occurred at distances of ≤ 5 km. From this subset, lions occurred at distances of ≤ 5 km with each other more often in Etosha (81.5%) than in Chobe (18.5%; $\varkappa^2 = 39.79$, df = 1, $p < 0.0001$). However, lions were frequently within 1-5 km of each other more often in Chobe ($\varkappa^2 = 21.05$, df = 1, $p < 0.0001$; Fig. 3.5), whereas lions were frequently within 0-10 m and 10-50 m of each other more often in Etosha $\varkappa^2 = 14.75$, df = 1, $p < 0.001$; and $\varkappa^2 = 20.81$, df = 1, $p < 0.0001$, respectively; Fig. 3.5). Furthermore, we found significant increases in lion activity, as well as in the travelling speeds, of Etosha lions when they were at closer distances to conspecifics (see Table S3.4a, Supporting Information). Conversely, lion activity was significantly higher when they were within competitor core areas in Chobe ($F = 51.31$, $p < 0.05$; Table S3.4b). During dusk/dawn periods, lions from both ecosystems showed increased activity when at closer distances to each other than when they were closer to spotted hyenas (Table S3.4a). Etosha lions also travelled faster when at close distances to conspecifics than when close to competitors (Table S3.4a). However, lions exhibited lower activity when inside the core area of conspecifics (Fig. 3.6; see Table S3.4b, Supporting Information). These trends were generally observed during dusk/dawn periods when our sampling interval was increased to 5 min, which suggests that the potential effects of inter- and intraspecific interactions are likely to be localized on a finer scale, irrespective of the type of ecosystem.

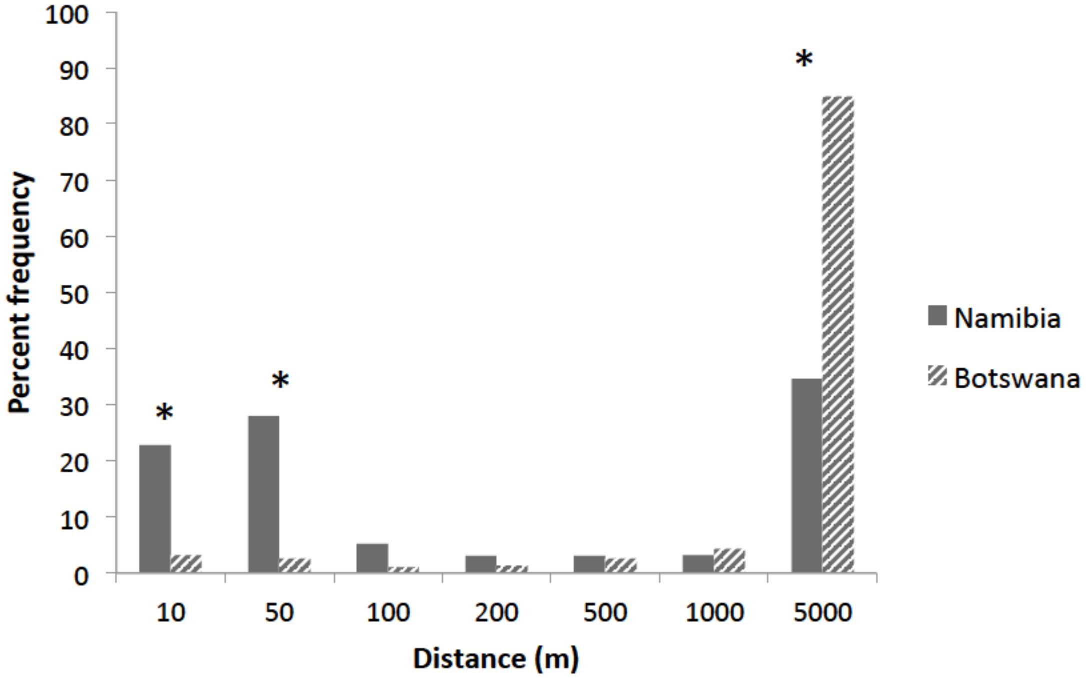

Figure 3.5. Percent frequency occurrence of time-matched distances between collared lions at distance intervals of 0-10 m, >10-50 m, >50-100 m, >100-200 m, >200-500 m, >0.5-1 km, >1-5 km. Bars reflect frequency of distances to conspecifics in the Etosha National Park, Namibia (dark grey bars) and the Chobe National Park / Linyanti Conservancy, Botswana (hatched bars). An asterisk denotes a significant difference.

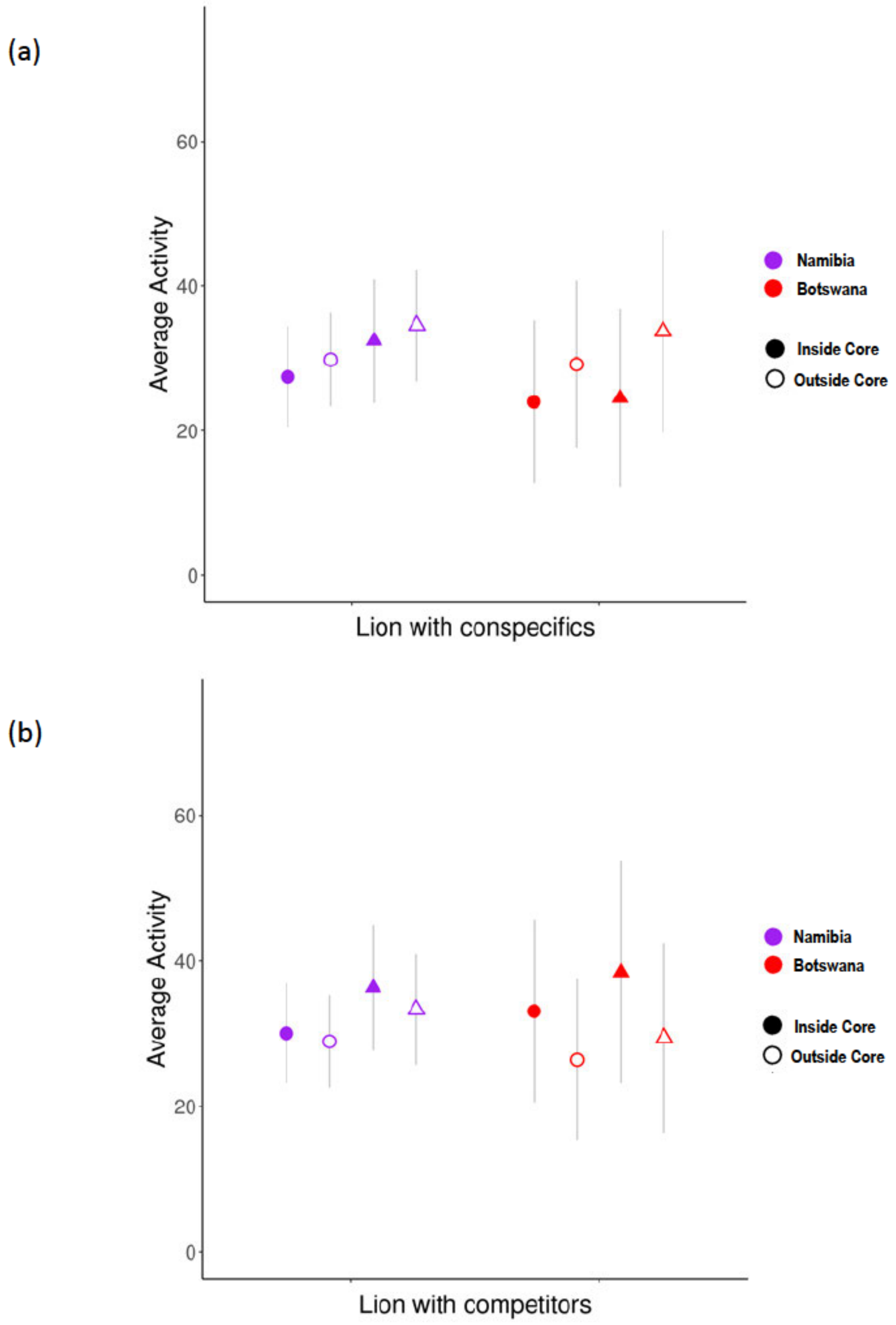

Figure 3.6. Average activity of lions with respect to (a) conspecific and (b) competitor core use areas from the Etosha National Park, Namibia (purple colours) and the Chobe National Park / Linynati Conservancy, Botswana (red colours). Inside core use areas are represented by solid shapes, and outside core use areas are represented by open shapes. Shapes represent the mean activity and error bars the standard error (SE). Activity X (circles) = forward/backward motion. Activity Y (triangles) = rotary/sideways motion.

3.4.4. Lion habitat selection and movement

For RSFs, models containing social interaction variables had more weight of evidence than base models for 24 h and nocturnal periods for both of the dry and wet seasons in both ecosystems (Table 3.3a, and see Table S3.5a in Supporting Information). The social interaction covariates representing the probability of competitor/conspecific use areas were consistently selected as the best model over models with social interaction covariates consisting of the measured distances to the nearest competitor/conspecific. For nocturnal and dusk/dawn SSFs, the model with social interaction variables consistently had more weight of evidence than base models for both seasons in both ecosystems (Table 3.3b, and see Table S3.5b in Supporting Information). Probability of competitor/conspecific use covariates were again selected over distances to the nearest competitor/conspecific for all groups For all RSF and SSF models, the backward stepwise selection procedure retained the social interaction variables as predictors included in the most parsimonious models for all groups with social interaction covariates (i.e., excluding Okavango lions). The direction of the relationship of the variables and significant predictors from these models are indicated in Table 3.4. Within these models, lions consistently responded to specific variables, in spite of substantial individual variation among the coefficient values that contributed to large standard errors (Table 3.4, and see Table S3.6 in Supporting Information).

Inter- and intraspecific interactions had a seasonal influence on lion response. Despite the high individual variation among lions in habitat selection and movements, social interaction variables were consistently selected during the dry season. When accounting for other habitat characteristics, lions were consistent in their responses to competitor and conspecific probabilities between 24 h and nocturnal periods for RSFs, and between nocturnal and dusk/dawn periods for SSFs. Competitor and conspecific probabilities did not affect lion habitat selection and movements during the wet season. During the dry season, lions from both Etosha and Chobe used habitats in response to competitor and conspecific probabilities (Table 3.4a, and see Table S3.6a). Lions used areas within their home ranges with a lower probability of competitors for the 24 h period in Etosha, and for both the 24 h and nocturnal periods in Chobe (Fig. 3.7.a-d). Additionally, lions from Chobe used areas with a higher probability of conspecifics during the 24 h and nocturnal periods. Similarly, lion movements in both Etosha and Chobe were influenced by the probability of competitors and conspecifics during the dry season (Table 3.4b, and see Table S3.6b). Etosha lions moved through areas with a lower probability of competitors during dusk/dawn periods (Fig. 3.7.e). Contrarily, lion movements from Chobe were consistent between nocturnal and dusk/dawn periods, selecting steps in areas with a lower probability of competitors but with an increased probability of conspecifics (Fig. 3.7.f-g).

In addition to social interaction covariates, lion responses were influenced by various landscape features (Table 3.4-5, see Table S3.6 and Appendix S3.3 in Supporting Information; and see Supplementary materials to Chapter 3 results for additional details). Although Etosha lions used different types of land covers between the seasons, they consistently used areas within their home range with median NDVI values (i.e., shrubland, closed grassland). They also used areas closer to seasonal water sources during the dry season, and areas with higher probabilities of site-attracted foraging ungulates (Table 3.5; see S3.6a and Appendix S3.3.1a, Supporting Information). Conversely, lions from Chobe consistently used certain land cover types within their habitats across seasons and periods of higher NDVI values (i.e., closed shrublands, woodland) (Table 3.5; see Table S3.6a and Appendix S3.3.2a, Supporting Information).

However, lions from the Okavango Delta were similar to Etosha in that they used habitats with median NDVI values corresponding to closed shrubland, open grassland (Table 3.5; Table S3.6a and Appendix S3.3.3, Supporting Information). Chobe lions also used areas closer to seasonal water sources in the dry season, and areas at further distances from anthropogenic features but closer to roads (Table 3.5; Table S3.6a and Appendix S3.3.2a, Supporting Information). Contrarily to Chobe and Etosha lions, Okavango lions consistently used areas within their home range further from seasonal water sources across both periods for both seasons (Table 3.5; Table S3.6a and Appendix S3.3.3, Supporting Information).

Table 3.3. Akaike information criterion (AIC) for best population level model selection results for dry and wet season (a) resource selection function (RSF) models during the 24-hour (18h00-18h00) and nocturnal periods (18h00-6h00 and 17h00-8h00), and (b) step selection function (SSF) models of nocturnal periods (18h00-6h00 and 17h00-8h00), and dusk/dawn periods (19h00-21h00 and 4h00-6h00) fit to 11 lions in the Etosha National Park, Namibia and to 6 lions in the Chobe National Park and Linyanti Conservancy, Botswana. Due to correlations between the interaction variables distance to competitor/conspecific and competitor/conspecific probability, those variables were interchanged within the models to see which variable best-predicted lion (a) resource selection and (b) step selection. The covariates within the model, the type of model whether interaction or base, the Akaike (AIC) values, and Akaike weight (ω_i) are presented.

(a)

Name	Period	Model Covariates	Model Type	AIC	ω_i
Etosha Dry season	24-hour	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	23383.00	1.0000
	Nocturnal	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	94028.27	1.0000
Etosha Wet season	24-hour	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	16679.40	1.0000
	Nocturnal	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	70001.08	1.0000
Chobe/ Linyanti Dry season	24-hour	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb*	interaction	17486.50	1.0000
	Nocturnal	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb + cnsp_prb*	interaction	28430.30	1.0000
Chobe/ Linyanti Wet season	24-hour	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb + cnsp_prb*	interaction	36263.14	1.0000
	Nocturnal	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb + cnsp_prb*	interaction	166865.63	1.0000

(b)

Name	Period	Model Covariates	Model Type	AIC	ω_i
Etosha Dry season	Nocturnal	*elvtn + d_anthr + d_ssnwtr + d_rds + d_crcs + moon_ill + cmp_prb + cnsp_prb*	interaction	271777.34	1.0000
	Dusk/ dawn	*elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cmp_prb + cnsp_prb*	interaction	540581.24	1.0000
Etosha Wet season	Nocturnal	*elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cmp_prb + cnsp_prb*	interaction	288053.93	0.6972
	Dusk/ dawn	*elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + cmp_prb + cnsp_prb*	interaction	567843.20	1.0000
Chobe/ Linyanti Dry season	Nocturnal	*elvtn + d_anthr + d_prmwtr + d_rds + temp + cmp_prb + cnsp_prb*	interaction	106099.74	1.0000
	Dusk/ dawn	*elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cmp_prb + cnsp_prb*	interaction	211079.32	1.0000
Chobe/ Linyanti Wet season	Nocturnal	*elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cmp_prb + cnsp_prb*	interaction	182157.51	1.0000
	Dusk/ dawn	*elvtn + d_anthr + d_ssnwtr + d_rds + temp + cmp_prb + cnsp_prb*	interaction	371617.52	1.0000

Table 3.4. Summary of variable coefficients indicating the direction of the relationship (**+** and **−**), and whether it is significant for all best models. (a) Resource selection function (RSF) models of the 24-hour (18h00-18h00) and nocturnal periods (18h00-6h00 and 17h00-8h00), and (b) step selection function (SSF) models of the nocturnal (18h00-6h00 and 17h00-8h00) and dusk/dawn periods (19h00-21h00 and 4h00-6h00) were fitted to lions for the dry and wet (shaded columns) seasons from the Etosha National Park (ENP), Namibia, the Chobe National Park and Linyanti Conservancy (CNP), and the NG32 concession in the Okavango Delta, Botswana. Emboldened signs indicate significance for that model at $p < 0.05$.

(a)

Variable	ENP				CNP				NG32			
	24 h		Nocturnal		24 h		Nocturnal		24 h		Nocturnal	
elvtn	**+**	**+**	**+**	**+**	–	**+**	**+**	**+**	**+**	**+**	**+**	**+**
xhr_day	+	+			–				+	–		
xhr_night			**+**	+			+	**+**			+	**+**
ndvi	**−**	**−**	–	–	+	–	**+**	–		**−**	**−**	**−**
precip_mnth									**−**			
sp_forest					+		+	–	–	–	+	+
woodland	+	+	+	+		**+**	**−**		**+**	**+**	**+**	**+**
grassland	–	**+**	+	+								
clsd_grass					**+**	**+**	**+**	**+**	–	–	+	+
opn_grass					**+**	**+**	**+**	**+**			**+**	**+**
savanna_grass	–	+		+								
shrub	**−**		–	+								
clsd_shrub					**+**		**+**	**+**	**+**	–	**+**	**+**
opn_shrub					–	**+**			**−**	–	**+**	**+**
crop	**+**	–		+	+	**+**	–	**+**	+	+	**+**	**+**
veget_wetland	–	**+**	+	+	+		–	**+**	**−**	**−**	**−**	**+**
salt_pan	+			+								
floodplain					+	**+**	**+**	**−**				
settlement		**+**	+	+			**+**	**+**				
d_anthr	–	–	–	–	**+**	+	+	+				
d_ssnwtr	–	–	**−**	–	+	–	**−**	–	**+**	**+**	**+**	**+**
d_rds	–	–	–		–	**−**	–	**−**				
anthrx_prb	**+**	**+**	**+**	**+**								
sex		–		–								
age					+		+					
bc_score						–						
grp_size	–											
cmp_prb	**−**	–	–	+	**−**	+	**−**	+				
cnsp_prb	+	–	+	–	**+**	+	**+**	+				

(b)

Variable	ENP				CNP				NG32			
	Nocturnal		Dusk/dawn		Nocturnal		Dusk/dawn		Nocturnal		Dusk/dawn	
elvtn	**+**	**+**	**+**	**+**	**+**	**+**	**+**	**+**				
d_anthr	**−**	+	−	−	**+**	**+**		+				
d_prmwtr					−	**−**	−		−	−	−	−
d_ssnwtr		**−**		**−**				**−**				
d_rds			−	−	**−**	**−**	**−**	**−**				
anthrx_prb			**+**	+								
d_crcs	**−**											
temp			−	+								
moon_ill	−						−					
cmp_prb	−	−	**−**	−	**−**	−	**−**	−				
cnsp_prb	−	−	−	−	**+**	+	**+**	+				

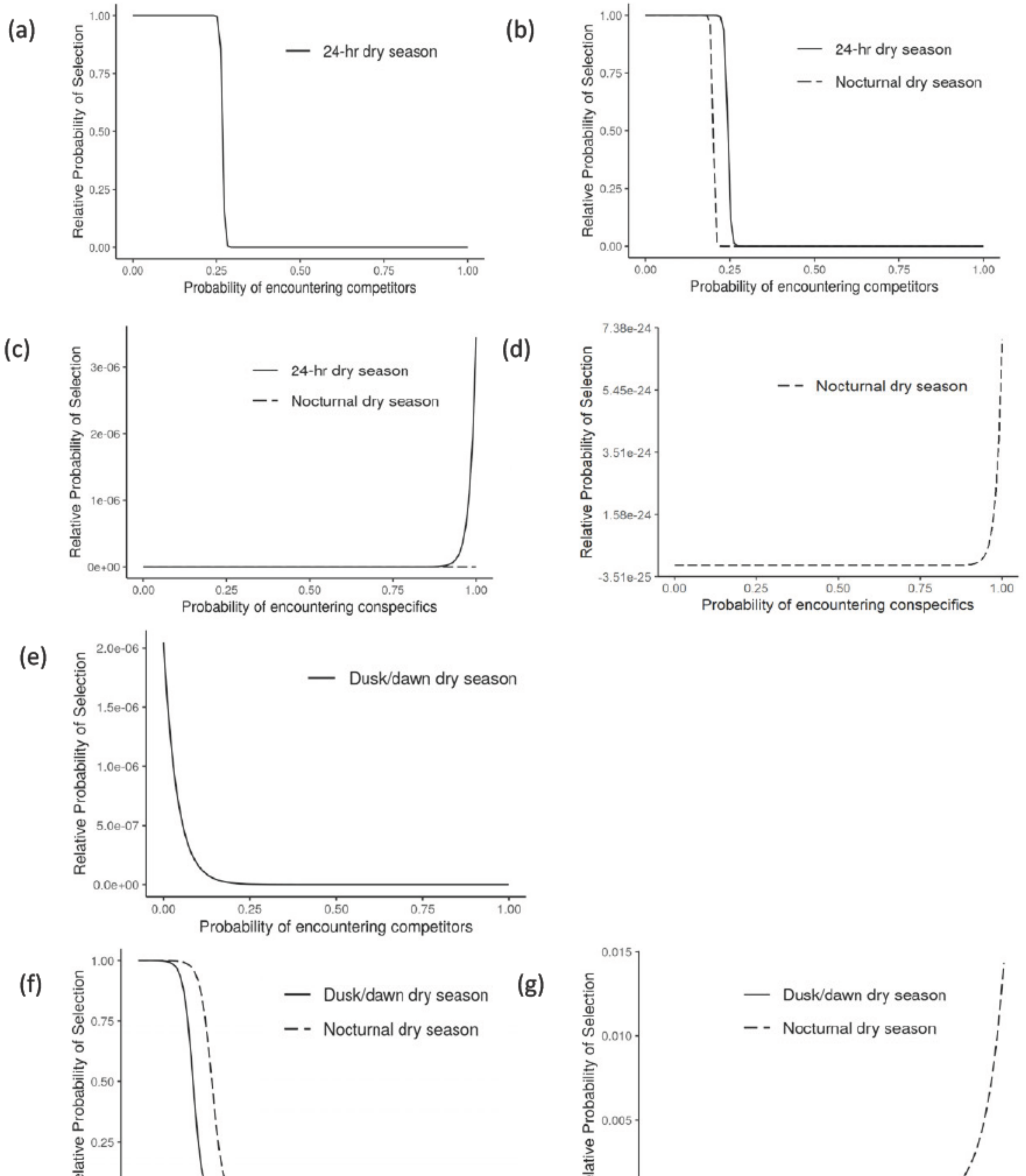

Figure 3.7. Relative probability of selection by lions indicated from RSF models (a-d) during 24-hour (18h00-18h00) and nocturnal (18h00-6h00 and 17h00-8h00) periods, and indicated from SSF models (e-g) during nocturnal (18h00-6h00 and 17h00-8h00), and dusk/dawn (19h00-21h00 / 4h00-6h00) periods. RSF models: probability of encountering (a) competitors in the Etosha National Park, Namibia; (b) competitors, or (c, d) conspecifics in the Chobe National Park and Linyanti Conservancy, Botswana. SSF models: probability of encountering (e) competitors in the Etosha National Park, Namibia; (f) competitors, or (g) conspecifics in the Chobe National Park and Linyanti Conservancy, Botswana.

Table 3.5. Comparison of selection for or against significant predictors associated with landscape features from (a) resource selection function (RSF) and (b) step selection function (SSF) models for lion groups from the Etosha National Park, Namibia, the Chobe National Park and Linyanti Conservancy, and the NG32[†] in Okavango Delta, Botswana. 24 hour periods (18h00-18h00), nocturnal periods (18h00-6h00 Etosha, and 17h00-8h00 Botswana groups), dusk/dawn periods (19h00-21h00 and 4h00-6h00) for the dry and wet seasons.

(a)

Lion group	**Period**	**Season**	**Selection**	**Landscape features**
Etosha	24 hour	Dry	For	NDVI values: -0.1 – 0.2, higher probabilities of site-attracted foragers to old anthrax carcass sites, cropland
			Against	shrubland
		Wet	For	NDVI values: -0.1 – 0.2, higher probabilities of site-attracted foragers to old anthrax carcass sites, grassland, vegetated wetland, settlement
			Against	
	Nocturnal	Dry	For	<5 km to seasonal water, higher probabilities of site-attracted foragers to old anthrax carcass sites
			Against	
		Wet	For	higher probabilities of site-attracted foragers to old anthrax carcass sites
			Against	
Chobe/ Linyanti	24 hour	Dry	For	>15 km to anthropogenic features, woodland, closed shrubland
			Against	
		Wet	For	<2 km to roads, woodland, open shrubland, closed & open grassland, floodplain, cropland
			Against	
	Nocturnal	Dry	For	NDVI values: >0.5, <1 km to seasonal water, woodland, closed shrubland
			Against	
		Wet	For	<2 km to roads, woodland, closed shrubland, closed & open grassland, wetland, cropland, settlement
			Against	floodplain
(NG32) Okavango Delta	24 hour	Dry	For	>2 km to seasonal water, woodland, closed shrubland,
			Against	open shrubland, wetland
		Wet	For	NDVI values: -0.3 – 0.3, >2 km to seasonal water, woodland
			Against	wetland
	Nocturnal	Dry	For	NDVI values: -0.3 – 0.3, >2 km to seasonal water, woodland, closed & open shrubland, open grassland, cropland
			Against	wetland
		Wet	For	NDVI values: -0.3 – 0.3, >2 km to seasonal water, woodland, closed & open shrubland, open grassland, wetland, cropland
			Against	

(b)

Lion group	**Period**	**Season**	**Selection**	**Landscape features**
Etosha	Nocturnal	Dry	For	<3 km to anthropogenic features, <5 km to available carcasses
			Against	
		Wet	For	<2 km to seasonal water,
			Against	
	Dusk/dawn	Dry	For	higher probabilities of site-attracted foragers to old anthrax carcass sites
			Against	
		Wet	For	<2 km to seasonal water,
			Against	
Chobe/ Linyanti	Nocturnal	Dry	For	>15 km to anthropogenic features, <2 km to roads
			Against	
		Wet	For	<2 km to permanent water, >15 km to anthropogenic features, <2 km to roads
			Against	
	Dusk/dawn	Dry	For	<2 km to roads
			Against	
		Wet	For	<2 km to seasonal water, <2 km to roads
			Against	

[†] *There were no significant predictors influencing the movements of Okavango Delta's NG32 lions.*

3.5. Discussion

The seasonal ranges of lions, and the larger ranges found in the drier ecosystem of Etosha concurs with other studies (Kittle et al. 2016, Zehnder et al. 2018). In this study, lion core areas were larger in arid systems than they were in mesic systems, comparable to the findings of Funston (2011) which reported unusually large home ranges in lions from the semi-arid Kgalagadi. Lions also exhibited larger ranges in the wet season in this present study, except in the Okavango Delta where they are constrained by the available space as a result of the changing floods, similar to Kotze et al. (2018). Constrained by the river to the north which acts as a natural barrier, and surrounded by human settlements and a heavily used tar road that cuts through the park, lions in Chobe experienced a higher degree of overlap within their home ranges than lions spread out at low densities over a large area in Etosha. Despite the spatial constraints in the free-ranging areas of Botswana, male lions adhered to the territorial behaviour of males in that their home ranges never intersected with each other, comparable to male lions from the vast areas of the Kalahari (Zehnder et al. 2018). Thus, in ecosystems currently experiencing human encroachment, such as within Transfrontier Conversation Areas (Watson et al. 2015), lions are at risk of either being relegated into habitats where they are subjected to increased competitive interactions from inter- and intragroups, or face substantial risk of conflict with humans (Di Minin et al. 2021), thereby exerting pressures on lion survival and fitness (Creel et al. 2013, Yiu et al. 2019).

Furthermore, our findings indicate that intra- and interspecific interactions influence lion habitat selection and movements during the dry season, in that lions used areas within their home range with a lower probability of competitors (spotted hyenas). This corresponds with the findings of other studies which have reported agonistic interactions among lions and spotted hyenas (Cooper 1991, Honer et al. 2002, Trinkel & Kastberger 2005, Périquet et al. 2015, Lehmann et al. 2017), which has resulted in the localized avoidance of spotted hyenas by lions (Périquet et al. 2021). Similarly, re-introduced lions altered their habitat selection patterns in response to competitive interactions among different lion prides (Yiu et al. 2019). However, our results demonstrated lions from Chobe used areas with a higher probability of conspecifics, whereas Etosha lions did not. Interestingly though, lions were within distances <5 km to conspecifics more often in Etosha than in Chobe. This difference in response may be the result of differences among habitats and areas with Etosha nearly twice as large as Chobe, and with more than twice the density of lions (Riggio et al., 2013; Funston, pers. comm). A caveat to note, however, is the likelihood that some of our collared groups on the periphery of the study area presumably interact with uncollared individuals beyond the border of our delineated study area. Thus, our findings may be biased towards the groups found in the middle of our study sites, as lion movement responses to uncollared individuals on the border of study sites may dilute some of the results for the groups on the periphery of the study area.

Male and female lions were found to have higher encounter frequencies in ecosystems with open habitat structures (i.e., Serengeti) than in closed habitat structures (i.e., Kruger National Park) (Funston et al. 1998). Perhaps when faced with a choice of either/or when selecting habitats or areas for movement, lions are preferentially selecting for areas with a higher probability of conspecifics as this would also inextricably be areas with a lower probability of competitors (Cooper 1991, Lehmann et al. 2017, Périquet et al. 2021). Most likely, lions are actively selecting for, and choosing to move towards areas with higher probabilities of conspecifics to maintain the sociality within a fission-fusion network, as has been noted in other studies through the formation and maintenance of subgroups (Kotze et al. 2018, Mbizah et al.

2020). Mosser and Packer (2009) demonstrated the benefits of living in groups for lions, in that larger prides gained and maintained access to the highest quality habitats, and had improved female fitness. Additionally, lions exhibit unique fission/fusion strategies in response to differences in inter-group interactions which may contribute to differences in the fitness of the individual (Packer et al. 1990, 2005, Yiu et al. 2019).

Conversely, lion habitat selection and movements in the wet season were not affected by intra- and interspecific interactions. This lack of a response is likely the result of a seasonal expansion in lion home ranges during periods of rainfall in the wet season (Kittle et al. 2016, Zehnder et al. 2018). This effectively spreads individuals occurring at low densities over a much larger area, thus decreasing the potential for interaction by reducing the probability of encountering other individuals (Linnell & Strand 2000, Trinkel & Kastberger 2005). These findings of a seasonal effect on lion habitat selection and movement responses, to select for areas with low probabilities of competitors, has important ramifications in light of the global trend towards a warmer world. The impacts of climate change has been linked to a decrease in lion densities through the reduction of prey biomass (Ogutu & Dublin 2004, Trinkel 2013), and shifts in lion ranges (Tuqa et al. 2014). With increases in temperatures and droughts brought on by climatic variability, the influences of inter- and intraspecific interactions on lion movements and habitat selection are likely to be amplified (Parmesan & Yohe 2003, Chen et al. 2011, Tuqa et al. 2014, Lenoir & Svenning 2015, Wiens 2016). Restricted to protected areas which are becoming increasingly fragmented, such effects may potentially drive lions outside reserve boundaries and into human dominated landscapes resulting in escalated conflicts, which poses a challenge for lion conservation (Kissui 2008, Creel et al. 2013, Di Minin et al. 2016, 2021, Weise et al. 2018).

Moreover, lion spatial patterns are largely food dependent, and are positively correlated to prey densities and prey biomass (Spong 2002, Hayward & Hayward 2007, Hayward & Slotow 2009). Despite Chobe lions using, and choosing to move through, areas that were far from anthropogenic sources, they also used, and consistently chose shorter steps closer to roads. Lions are likely attracted to roads as movement conduits, especially when travelling through denser vegetated environments, as was seen in North American wolves (*Canis lupus*) (Latham et al. 2011, Dickie et al. 2016), and African wild dogs (*Lycaon pictus*) (Abrahms et al. 2015). Our results indicate that lions consistently used land cover types that corresponded to shrub, grassland, and floodplains. As opportunistic stalk-and-ambush predators (Schaller 1972), lions frequent areas with landscape characteristics that increase the catchability of prey such as dense cover, embankments, and watering holes (Hopcraft et al. 2005, Kittle et al. 2016). Thus, lion response to land cover types is presumably a result of the need to search for, and obtain, resources. Our results also demonstrated that Etosha lions consistently used, and preferred to move through anthrax risk areas which possess a higher probability of foraging ungulates attracted to sites of previous anthrax carcasses (Turner et al. 2014). In the wet season, nearly all of our collared lions in Etosha shifted their home ranges either to encompass parts of the anthrax endemic area, or to different locales within the anthrax endemic area. In addition, the range of a lion initially outside of the anthrax endemic area also shifted to the savanna grassland environment, which is associated with an increase in anthrax ingestion in herbivores during the wet season (Turner et al. 2013). Further still, the home ranges of three lionesses', embedded within the anthrax endemic area, contracted instead of expanding as is typical of lion ranges in the wet season during this study and in other areas (Kittle et al. 2016, Zehnder et al. 2018). This response is likely driven by the potential of a resource-rich area, as the wet season in Etosha coincides with the anthrax season, and results in a prevalence of anthrax infected carcasses (Getz 2011). Although one of the lionesses was a lactating female with young cubs, which likely accounted for the reduction in her home range (Maruping-Mzileni et al. 2020), the home ranges of the other two lionesses presumably contracted in the wet season due to the proximity of a rich resource base within the central region of the anthrax endemic area. This behavioural plasticity has been observed in other carnivores with access to surplus anthropogenic food resources (Beckmann & Berger 2003), including a reduction in carnivore home ranges with access to refuse pits (Gilchrist & Otali 2002, Kolowski & Holekamp 2008, Gould & Andelt 2013).

The presence and densities of waterholes in semi-arid environments also contribute strongly to influence lion movements and spatial patterns (Valeix et al. 2010, Funston 2011). We found distance to water as a driver of lion space use patterns in all localities, although the effects were not homogenous. Lions in Etosha selected steps closer to seasonal water sources during the wet season, however, lions elected to move further from seasonal water and closer to anthropogenic features during the dry season. This is likely a result of the network of park infrastructure (i.e., anthropogenic features) which services the permanent water-holes in Etosha. During the dry season in Etosha, much of these pumped water-holes attract and sustain large aggregations of diverse prey taxa, providing lions and other carnivores with a regular and steady stream of potential food. Likewise, Valeix et al. (2010) found that lions frequented water holes in arid and semi-arid environments not only to obtain drinking water, but also to increase the potential for obtaining food resources as prey species aggregate around water-holes. Similarly, our results indicated that lions in Chobe moved towards seasonal water during dusk/dawn periods in the wet season, despite selecting to be in close proximity to permanent water (i.e., the river) during the night. Ungulate prey in northern Botswana typically migrates away from the river during the wet season, when they frequent seasonal water holes (Sianga et al. 2017). As Chobe lions were observed to concentrate their hunting efforts during crepuscular periods in this study, it is likely that the intended movement of lions away from an area of permanent water towards locations of seasonal water is not a result of requiring access to water, but rather to access the potential prey that visits these seasonal water areas (Davidson et al. 2013, Kittle et al. 2016).

Finally, the failure of our step-selection models to reveal significance in any of the predictors explaining for the movement of Okavango lions lends support for the inclusion of additional variables in the modelling process. As a group-living social carnivore, lions exhibit coordinated movements among individuals (Benhamou et al. 2014), engage in cooperative hunting (Scheel & Packer 1991), cooperative defense of kills (Cooper 1991) and territories (Heinsohn et al. 1996), while functioning as a fission-fusion society (Mbizah et al. 2019). Since the variables associated with inter- and intraspecific interactions were observed to consistently improve the models for both RSFs and SSFs for the Etosha and Chobe populations, this could potentially be an area of further research for the lions of Okavango. Behavioural variants among lions likely occurs as a function of the available habitat and seasonal effects, which has important implications for conservation (Kotze et al. 2018, Yiu et al. 2019). We have found the movement behaviour of Okavango lions differs from the behaviour of lions in other areas, in that they select for areas away from seasonal water as they are constrained by the available areas due to encroaching flood waters. Therefore, this presents a unique challenge in determining the underlying factors that dictate lion movements within the Delta ecosystem. Increasing threats to the Delta system caused by human activities such as agricultural and irrigation practices (Kgathi et al. 2006), in combination with the environmental impacts of climate change, are likely to disrupt the ecology of an apex predator within these areas.

3.6. Conclusions

Our results suggest that the potential for interaction with spotted hyenas during the dry season drives lions to select for areas with low hyena probabilities, and to select for steps further away from high hyena probabilities. Our results have implications for the conservation planning and reserve design of lions, to not only ensure that different environmental characteristics are incorporated within lion habitats, but also that such habitats allow for movements that may mitigate the effects of inter- and intraspecific interactions on lion space use patterns (Trinkel & Kastberger 2005, Yiu et al. 2019, Périquet et al. 2021). The conservation of lions has long relied on designated, demarcated protected areas which reduces the potential for lion interaction with humans. Hence, keeping lions away from potential conflict with humans is a conservation priority. Nonetheless, it ignores not only the potential effects of environmental and landscape changes that may occur as a result of climatic variability (Trinkel 2013, Tuqa et al. 2014), but also discounts the effects of competitive interactions both among lions and with other sympatric predators, which may impose a greater influence on lion behaviour than the environment alone (Kotze et al. 2018, Périquet et al. 2021).

Therefore, and ideally, the maintenance of large enough protected areas or the linking of several smaller reserves with the use of wildlife corridors away from the pressures of anthropogenic influences, is a conservation priority for lions who share their ranges with spotted hyenas. However as wild lands become increasingly fragmented and interspersed with human activities, strong resistance is likely to ensue when attempting to establish wildlife corridors for the protection of carnivores. Thus, limiting the types and amounts of human activities seasonally, or during periods of droughts, will become a crucially important tool for reducing the impacts on wildlife, especially when carnivores move outside of protected areas into human-use landscapes where the potential for conflict with humans becomes amplified (Woodroffe & Frank 2005, Ogutu et al. 2005, Di Minin et al. 2016). Wildlife managers will need to account for not only environmental heterogeneity, but also take into consideration the influences of competitive interactions that can impact lion movement behaviour, when designing and managing protected areas, and in constructing wildlife corridors when linking smaller reserves into larger conservation areas.

3.7. References

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3.8. Supplementary materials

Supplementary materials to Chapter 3 Results:

Lion range use, movement metrics and activity patterns

The net-squared displacement (NSD) over 24-hour periods for each lion indicates that individuals from both ecosystems typically exhibited a mixed type movement behaviour that consists of home range maintenance with frequent short-term migrations (Bunnefeld et al., 2011). However, one female lion (BE-35678) from the Linyanti Conservancy in Botswana exhibited a dispersal event towards the end of her net-squared displacement record (see right side of chart, Appendix S3.2.1, Supporting Information).

Our findings revealed that Etosha lions had overall significantly higher activity measures than lions from Botswana (mean ± SE: Etosha 35.17 ± 15.26 AMVs, Botswana 27.63 ± 20.35 AMVs, $t = 2.53$, df = 5.4, $p < 0.05$), despite moving at similar speeds (mean ± SE: Etosha 0.183 ± 0.09 m/s, Botswana 0.147 ± 0.12 m/s, $t = 1.32$, df = 12.4, $p > 0.05$; see Appendix S3.2.4; Table S3.2.1, Supporting Information). Lions from Etosha had larger mean step lengths and net-squared displacements than lions from Botswana during nocturnal periods (mean ± SE step lengths: Etosha 294.72 ± 133.61 m, Botswana 208.08 ± 166.54 m, $t = 2.19$, df = 13.8, $p < 0.05$; NSD: Etosha 13.10 ± 6.58 km^2, Botswana 5.21 ± 4.55 km^2, $t = 4.30$, df = 12.5, $p < 0.001$; see Appendix S3.2.5; Table S3.2.1, Supporting Information). Lions from both ecosystems characteristically exhibited increased step lengths and net-squared displacements over nocturnal periods between sunset and sunrise than diurnal periods between sunrise and sunset, for both the wet and dry seasons (mean ± SE step length: Etosha, nocturnal 1965.04 ± 559.44 m, diurnal

560.77 ± 310.50 m, $t = -12.89$, df = 14.0, $p < 0.0001$; Botswana, nocturnal 1281.79 ± 643.63 m, diurnal 505.42 ± 362.29 m, $t = -4.44$, df = 5.2, $p < 0.01$; NSD: Etosha, nocturnal 8.25 ± 6.05 km^2, diurnal 2.56 ± 2.16 km^2, $t = -6.29$, df = 13.0, $p < 0.0001$; Botswana, nocturnal 2.94 ± 3.23 km^2, diurnal 1.13 ± 1.36 km^2; $t = -2.77$, df = 8.0, $p < 0.05$; Appendix S3.2.5; Table S3.2.1).

During the nocturnal period, the dry season step lengths of Etosha male lions increase as the night progresses (mean ± SE 18h00-0h00: 304.33 ± 269.00 m, 0h00-6h00: 371.04 ± 336.04 m, $t = -3.96$, df = 2.5, $p < 0.05$; Appendix S3.2.5.c). Similarly, Etosha female lions have larger step lengths in the dry season during the period of the darkest part of the night to the morning twilight (mean ± SE 18h00-0h00: 273.75 ± 205.21 m, 0h00-6h00: 337.38 ± 227.70 m, $t = 2.51$, df = 5.7, $p < 0.05$; Appendix S3.2.5.c). Conversely, lions from Botswana exhibited a more crepuscular pattern, with larger step lengths during two periods of the night, from sunset to twilight end (18h00 – 20h00) and from late night to sunrise (3h00 – 7h00; Appendix S3.2.5.c). Although, lions in Botswana appeared to have larger step lengths in the early period of the night during the wet season with larger step lengths in the late period of the night during the dry season (Appendix S3.2.5.c), we found no significant seasonal differences between the two periods for Botswana lions. Moreover, Etosha lions demonstrated less tortuous movements than Botswana lions during nocturnal periods of the dry season (mean ± SE: Etosha 0.018 ± 0.85, Botswana -0.068 ± 0.86, Watson's test statistic: 0.177, $0.05 < p < 0.10$; see Appendix S3.2.6.a and Table S3.2.1, Supporting Information). Overall, Etosha lions were consistently more directional than Botswana lions in their nocturnal movements, with the Watson's test of homogeneity indicating significance for the following time intervals: 22h00-23h00, 1h00-2h00, 3h00-4h00 (Watson's test statistic: 0.215, 0.204, 0.205, all p-values < 0.05), and for 4h00-5h00 (Watson's test statistic: 0.161, $0.05 < p < 0.10$; see Appendix S3.2.6.b, Supporting Information). Conversely, Botswana lions presented with more directional movements only for the early period of the night (19h00 – 20h00, Watson's test statistic: 0.193, p < 0.05; Appendix S3.2.6.b).

The relationship between lion age and home range/core area size were not significant (Spearman's correlation: home range 0.46, core areas 0.37; adjusted R^2= home range 0.01, core areas 0.12, all p-values > 0.05). Similarly, the relationship between lion body condition scores and home range size was insignificant (Spearman's correlation: -0.14; adjusted R^2 = -0.06, p > 0.05). However, there was a significant two-way interaction between season and body condition scores on the traveling speed and path tortuosity of Etosha lions during dusk/dawn periods (F = 25.38, p < 0.05; F = 19.65, p < 0.05, respectively; Table S3.2.2d), whereas there was only a seasonal effect on the nocturnal travelling speed of lions with different body condition scores from Botswana (F = 18.57, p < 0.05; Table S3.2.2d). In addition, the relationship between the size of the lion pride and home range size were also insignificant (Spearman's correlation: -0.11, adjusted R^2 = -0.05, p > 0.05).

Furthermore, male lions have larger nocturnal mean step lengths and net-squared displacements than females in Etosha (mean ± SE step length: males 9081.58 ± 3554.94 m, females 7652.30 ± 1715.24 m, t = 2.64, df = 7.0, p < 0.05; NSD: males 17.72 ± 25.50 km^2, females 11.03 ± 8.39 km^2, t = 3.03, df = 3.7, p < 0.05), whereas we found no differences between the sexes in Botswana (see Appendix S3.2.7 and Table S3.2.2a, Supporting Information). Although we found male lions from the Okavango Delta had considerably smaller nocturnal step lengths and net-squared displacements than the single male from Chobe (mean ± SE step length: Okavango 3838.21 ± 1553.28 m, Chobe 5603.85 ± 2541.85 m, t = -3.13, df = 7.3, p < 0.05; NSD: Okavango 3.73 ± 3.86 km^2, Chobe 19.45 ± 21.48 km^2, t = -3.89, df = 4.3, p < 0.05; Table S3.2.2b), we note the low statistical power of such a small sample size. In addition, female lions in Etosha have more tortuous movements than male lions during nocturnal periods of the wet season (mean ± SE: females 0.203 ± 0.76, males 0.043 ± 1.01, Watson's test statistic: 0.192, $p < 0.05$). Conversely, male lions in Botswana demonstrated more tortuous movements than female lions during 24-hour periods of the wet season (mean ± SE: males -0.641 ± 1.46, females 0.560 ± 0.93, Watson's test statistic: 0.177, $0.05 < p < 0.10$; see Appendix S3.2.7, and Table S3.2.2a, Supporting Information).

Older lions (> 10 years, $n = 4$) and young lions (< 5 years, $n = 5$) have larger mean step lengths during nocturnal and 24-hour periods than adult lions (5-10 years, $n = 10$) (mean ± SE nocturnal: old lions 7112.75 ± 760.53 m, adult lions 4881.98 ± 460.59 m, $t = 4.95$, df = 63.0, $p < 0.0001$; adult lions 4881.98 ± 460.59 m, young lions 6975.76 ± 944.17 m, $t = 3.66$, df = 27.4, $p < 0.005$; 24-hour: old lions 6402.21 ± 710.03 m, adult lions 5078.80 ± 389.25 m, $t = 3.52$, df = 79.0, $p < 0.001$; adult lions 5078.80 ± 389.25 m, young lions 6577.31 ± 920.76 m, $t = -3.48$, df = 36.8, $p < 0.005$; see Table S3.2.2c, Supporting Information). Although the tortuosity of older lions differed from young and adult lions which were more similar (see Appendix S3.2.8, Supporting Information), young males ($n = 2$) had more tortuous movements than young females ($n = 3$) during nocturnal periods (mean ± SE: young males 0.064 ± 1.02, young females -0.044 ± 1.32, Watson's test statistic: 0.153, $0.05 < p < 0.10$; Table S3.2.2c). In addition, the mixed ANOVA resulted in significant differences for the net-squared displacements among the age categories of Etosha lions (mean ± SE NSD: young 19.40 ± 19.09 km^2, adult 26.42 ± 42.46 km^2, old 22.07 ± 18.47 km^2, F = 28.87, $p < 0.05$). Furthermore, there was also a significant interaction between sex and age categories for the net-squared displacements of Etosha lions, with males consistently having larger net-squared displacements than their counterparts (mean ± SE NSD: young male 21.90 ± 1.82 km^2, young female 18.14 ± 1.65 km^2, adult male 37.59 ±

2.88 km^2, adult female 20.84 ± 2.12 km^2, old male 37.66 ± 4.40 km^2, old female 16.87 ± 1.46 km^2, F = 27.86, $p < 0.05$).

Pride demographics contribute to differences in female lion movement behaviours, specifically the size of the pride and whether the female is with or without cubs. Females with cubs ($n = 7$) from either large prides (10 or more individuals) or small prides (less than 5 individuals) have smaller nocturnal net-squared displacements (mean ± SE: 6.73 ± 5.75 km^2, and 12.58 ± 11.84 km^2, respectively), while females without cubs ($n = 6$) from large and small prides had larger net-squared displacements (mean ± SE: 13.99 ± 15.24 km^2, $t = 3.66$, df = 2.9, $p < 0.05$; and 19.31 ± 15.51 km^2, $t = 15.70$, df = 1.5, $p < 0.05$, respectively; see Appendix S3.2.9, and Table S3.2.2e, Supporting Information). Females without cubs from large prides ($n = 2$) have higher net-squared displacements (mean ± SE: 13.99 ± 15.24 km^2) than females without cubs from smaller sized prides of between 6-9 individuals ($n = 2$, mean ± SE: 4.46 ± 6.04 km^2; $t = 5.10$, df = 2.0, $p < 0.05$; Table S3.2.2e). Regardless of pride size, females with cubs ($n = 7$) tend to have smaller net-squared displacements than females without cubs ($n = 6$) (mean ± SE: with cubs 12.16 ± 5.70 km^2, without cubs 17.12 ± 8.19 km^2, F = 2769.51, $p < 0.05$). Moreover, females with cubs from large prides ($n = 4$) tend to have more tortuous movements during nocturnal periods (mean ± SE: 0.108 ± 1.24) than females with cubs from smaller prides ($n = 3$, mean ± SE: -0.032 ± 1.23; Watson's test statistic: 0.167, $0.05 < p < 0.10$; Table S3.2.2e).

We found lion activity to be relatively consistent among various landcover classes inside protected areas, with the lowest average activity for Botswana lions occurring in woodland habitats (mean ± SE: 15.10 ± 1.73 AMVs) and the highest activity occurring within human settlements (mean ± SE: 61.16 ± 10.13 AMVs; Fig. 3.3; see Table S3.2.4, Supporting Information). The lowest and highest average activity for Etosha lions occurred in the pan (mean ± SE: 23.37 ± 0.48 AMVs) and among human settlements respectively (mean ± SE: 49.08 ± 6.9 AMVs; Fig. 3.3; Table S3.2.4). Lion activity within the protected areas (excluding croplands and settlements) were higher for Etosha individuals than they were for individuals from Botswana for both the nocturnal and dusk/dawn periods (mean ± SE nocturnal: Etosha 34.75 ± 5.96 AMVs, Botswana 24.68 ± 7.81 AMVs, $t = 3.92$, df = 59.9, $p < 0.001$; dusk/dawn: Etosha 34.24 ± 6.86 AMVs, Botswana 27.12 ± 9.18 AMVs, $t = 2.15$, df = 54.6, $p < 0.05$; Table S3.2.4). However, when outside of protected areas and in human-use landscapes, lion activity was seen to significantly increase when inside of human settlements and Namibian croplands during dusk/dawn periods (mean ± SE: protected areas 32.21 ± 5.28 AMVs, settlements & croplands 68.34 ± 14.85 AMVs, $t = 3.73$, df = 12.9, $p < 0.01$). In addition, lions moved faster and when inside of human-used areas (mean ± SE: protected areas 0.180 ± 0.03 m/s, settlements & croplands 0.540 ± 0.08 m/s, $t = -3.48$, df = 11.3, $p < 0.005$). Although lions exhibited mostly directional movements when in human-use areas during nocturnal and dusk/dawn periods for both ecosystems (see Appendix S3.2.10, Supporting Information), the Watson's test indicated that within grassland habitats, Botswana lions had significantly more tortuous paths than Etosha lions during both the nocturnal (mean ± SE: Etosha 0.028 ± 0.60, Botswana -0.023 ± 0.88, Watson's test statistic: 0.222, $p < 0.05$) and dusk/dawn periods (mean ± SE: Etosha 0.054 ± 0.75, Botswana -2.547 ± 1.06, Watson's test statistic: 0.204, $p < 0.05$; Table S3.2.4).

Furthermore, lions exhibited markedly different seasonal responses and temporal differences between the two ecosystems with respect to the lunar cycle. During the dry season, lions had higher overall mean activity on new moon nights with Botswana lions peaking during dusk and dawn periods (Fig. 3.4). Etosha lions have their highest activity during the darker periods of the night, from nadir to night-end for new moon nights and during night end to dawn on full moon nights (see Table S3.2.3a, Supporting Information). Conversely, mean activity was interchangeable between full and new moon nights for the wet season, with Botswana lions peaking at dusk during full moon nights and decreasing to dawn. However Etosha lions continued to exhibit their highest activity during nadir to night-end but on full moon nights with relatively consistent mean activity throughout the nocturnal period from dusk to dawn for new moon nights (Fig. 3.4; Table S3.2.3a).

The mixed ANOVA resulted in significant differences in the activity, speed, and tortuosity among the nocturnal and dusk/dawn periods of Etosha lions across the various moon phases of new/full moon, waxing/waning crescent, first/last quarter, and waxing/waning gibbous (nocturnal: activity $F = 11.33$, $p < 0.0001$; speed $F = 16.36$, $p < 0.0001$; tortuosity $F = 34.10$, $p < 0.0001$; dusk/dawn: activity $F = 4.91$, $p < 0.001$; speed $F = 13.69$, $p < 0.0001$; see Table S3.2.3b, Supporting Information). In addition, there was also a significant interaction between sex and moon phase for the activity and speed of Etosha lions during nocturnal and dusk/dawn periods (nocturnal: activity $F = 5.71$, $p < 0.001$; speed $F = 13.01$, $p < 0.0001$; dusk/dawn: activity $F = 2.92$, $p < 0.05$; speed $F = 11.16$, $p < 0.0001$; Table S3.2.3b).

During nocturnal periods of the dry season, Etosha lions had more tortuous movements during new moon nights than full moon nights (mean ± SE: new moon 0.351 ± 0.86, full moon 0.013 ± 0.84, $F = 22.99$, $p < 0.05$; Table S3.2.3b). Although males from Etosha had more tortuous movements than females (mean ± SE: males -0.096 ± 0.73, females 0.012 ± 0.34, $F = 33.19$, $p < 0.05$), the interaction between sex and new/full moon indicated that the tortuosity of males and females in Etosha differed between new and full moon nights (mean ± SE new moon: males 1.133 ± 0.24, females 0.171 ± 0.96; full moon: males -0.081 ± 0.13, females 0.037 ± 0.95; $F = 14.80$, $p < 0.05$). In addition, there also existed interactions between sex and moon phase for Etosha lions during both the nocturnal and dusk/dawn periods. Thus, the tortuosity of male and female lions in Etosha differs among the phases of the lunar cycle (nocturnal: F = 29.84, $p < 0.0001$; dusk/dawn: F = 2.82, $p < 0.05$).

Alternatively, the wet season tortuosity of Botswana lions differed across moon phases during the dusk/dawn period, with mostly directional movements during waxing gibbous and more tortuous movements during first quarter and waning gibbous phases (F = 2.51, $p < 0.05$; Table S3.2.3b). Moreover, Botswana lions also had higher activity and travelled at faster speeds on new moon nights than they did on full moon nights during nocturnal periods of the dry season (mean ± SE activity: new moon 30.28 ± 20.51 AMVs, full moon 26.42 ± 19.85 AMVs, F = 20.30, $p < 0.05$; speed: new moon 0.159 ± 0.09 m/s, full moon 0.124 ± 0.08 m/s, F = 8.21, $p < 0.05$; Table S3.2.3b). In addition, Botswana lions also travelled at faster speeds on new moon nights during dusk/dawn periods (mean ± SE speed: new moon, 0.163 ± 0.12 m/s; full moon, 0.134 ± 0.11 m/s; F = 10.90, $p < 0.05$; Table S3.2.3b).

Intra- and interspecific interactions

During dusk/dawn periods, lions from both ecosystems showed increased activity when at closer distances to each other than when they were closer to spotted hyenas (mean ± SE Etosha: 100-200 m to conspecifics 53.66 ± 20.30 AMVs, to competitors 23.32 ± 20.50 AMVs, t = -3.77, df = 8.9, $p < 0.01$; Chobe: 500-600 m to conspecifics 45.55 ± 36.94 AMVs, to competitors 29.50 ± 0.10 AMVs, t = -80.71, df = 1, $p < 0.01$; see Table S3.4a, Supporting Information). Etosha lions also travelled faster when at close distances to conspecifics than when close to competitors (mean ± SE: 100-200 m to conspecifics 0.412 ± 0.14 m/s, to competitors 0.082 ± 0.10 m/s, t = -6.78, df = 6.7; 200-300 m to conspecifics 0.337 ± 0.14

m/s, to competitors 0.155 ± 0.12 m/s, t = -3.78, df = 6.8; 300-400 m to conspecifics 0.302 ± 0.16 m/s, to competitors 0.085 ± 0.08 m/s, t = -4.96, df = 5.9; 400-500 m to conspecifics 0.396 ± 0.15 m/s, to competitors 0.135 ± 0.10 m/s, t = -3.25, df = 10.4; 700-800 m to conspecifics 0.319 ± 0.16 m/s, to competitors 0.162 ± 0.13 m/s, t = -3.62, df = 9.6; all p-values < 0.01; Table S3.4a).

In addition, lions exhibited lower average activity when inside the core area of conspecifics and higher average activity when inside the core area of competitors in relation to when they were outside of conspecific and competitor core areas (Fig. 3.6; see Table S3.4b, Supporting Information). However, the mixed ANOVA resulted in significance only for the activity of Chobe lions with respect to competitor core areas during dusk/dawn periods (mean ± SE inside competitor core areas: 34.29 ± 29.38 AMVs, outside competitor core areas: 30.66 ± 25.08 AMVs; $F = 51.31$, $p < 0.05$; Table S3.4b).

Habitat use selection and movement

Lions from the Etosha National Park, the Chobe National Park and Linyanti Conservancy, Botswana selected habitats within their home range with a lower probability of competitors. Lions from Chobe also selected for areas with a higher probability of conspecifics. In addition, lions from Etosha selected steps in areas with a lower probability of competitors during dusk/dawn periods, while selecting steps in areas with a lower probability of conspecifics during nocturnal periods. Alternatively, lions from Chobe chose to move through areas with a lower probability of competitors, but with a higher probability of conspecifics.

In addition to interaction covariates, lion responses were influenced by various landscape features. Etosha lions consistently selected for areas within their home range that had higher probabilities of site-attracted foraging ungulates for both the 24-hour and nocturnal periods of the dry and wet season (Table S3.6a; Appendix S3.3.1a). Furthermore, Lions from Etosha selected for areas within their habitats with median NDVI values (i.e., shrubland, closed grassland) during 24-hour periods for both seasons, although lions selected for different types of landcover classes between the seasons. Lions selected for shrub and crop lands in the dry season while opting for grassland, vegetated wetlands and settlements in the wet season (Table S3.6a; Appendix S3.3.1a).

Conversely, lions from Botswana consistently selected for certain landcover types within their habitats throughout both 24-hour and nocturnal periods across seasons. Lions from Chobe selected for closed and open grassland areas, while lions from the Okavango Delta selected for woodland and wetland habitats (Table S3.6a; Appendix S3.3.2a-3). Additionally, Chobe lions also selected for open shrubland, floodplains and crop lands during 24-hour periods of the wet season. Similarly to Etosha lions, Okavango lions also chose areas within their home range with median NDVI values corresponding to woodland, shrubland, open grassland and wetland across both seasons (Table S3.6a; Appendix S3.3.3). For the nocturnal period, lions from Chobe selected for closed shrubland, floodplains and settlements in both seasons, while also selecting for crop lands and wetlands in the wet season (Table S3.6a; Appendix S3.3.2a). Alternatively, Okavango lions selected for open grassland, closed/open shrublands, and croplands in both season (Table S3.6a; Appendix S3.3.3).

Furthermore, lions from both Etosha and Chobe selected for areas within their habitats closer to seasonal water sources during nocturnal periods in the dry season (Table S3.6a; Appendix S3.3.1-2a). However, Okavango lions consistently selected for areas within their home range farther from seasonal water sources (>3 km) in both periods for both seasons (Table

S3.6a; Appendix S3.3.3). In addition, for the dry season, lions from Chobe selected for areas within their habitats at farther distances from anthropogenic features during the 24-hour period, while choosing areas with NDVI values associated with increasing vegetation (i.e., closed shrublands, woodland) during nocturnal periods. Alternatively, during the wet season, Chobe lions selected for areas within their habitats closer to roads for both the 24-hour and nocturnal periods (Table S3.6a; Appendix S3.3.2a).

Lion movements in Etosha and Chobe were influenced by different landscape features, although there were no significant predictors influencing the movements of Okavango lions (Table S3.6b). In the wet season, lions from Etosha were more likely to select steps that were closer to seasonal water sources during nocturnal and dusk/dawn periods. However, in the dry season, lions selected for steps during nocturnal periods that took them farther away from seasonal water sources, but closer to anthropogenic features (Table S3.6b; Appendix S3.3.1b). In addition, Etosha lions preferred to move through areas with a higher probability of encountering site-attracted foraging ungulates during dusk/dawn periods (Table S3.6b; Appendix S3.3.1b). Similarly, lion movements in Chobe were also influenced by distance to water in the wet season (Table S3.6b; Appendix S3.3.2b). Lions in Chobe selected steps that took them closer to permanent water sources during nocturnal periods, with greater selection for steps closer to seasonal water during dusk/dawn periods (Table S3.6b; Appendix S3.3.2b). Lions also preferred to move through areas far from anthropogenic features during nocturnal periods in both seasons, and consistently selected steps closer to roads during both nocturnal and dusk/dawn periods in all seasons (Table S3.6b; Appendix S3.3.2b).

Table S3.1. Kernel density (a) and *a*-LoCoH (b) area measures for home ranges and core use areas (km^2) of lion individuals. CS = combined seasons, DS = dry season, WS = wet season. Upper panels consist of individuals from the Etosha National Park, Namibia, and lower panels consist of individuals from the Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana.

(a)

	HOME RANGE (95%)									CORE AREA (50%)								
						DRY SEASON		WET SEASON							DRY SEASON		WET SEASON	
INDIVIDUAL	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**
OK-33863	456	284	457	604	586	326	308	604	586	129	62	128	170	168	73	69	170	168
RE-33864	538	117	539	691	674	120	119	691	674	106	23.7	107	137	134	24.8	27.1	137	134
NU-33865	841	614	653	1067	1051	837	825	842	834	198	172	158	252	245	230	227	215	208
MO-33866	1192	1111	871	1440	1433	1497	1487	1130	1128	277	188	242	370	367	296	290	307	308
OJ-33867	787	415	765	937	979	443	474	937	979	168	87	160	224	221	97	103	224	224
SU-33868	667	495	646	915	872	810	726	897	868	112	74	114	159	147	159	141	162	149
OM-34308	369	131	375	487	490	131	144	487	490	87	24.2	90	116	117	25.1	28.2	116	117
LU-34308	214	185	129	241	254	212	220	195	191	29.3	27.5	33.5	36.3	34.6	34.5	32.4	49.7	48.6
OF-34309	375	436	361	418	424	433	472	418	424	87	56	87	125	119	62	67	125	119
G2-35678	329	329	127	439	424	439	424	-	-	62	62	27.7	83	83	83	83	-	-
Mean	***577***	***411***	***435***	***724***	***719***	***525***	***520***	***688***	***686***	***125***	***135***	***115***	***167***	***163***	***109***	***107***	***167***	***164***
SD	***297***	***294***	***276***	***364***	***361***	***422***	***411***	***293***	***296***	***72***	***189***	***63***	***95***	***94***	***92***	***88***	***74***	***75***
SW-33950	255	208	272	314	331	278	290	341	356	56	45.5	63	69	72	62	64	79	82
AF-34308	210	40.0	236	284	297	61	58	326	341	36.8	10.7	43.8	56	54	17.4	16.1	69	68
BE-35678	727	38.5	720	1196	1096	-	-	1196	1099	213	11.4	211	335	316	-	-	335	317
BO-35947	296	304	216	399	399	451	461	270	265	67	79	46.6	84	85	120	124	56	56
AM-36714	1032	710	1171	1378	1386	901	971	1693	1612	132	71	214	258	226	154	137	381	337
BA-36715	47.0	49.8	38.1	48.9	48.1	42.8	40.0	50	50	8.0	7.7	7.5	8.0	8.1	7.5	7.3	8.5	8.8
KW-36716	244	125	304	283	304	147	161	388	404	39.5	29.6	59	48.5	53	34.4	37.8	81	88
KB-36717	97	72	113	126	137	75	74	164	190	11.3	9.3	14.6	15.6	17.5	11.1	11.3	23.7	28.5
Mean	***363***	***193***	***384***	***504***	***500***	***279***	***294***	***554***	***540***	***70***	***33.0***	***82***	***109***	***104***	***58***	***57***	***129***	***123***
SD	***339***	***229***	***377***	***498***	***477***	***311***	***335***	***576***	***533***	***69***	***29.0***	***83***	***120***	***109***	***58***	***54***	***144***	***129***

(b)

	HOME RANGE (95%)									**CORE AREA (50%)**								
						DRY SEASON		**WET SEASON**							**DRY SEASON**		**WET SEASON**	
INDIVIDUAL	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**CS**	**DS**	**WS**	**DAY**	**NIGHT**	**DAY**	**NIGHT**	**DAY**	**NIGHT**
OK-33863	295	54	283	209	269	39.8	69	209	269	144	16.1	123	84	134	6.5	17.3	84	134
RE-33864	345	41.8	335	309	362	0.2	38.6	309	362	92	12.2	85	96	91	0.1	14.9	96	91
NU-33865	580	362	358	553	609	326	371	384	449	174	120	131	177	212	167	185	169	189
MO-33866	622	370	294	734	829	446	554	454	507	178	103	77	232	298	99	114	176	208
OJ-33867	348	105	273	265	393	41.7	101	265	393	165	33.3	98	92	160	33.8	21.6	92	160
SU-33868	484	162	375	537	503	161	228	412	423	101	46.9	99	97	106	23.1	25.1	99	106
OM-34308	221	66	233	189	244	29.5	69	189	244	91	14.4	74	68	90	11.4	18.3	68	90
LU-34308	170	150	43.8	149	210	129	167	39.0	44.7	31.1	28.6	18.5	33.9	44.2	43.3	33.7	18.6	21.5
OF-34309	327	141	254	201	256	15.1	200	201	256	104	16.1	71	91	63	5.5	27.1	91	63
G2-35678	229	229	-	220	258	220	258	-	-	55	54.5	-	78	81	78	81	-	-
Mean	***362***	***168***	***272***	***337***	***394***	***141***	***206***	***273***	***328***	***113***	***44.5***	***86***	***105***	***128***	***46.8***	***54***	***99***	***118***
SD	***153***	***118***	***98***	***199***	***200***	***150***	***160***	***131***	***140***	***50***	***38.2***	***33.1***	***57***	***77***	***53***	***57***	***48.2***	***60***
SW-33950	171	113	171	163	194	134	106	134	181	43.2	25.9	40.2	61	51	64	32.2	64	73
AF-34308	87	16.0	89	117	120	14.3	17.2	117	125	30.5	5.8	27.8	35.0	28.3	5.3	6.6	40.0	25
BE-35678	282	1.5	275	241	314	-	-	241	310	59	0.8	57	79	144	-	-	79	140
BO-35947	271	230	180	243	316	191	274	166	185	70	73	46.1	82	83	82	99	56	50
AM-36714	934	604	849	751	692	161	-	729	651	195	168	182	353	125	43.3	49	418	358
BA-36715	52	49	47.4	44.8	43	30.2	29.6	39.0	38.2	9.8	8.8	10.9	11.6	11.5	7.6	6.6	11.0	10.7
KW-36716	174	89	167	183	208	79	85	192	225	36.5	21.5	37.5	34.2	44.7	29.5	27.7	42.7	67
KB-36717	88	59	83	74	78	42.1	32.1	75	68	11.6	7.1	10.9	19.2	16.5	18.7	11.6	22.6	18.2
Mean	***257***	***145***	***233***	***227***	***246***	***93***	***91***	***212***	***223***	***57***	***38.9***	***52***	***84***	***63***	***35.7***	***33.2***	***92***	***93***
SD	***286***	***199***	***259***	***223***	***206***	***69***	***97***	***219***	***193***	***60***	***57***	***55***	***112***	***49.6***	***28.8***	***32.9***	***134***	***115***

Table S3.2.1. Movement metrics of lions from the Etosha National Park, Namibia, and the Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. Movement metrics consist of the means ± standard deviations for activity (activity monitor values [AMVs]), speed (m/s), step length (m), net-squared displacement (NSD, km^2), and path tortuosity (radian).

Metric		**Namibia**	**Botswana**
Activity (AMVs)		35.17 ± 50.6	27.63 ± 45.5
Speed (m/s)		0.183 ± 0.31	0.147 ± 0.27
30 min nocturnal step length (m)		294.72 ± 443.14	208.08 ± 372.40
12 h nocturnal step length from 4 h fixes (m)		1965.04 ± 1855.44	1281.79 ± 1439.21
12 h diurnal step length from 4 h fixes (m)		560.77 ± 1029.83	505.42 ± 810.10
12 h nocturnal NSD from 30 min fixes (km^2)		13.1 ± 20.8	6.8 ± 21.6
12 h nocturnal NSD from 4 h fixes (km^2)		8.3 ± 19.1	2.9 ± 9.1
12 h diurnal NSD from 4 h fixes (km^2)		2.6 ± 6.8	1.1 ± 3.9
18h00 – 0h00 step length (m)	Dry season – Male	285.65 ± 463.03	155.25 ± 313.71
	Wet season – Male	322.42 ± 476.53	190.25 ± 336.12
	Dry season – Female	273.94 ± 410.53	237.75 ± 396.01
	Wet season – Female	284.30 ± 391.77	233.98 ± 402.40
0h00 – 6h00 step length (m)	Dry season – Male	414.46 ± 570.83	240.70 ± 415.81
	Wet season – Male	412.59 ± 551.72	185.94 ± 358.39
	Dry season – Female	337.45 ± 455.03	254.20 ± 414.61
	Wet season – Female	292.74 ± 426.07	177.58 ± 349.11
24 h path tortuosity (4 h fixes)		0.080 ± 2.07	0.432 ± 2.41
	Dry season	0.070 ± 2.07	0.296 ± 2.33
	Wet season	-0.022 ± 2.07	0.209 ± 2.35
	Male	0.194 ± 1.98	-0.044 ± 2.63
	Female	0.029 ± 2.09	0.612 ± 2.05
Nocturnal path tortuosity (30 min fixes)		0.135 ± 1.90	0.052 ± 2.48
	Dry season	0.018 ± 1.89	-0.068 ± 2.44
	Wet season	0.151 ± 1.93	0.003 ± 2.49
	Male	0.046 ± 1.78	0.095 ± 2.46
	Female	0.172 ± 1.92	0.026 ± 2.52
Dusk/dawn path tortuosity (5 min fixes)		0.053 ± 2.43	0.847 ± 1.92
	Dry season	-0.012 ± 2.40	0.024 ± 2.01
	Wet season	0.097 ± 2.42	1.062 ± 1.85
	Male	-0.094 ± 2.33	3.067 ± 1.82
	Female	0.123 ± 2.45	0.448 ± 2.19

Table S3.2.2. Lion movement metrics according to (a) sex, (b) males from regions of Botswana (c) age, (d) body condition scores, and (e) different pride sizes with cubs from the Etosha National Park, Namibia, and the Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. Step length (m), net-squared displacements (NSD, km^2), and path tortuosity (radian) of (a) male and female lions of the dry and wet seasons; (b) of male lions from Chobe and the NG32 in Okavango Delta, and of (c) young (<5 years), adult (5-10 years), and old (>10 years) lions from nocturnal (30 min fixes) and 24 h (4 h fixes) periods. (d) Speed (m/s) and path tortuosity (radian) according to lion body condition scores during nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods of the dry and wet seasons. (e) Net-squared displacements (NSD, km^2) and path tortuosity (radian) of females from large, medium, and small prides with and without cubs during nocturnal (30 min fixes) periods. Large prides consists of 10 or more individuals, medium prides between 6-9 individuals and small prides five or fewer individuals. Values consist of the means ± standard deviations.

(a)

Period	**Sex**	**Season**	**12 h Step length (m)**		**12 h NSD (km^2)**		**Tortuosity**	
			Namibia	**Botswana**	**Namibia**	**Botswana**	**Namibia**	**Botswana**
Nocturnal periods	Male		9081.58 ± 6157.34	4532.35 ± 4741.40	17.7 ± 44.2	9.6 ± 32.8	0.046 ± 1.78	0.095 ± 2.46
		Dry season	8476.97 ± 7637.36	4504.25 ± 4042.81	22.05 ± 65.93	7.65 ± 13.80	0.062 ± 2.07	0.063 ± 2.39
		Wet season	9106.71 ± 5848.13	4428.11 ± 4976.66	17.64 ± 39.40	9.69 ± 37.44	0.043 ± 1.74	0.125 ± 2.51
	Female		7652.30 ± 4538.09	3327.61 ± 3605.74	11.0 ± 22.2	5.1 ± 13.7	0.172 ± 1.92	0.026 ± 2.52
		Dry season	7693.62 ± 4342.73	3866.30 ± 3854.98	10.11 ± 22.04	4.15 ± 11.82	0.006 ± 1.88	-0.188 ± 2.51
		Wet season	7300.80 ± 4614.17	3395.90 ± 3472.71	10.41 ± 22.28	6.16 ± 15.02	0.203 ± 2.00	-0.079 ± 2.47
24-hour periods	Male		8721.12 ± 6272.62	4648.71 ± 3676.83	32.38 ± 89.07	20.42 ± 56.72	0.194 ± 1.98	-0.044 ± 2.63
		Dry season	8324.94 ± 7931.63	4966.85 ± 3749.04	46.18 ± 145.34	21.55 ± 35.22	0.700 ± 2.08	-0.035 ± 2.52
		Wet season	8791.84 ± 5993.44	4522.34 ± 3646.05	31.69 ± 76.63	19.84 ± 63.11	0.155 ± 1.95	-0.641 ± 2.52
	Female		6914.46 ± 4103.34	4348.69 ± 3284.74	18.37 ± 33.48	9.34 ± 19.41	0.029 ± 2.09	0.612 ± 2.05
		Dry season	7069.84 ± 3858.23	5292.74 ± 3076.09	17.73 ± 33.09	6.46 ± 16.97	-0.093 ± 2.07	0.485 ± 2.02
		Wet season	6406.74 ± 4208.10	4606.11 ± 3003.38	16.44 ± 32.24	10.78 ± 20.76	-0.117 ± 2.12	0.560 ± 2.08

(b)

Period	**Botswana regions**	**12 h Step length (m)**	**12 h NSD (km^2)**	**Tortuosity**
Nocturnal periods	CNP*	5603.85 ± 5683.74	19.45 ± 48.04	0.108 ± 1.67
	NG32	3838.21 ± 3804.74	3.73 ± 9.47	-0.009 ± 1.80
24-hour periods	CNP*	3861.18 ± 3965.14	42.55 ± 82.34	-0.136 ± 1.91
	NG32	4768.75 ± 3344.75	7.58 ± 19.08	-0.040 ± 1.75

**one male lion with 5 seasons (3 dry and 2 wet)*

(c)

Age group	Gender	12 h Step length (m)		12 h NSD (km^2)		Tortuosity	
		24-hours	Nocturnal	24-hours	Nocturnal	24-hours	Nocturnal
Young		6577.31 ± 4013.50	6975.76 ± 4115.53	15.08 ± 29.32	9.48 ± 19.72	0.177 ± 2.09	-0.033 ± 2.24
	Male	8594.26 ± 5513.00	8888.59 ± 5216.11	22.80 ± 34.63	15.40 ± 25.95	0.171 ± 1.98	0.064 ± 1.76
	Female	6199.14 ± 3740.40	6617.10 ± 3969.64	13.63 ± 28.46	8.4 ± 18.67	0.179 ± 2.10	-0.044 ± 2.29
Adult		5078.80 ± 3713.24	4881.98 ± 4393.76	17.41 ± 50.43	9.04 ± 28.19	0.093 ± 2.15	0.070 ± 2.29
	Male	5254.34 ± 4038.01	5312.98 ± 4836.84	23.53 ± 63.51	11.38 ± 34.34	-0.242 ± 2.26	0.118 ± 2.43
	Female	4914.47 ± 3235.18	4478.48 ± 3699.59	11.69 ± 24.40	6.86 ± 16.16	0.235 ± 2.01	0.038 ± 2.08
Old		6402.21 ± 4078.83	7112.75 ± 4368.91	19.18 ± 36.28	11.08 ± 23.59	0.180 ± 2.09	0.057 ± 1.93
	Male	8537.69 ± 6151.20	9689.05 ± 6456.06	30.69 ± 80.36	15.98 ± 46.21	0.274 ± 1.92	0.050 ± 1.66
	Female	6188.67 ± 3908.31	6855.12 ± 4202.57	18.03 ± 31.29	10.59 ± 21.26	0.148 ± 2.10	0.060 ± 1.94

(d)

Period	Season	BCS	Speed (m/s)		Tortuosity	
			Namibia	Botswana	Namibia	Botswana
Nocturnal periods	Dry season	Low BCS	0.175 ± 0.26	0.123 ± 0.22	0.009 ± 1.72	0.114 ± 1.77
		Medium BCS	0.171 ± 0.24	0.112 ± 0.21	-0.022 ± 1.68	0.014 ± 1.79
		High BCS	0.179 ± 0.24	0.135 ± 0.21	0.023 ± 1.64	0.062 ± 1.77
	Wet season	Low BCS	0.196 ± 0.26	0.107 ± 0.21	-0.025 ± 1.59	0.000 ± 1.73
		Medium BCS	0.157 ± 0.24	0.104 ± 0.19	0.048 ± 1.71	0.001 ± 1.70
		High BCS	0.200 ± 0.29	0.122 ± 0.21	0.023 ± 1.63	0.026 ± 1.78
Dusk/dawn periods	Dry season	Low BCS	0.206 ± 0.37	0.134 ± 0.23	0.033 ± 1.85	0.114 ± 1.86
		Medium BCS	0.189 ± 0.30	0.150 ± 0.28	0.008 ± 1.80	0.032 ± 1.84
		High BCS	0.192 ± 0.31	0.187 ± 0.30	-0.005 ± 1.78	-0.006 ± 1.85
	Wet season	Low BCS	0.240 ± 0.33	0.111 ± 0.22	-0.026 ± 1.74	0.016 ± 1.85
		Medium BCS	0.174 ± 0.29	0.135 ± 0.26	-0.000 ± 1.86	0.019 ± 1.85
		High BCS	0.228 ± 0.37	0.206 ± 0.32	0.074 ± 1.75	-0.003 ± 1.81

(e)

Pride sizes	12 h NSD (km^2)		Tortuosity	
	With cubs	Without cubs	With cubs	Without cubs
Large (≥ 10)	6.73 ± 9.97	13.99 ± 21.55	0.108 ± 2.14	0.094 ± 1.82
Medium (6 – 9)	7.77 ± 11.61	4.46 ± 8.55	0.074 ± 2.07	-0.064 ± 2.33
Small (≤ 5)	12.58 ± 11.84	19.31 ± 21.94	-0.032 ± 1.74	0.009 ± 1.85

Table S3.2.3. Lion activity (AMVs), speed (m/s), and path tortuosity in relation to the lunar cycle in the Etosha National Park, Namibia, and the Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. (a) Means ± standard deviations of lion activity during the seven periods of a 24 h cycle during new moon and full moon nights. The 24 h cycle was subdivided into seven different periods. Night/nadir/night end consists of the end of evening twilight to the beginning of morning twilight divided into three equal intervals. Afternoon = noon to sundown; dusk = sundown to twilight end; dawn = beginning of morning twilight to sunrise; morning = sunrise to noon. (b) Seasonal means ± standard deviations of lion activity, speed (m/s) and path tortuosity (radian) during nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods during the eight different phases of the lunar cycle.

(a)

Season	24 h period cycle	New Moon		Full Moon	
		Namibia	Botswana	Namibia	Botswana
Dry season	**Afternoon**	6.49 ± 11.93	5.47 ± 10.30	4.97 ± 9.87	6.10 ± 11.53
	Dusk	24.35 ± 40.59	31.30 ± 48.54	23.20 ± 43.14	25.90 ± 44.05
	Night	33.72 ± 34.28	25.07 ± 30.98	25.67 ± 32.85	20.35 ± 28.26
	Nadir	41.01 ± 38.98	30.31 ± 32.03	35.95 ± 38.61	28.52 ± 32.80
	Night end	41.64 ± 39.22	31.60 ± 33.84	39.63 ± 38.25	29.77 ± 33.69
	Dawn	34.07 ± 51.66	38.74 ± 51.01	39.02 ± 55.81	32.40 ± 47.98
	Morning	11.67 ± 17.31	15.20 ± 19.70	13.98 ± 20.63	11.98 ± 18.01
Wet season	**Afternoon**	8.12 ± 13.99	9.48 ± 14.32	6.93 ± 13.03	10.54 ± 14.25
	Dusk	31.48 ± 55.97	34.01 ± 48.31	30.42 ± 44.76	37.52 ± 48.07
	Night	31.14 ± 43.57	30.69 ± 31.50	28.17 ± 34.34	25.15 ± 33.04
	Nadir	31.52 ± 44.39	28.56 ± 33.30	35.06 ± 40.30	23.73 ± 30.56
	Night end	28.51 ± 40.47	25.82 ± 34.28	34.91 ± 39.89	25.91 ± 32.34
	Dawn	28.02 ± 50.06	24.47 ± 43.64	28.73 ± 48.65	22.54 ± 36.63
	Morning	11.70 ± 20.30	10.50 ± 15.62	10.61 ± 17.86	10.31 ± 14.98

(b)

Period	Lunar phase	Activity		Speed (m/s)		Tortuosity	
		Namibia	Botswana	Namibia	Botswana	Namibia	Botswana
Nocturnal combined seasons	**New moon**	32.67 ± 49.27	29.34 ± 45.53	0.170 ± 0.24	0.135 ± 0.23	0.367 ± 2.21	-0.272 ± 2.26
	Full moon	33.39 ± 48.98	27.16 ± 44.46	0.185 ± 0.25	0.124 ± 0.22	-0.011 ± 1.81	0.442 ± 2.58
Nocturnal dry season	**New moon**	38.46 ± 52.31	30.28 ± 45.85	0.169 ± 0.25	0.159 ± 0.23	0.351 ± 1.93	-0.162 ± 2.29
	Waxing crescent	45.35 ± 53.94	31.19 ± 47.54	0.223 ± 0.26	0.153 ± 0.24	0.014 ± 1.82	-0.030 ± 2.24
	First quarter	27.17 ± 48.32	27.73 ± 44.82	0.160 ± 0.24	0.146 ± 0.23	-0.170 ± 2.03	0.077 ± 2.32
	Waxing gibbous	23.75 ± 45.48	30.39 ± 49.22	0.135 ± 0.22	0.161 ± 0.25	-0.245 ± 2.05	-0.243 ± 2.29
	Full moon	33.23 ± 50.35	26.42 ± 44.38	0.182 ± 0.25	0.124 ± 0.21	0.013 ± 1.88	-0.024 ± 2.49
	Waning gibbous	36.16 ± 50.15	27.85 ± 47.76	0.184 ± 0.24	0.135 ± 0.23	0.164 ± 1.82	-0.057 ± 2.36
	Last quarter	37.39 ± 52.07	32.60 ± 46.91	0.186 ± 0.25	0.154 ± 0.22	-0.223 ± 1.80	-0.135 ± 2.56

	Waning crescent	37.22 ± 53.67	29.47 ± 49.82	0.216 ± 0.27	0.141 ± 0.24	-0.009 ± 2.00	0.259 ± 2.30
Nocturnal wet season	**New moon**	29.41 ± 46.60	27.87 ± 45.19	0.156 ± 0.23	0.128 ± 0.23	0.279 ± 2.40	-0.128 ± 2.18
	Waxing crescent	34.29 ± 49.79	27.51 ± 44.07	0.186 ± 0.25	0.123 ± 0.23	0.094 ± 1.90	-0.182 ± 2.38
	First quarter	34.05 ± 48.81	24.31 ± 41.38	0.187 ± 0.25	0.117 ± 0.21	-0.085 ± 1.87	-0.024 ± 2.53
	Waxing gibbous	36.90 ± 50.21	25.59 ± 44.34	0.211 ± 0.26	0.119 ± 0.23	0.200 ± 1.91	0.377 ± 2.41
	Full moon	32.68 ± 47.55	27.30 ± 43.68	0.177 ± 0.24	0.123 ± 0.22	0.017 ± 1.76	0.674 ± 2.49
	Waning gibbous	36.53 ± 51.71	23.79 ± 41.63	0.190 ± 0.25	0.112 ± 0.22	0.139 ± 1.78	0.519 ± 2.60
	Last quarter	36.05 ± 51.51	28.79 ± 44.52	0.186 ± 0.26	0.122 ± 0.22	-0.110 ± 1.92	0.230 ± 2.35
	Waning crescent	34.63 ± 49.27	28.29 ± 44.71	0.167 ± 0.24	0.120 ± 0.22	0.072 ± 2.10	0.127 ± 2.33
Dusk/dawn combined seasons	**New moon**	32.25 ± 48.36	31.44 ± 47.38	0.182 ± 0.29	0.163 ± 0.28	-1.173 ± 2.38	0.844 ± 1.91
	Full moon	34.49 ± 47.63	28.53 ± 44.50	0.206 ± 0.29	0.134 ± 0.26	-0.033 ± 2.44	1.506 ± 1.74
Dusk/dawn dry season	**New moon**	40.25 ± 52.00	33.80 ± 46.61	0.184 ± 0.31	0.141 ± 0.26	-0.654 ± 2.47	-0.023 ± 1.94
	Waxing crescent	44.32 ± 53.96	32.81 ± 47.82	0.257 ± 0.35	0.149 ± 0.28	0.038 ± 2.19	-0.356 ± 1.92
	First quarter	24.61 ± 48.13	32.81 ± 45.07	0.168 ± 0.31	0.155 ± 0.27	-3.045 ± 2.43	-0.539 ± 1.87
	Waxing gibbous	24.67 ± 44.71	32.34 ± 49.42	0.151 ± 0.28	0.153 ± 0.29	-0.106 ± 2.26	-0.038 ± 2.07
	Full moon	34.56 ± 48.77	29.13 ± 44.30	0.175 ± 0.30	0.132 ± 0.25	-0.054 ± 2.45	2.994 ± 1.75
	Waning gibbous	34.39 ± 49.85	35.13 ± 50.05	0.193 ± 0.31	0.141 ± 0.27	0.141 ± 2.27	1.068 ± 1.94
	Last quarter	34.85 ± 50.04	34.75 ± 48.97	0.198 ± 0.32	0.140 ± 0.25	0.147 ± 2.22	-0.013 ± 1.77
	Waning crescent	35.05 ± 52.38	33.54 ± 51.74	0.214 ± 0.34	0.133 ± 0.28	-0.011 ± 2.31	0.354 ± 2.03
Dusk/dawn wet season	**New moon**	30.13 ± 45.49	30.71 ± 47.94	0.178 ± 0.27	0.142 ± 0.26	-2.659 ± 2.25	0.785 ± 1.92
	Waxing crescent	35.09 ± 48.60	31.83 ± 44.60	0.207 ± 0.30	0.133 ± 0.25	-0.163 ± 2.35	0.862 ± 1.85
	First quarter	36.24 ± 49.59	29.70 ± 43.85	0.227 ± 0.32	0.127 ± 0.25	-0.107 ± 2.29	1.818 ± 1.93
	Waxing gibbous	39.36 ± 51.94	31.46 ± 48.08	0.252 ± 0.33	0.132 ± 0.27	-0.195 ± 2.20	0.145 ± 1.76
	Full moon	34.21 ± 46.13	29.44 ± 44.54	0.195 ± 0.28	0.127 ± 0.25	-0.228 ± 2.11	1.232 ± 1.73
	Waning gibbous	34.27 ± 50.36	28.11 ± 43.15	0.199 ± 0.31	0.119 ± 0.24	0.180 ± 2.30	-1.526 ± 1.77
	Last quarter	33.68 ± 48.72	32.28 ± 46.56	0.193 ± 0.31	0.129 ± 0.25	-0.282 ± 2.42	0.988 ± 1.81
	Waning crescent	30.61 ± 44.76	33.68 ± 46.29	0.166 ± 0.28	0.144 ± 0.25	0.037 ± 2.41	-1.314 ± 1.78

Table S3.2.4. Lion activity, speed, and path tortuosity in different land cover types from the Etosha National Park, Namibia, and the Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. Values consist of the means ± standard deviations of activity (AMVs) averaged daily from 24 h periods, with the speed (m/s) and path tortuosity (radian) from nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods.

Land cover	Activity (24 h)		Speed (m/s)				Tortuosity			
	Namibia	Botswana	Namibia		Botswana		Namibia		Botswana	
			Nocturnal	Dusk/dawn	Nocturnal	Dusk/dawn	Nocturnal	Dusk/dawn	Nocturnal	Dusk/dawn
Forest	-	24.18 ± 0.39	-	-	0.118 ± 0.23	0.137 ± 0.31	-	-	0.147 ± 2.34	3.079 ± 2.31
Grassland	30.17 ± 0.26	21.68 ± 0.24	0.182 ± 0.25	0.207 ± 0.37	0.117 ± 0.21	0.158 ± 0.28	0.028 ± 1.89	-0.054 ± 2.37	-0.023 ± 2.48	-2.567 ± 2.36
Shrubland	27.56 ± 0.45	23.79 ± 0.20	0.196 ± 0.23	0.223 ± 0.27	0.120 ± 0.22	0.153 ± 0.29	0.182 ± 1.91	0.144 ± 2.67	-0.026 ± 2.32	0.465 ± 1.86
Woodland	28.78 ± 0.46	15.10 ± 2.81	0.192 ± 0.23	0.177 ± 0.30	0.131 ± 0.22	0.172 ± 0.31	0.108 ± 1.86	0.012 ± 2.49	2.66 ± 2.14	3.054 ± 1.72
Cropland	37.78 ± 10.41	-	0.117 ± 0.15	0.230 ± 0.34	-	-	0.721 ± 1.29	0.021 ± 1.93	-	-
Wetland	-	22.87 ± 0.34	-	-	0.101 ± 0.18	0.125 ± 0.29	-	-	0.523 ± 2.55	3.122 ± 2.28
Pan	23.37 ± 0.76	-	0.150 ± 0.24	0.168 ± 0.30	-	-	0.062 ± 2.09	0.222 ± 2.60	-	-
Settlement	49.08 ± 10.48	61.16 ± 16.16	0.113 ± 0.23	0.257 ± 0.30	0.481 ± 0.46	0.530 ± 0.31	2.68 ± 1.73	-0.839 ± 1.61	2.08 ± 1.50	0.263 ± 1.37

Table S3.3.1. Total overlapped areas in km^2 shared between lions' home ranges (95%) and core areas (50%) in the (a) Etosha National Park, Namibia; (b) Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. Lion utilization distributions were generated with 95% (home range) and 50% (core areas) *a*-LoCoH isopleths. Males are underlined. An asterisk denotes an observed mating pair.

(a)

HOME RANGE (95%)

	DRY SEASON										WET SEASON									
	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2
OK-33863					3.4										93.2*					-
RE-33864			0	32.7		28.6			0	0			0	0.3		231.4*			2.3	-
NU-33865		0		75.3		0						0		118.3		0.8				-
MO-33866		32.7	75.3			41.7						0.3	118.3			15.8				-
OJ-33867	3.4						0	34.5*			93.2*						0	2.4		-
SU-33868		28.6	0	41.7			0			24.7		231.4*	0.8	15.8			0			-
OM-34308					0	0		0.9	0	1.4					0	0		0	0	-
LU-34308					34.5*		0.9			5.7					2.4		0			-
OF-34309		0					0			1.1		2.3					0			-
G2-35678		0				24.7	1.4	5.7	1.1		-	-	-	-	-	-	-	-	-	

CORE (50%)

	DRY SEASON										WET SEASON									
	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2
OK-33863					0										15.4*					-
RE-33864			0	3.2		7.6			0	0			0	0		60.3*			0	-
NU-33865		0		7.8		0						0		5.8		0				-
MO-33866		3.2	7.8			16.0						0	5.8			0				-
OJ-33867	0						0	0.2*			15.4*						0	0.2		-
SU-33868		7.6	0	16.0			0			0		60.3*	0	0			0			-
OM-34308					0	0		0	0	0					0	0		0	0	-
LU-34308					0.2*		0			0					0.2		0			-
OF-34309		0					0			0		0					0			-
G2-35678		0				0	0	0	0		-	-	-	-	-	-	-	-	-	

(b)

HOME RANGE (95%)

	DRY SEASON								WET SEASON							
	SW	AF	BE	BO	AM	BA	KW	KB	SW	AF	BE	BO	AM	BA	KW	KB
SW-33950							0	9.8							0	8.4
AF-34308			0.1		15.9						13.2		86.5*			
BE-35678		0.1			1.5					13.2			163.1			
BO-35947																
AM-36714		15.9	1.5							86.5*	163.1					
BA-36715																
KW-36716	0							31.2	0							43.1
KB-36717	9.8						31.2		8.4						43.1	

CORE (50%)

	DRY SEASON								WET SEASON							
	SW	AF	BE	BO	AM	BA	KW	KB	SW	AF	BE	BO	AM	BA	KW	KB
SW-33950							0	0							0	0
AF-34308			0		4.7						0.1		27.3*			
BE-35678		0			0.2					0.1			17.0			
BO-35947																
AM-36714		4.7	0.2							27.3*	17.0					
BA-36715																
KW-36716	0							1.4	0							3.0
KB-36717	0						1.4		0						3.0	

Table S3.3.2. Total proportion of lions' (vertical column) home ranges and core areas overlapped by other lions (horizontal column) in the (a) Etosha National Park, Namibia; (b) Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. Lion utilization distributions were generated with 95% (home range) and 50% (core areas) *a*-LoCoH isopleths. Males are underlined. An asterisk denotes an observed mating pair.

(a)

	HOME RANGE (95%)																			
	DRY SEASON										WET SEASON									
	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2
OK-33863					0.063										0.329*					-
RE-33864			0	0.78		0.68			0	0			0	0.00089		0.69*			0.0069	-
NU-33865		0		0.21		0						0		0.33		0.0022				-
MO-33866		0.088	0.204			0.113						0.001	0.402			0.054				-
OJ-33867	0.032						0	0.328*			0.341*						0	0.0088		-
SU-33868		0.177	0	0.258			0			0.153		0.618*	0.0021	0.042			0			-
OM-34308					0	0		0.014	0	0.021					0	0		0	0	-
LU-34308					0.23*		0.006			0.038					0.055		0			-
OF-34309		0					0			0.0078		0.0091					0			-
G2-35678		0				0.11	0.0061	0.025	0.0048		-	-	-	-	-	-	-	-	-	

	CORE (50%)																			
	DRY SEASON										WET SEASON									
	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2	OK	RE	NU	MO	OJ	SU	OM	LU	OF	G2
OK-33863					0										0.125*					-
RE-33864			0	0.262		0.623			0	0			0	0		0.71*			0	-
NU-33865		0		0.065		0						0		0.044		0				-
MO-33866		0.031	0.076			0.156						0	0.075			0				-
OJ-33867	0						0	0.006*			0.158*						0	0.002		-
SU-33868		0.162	0	0.341			0			0		0.61*	0	0			0			-
OM-34308					0	0		0	0	0					0	0		0	0	-
LU-34308					0.007*		0			0					0.011		0			-
OF-34309		0					0			0		0					0			-
G2-35678		0				0	0	0	0		-	-	-	-	-	-	-	-	-	

(b)

HOME RANGE (95%)

	DRY SEASON								WET SEASON							
	SW	AF	BE	BO	AM	BA	KW	KB	SW	AF	BE	BO	AM	BA	KW	KB
SW-33950							0	0.087							0	0.049
AF-34308			0.0063		0.994						0.148		0.97*			
BE-35678		0.067			1.00					0.0479			0.592			
BO-35947																
AM-36714		0.026	0.0025							0.102*	0.192					
BA-36715																
KW-36716	0							0.351	0							0.258
KB-36717	0.166						0.53		0.101						0.518	

CORE (50%)

	DRY SEASON								WET SEASON							
	SW	AF	BE	BO	AM	BA	KW	KB	SW	AF	BE	BO	AM	BA	KW	KB
SW-33950							0	0							0	0
AF-34308			0		0.81						0.0036		0.982*			
BE-35678		0			0.25					0.0017			0.297			
BO-35947																
AM-36714		0.028	0.0012							0.15*	0.093					
BA-36715																
KW-36716	0							0.065	0							0.08
KB-36717	0						0.197		0						0.275	

Table S3.4. Lion activity (AMVs), speed (m/s), and path tortuosity (radian) in relation to intraspecific and interspecific competitors during nocturnal (30 min fixes) and dusk/dawn (5 min fixes) periods from the Etosha National Park, Namibia, and the Chobe National Park, Linyanti Conservancy, and the NG32 in Okavango Delta, Botswana. Values consist of the means ± standard deviations (a) at distance intervals in metres to the nearest conspecific (intraspecific) and competitor (interspecific), and (b) inside and outside of conspecific and competitor core use areas.

(a)

Period	Region	Distance Interval (m)	Conspecific			Competitor		
			Activity	Speed (m/s)	Tortuosity	Activity	Speed (m/s)	Tortuosity
Nocturnal	Namibia	**0-100**	26.26 ± 33.29	0.127 ± 0.19	0.169 ± 2.07	22.33 ± 30.74	0.100 ± 0.22	-2.912 ± 1.66
		100-200	53.78 40.41	0.313 ± 0.26	0.170 ± 1.12	23.00 ± 30.16	0.044 ± 0.11	2.775 ± 1.58
		200-300	41.75 ± 41.82	0.245 ± 0.26	-0.155 ± 1.52	29.52 45.83	0.139 ± 0.25	1.047 ± 1.65
		300-400	34.01 ± 39.56	0.212 ± 0.29	0.014 ± 1.46	31.41 ± 35.05	0.080 ± 0.15	-2.159 ± 1.73
		400-500	51.92 ± 44.42	0.289 ± 0.27	-0.001 ± 1.21	18.67 ± 28.12	0.059 ± 0.12	2.305 ± 1.27
		500-600	26.49 ± 31.14	0.105 ± 0.19	0.897 ± 1.56	40.03 ± 45.91	0.094 ± 0.15	0.055 ± 1.12
		600-700	53.74 ± 47.67	0.224 ± 0.28	-0.011 ± 1.34	31.88 ± 37.33	0.151 ± 0.23	0.626 ± 1.65
		700-800	48.83 ± 50.73	0.226 ± 0.26	0.293 ± 1.51	36.89 ± 40.20	0.135 ± 0.23	0.401 ± 1.71
		800-900	40.74 ± 38.65	0.271 ± 0.25	0.093 ± 1.57	29.80 ± 33.87	0.185 ± 0.28	1.147 ± 1.65
		900-1000	35.72 ± 45.01	0.168 ± 0.24	1.761 ± 1.59	34.28 ± 42.46	0.150 ± 0.23	-0.223 ± 1.89
	Botswana	**0-100**	-	0.024 ± 0.09	-2.162 ± 2.16	9.71 ± 4.73	0.041 ± 0.03	2.799 ± 1.58
		100-200	46.86 ± 28.76	0.128 ± 0.02	-2.342 ± 1.71	28.57 ± 36.33	0.014 ± 0.02	-2.134 ± 1.50
		200-300	51.45 ± 48.20	0.069 ± 0.05	1.911 ± 1.45	37.47 ± 48.78	0.082 ± 0.20	0.380 ± 1.25
		300-400	11.42 ± 24.22	0.101 ± 0.34	-2.775 ± 2.46	14.20 ± 15.97	0.022 ± 0.02	-0.762 ± 1.46
		400-500	51.54 ± 42.14	0.073 ± 0.07	-0.739 ± 2.30	37.89 ± 57.70	0.128 ± 0.25	1.460 ± 1.67
		500-600	-	0.057 ± 0.11	-0.340 ± 2.08	26.63 ± 47.72	0.115 ± 0.25	-1.710 ± 1.62
		600-700	-	0.031 ± 0.04	2.567 ± 1.82	2.08 ± 2.92	0.079 ± 0.11	-0.844 ± 2.36
		700-800	-	0.126 ± 0.19	-0.078 ± 1.86	12.64 ± 23.05	0.041 ± 0.10	-1.433 ± 2.15
		800-900	21.33 ± 35.93	0.053 ± 0.13	0.739 ± 1.60	32.19 ± 58.03	0.076 ± 0.19	2.083 ± 2.08
		900-1000	-	0.024 ± 0.04	0.929 ± 1.76	19.45 ± 24.51	0.207 ± 0.38	0.120 ± 1.87
Dusk/dawn	Namibia	**0-100**	26.84 ± 37.69	0.108 ± 0.21	-1.533 ± 2.39	32.26 ± 43.67	0.063 ± 0.14	-3.037 ± 2.03
		100-200	53.66 ± 49.73	0.412 ± 0.34	0.076 ± 1.14	23.32 ± 50.22	0.082 ± 0.24	3.130 ± 1.73
		200-300	46.28 ± 50.56	0.337 ± 0.34	0.145 ± 1.43	35.13 ± 52.09	0.155 ± 0.26	1.620 ± 1.79
		300-400	50.00 ± 51.91	0.302 ± 0.39	0.102 ± 1.92	31.35 ± 42.61	0.085 ± 0.21	-2.571 ± 1.94
		400-500	79.47 ± 47.28	0.396 ± 0.37	0.058 ± 1.48	33.79 ± 44.56	0.135 ± 0.26	-2.666 ± 1.88
		500-600	35.86 ± 46.90	0.184 ± 0.34	-0.131 ± 2.03	20.41 ± 38.26	0.188 ± 0.33	2.414 ± 1.77
		600-700	50.93 ± 58.36	0.254 ± 0.43	0.624 ± 1.71	42.27 ± 59.37	0.257 ± 0.36	0.906 ± 1.37
		700-800	49.20 ± 57.70	0.319 ± 0.40	-0.057 ± 1.57	27.42 ± 41.12	0.162 ± 0.33	-2.842 ± 1.70
		800-900	70.72 ± 58.96	0.325 ± 0.40	-0.351 ± 1.47	46.56 ± 56.70	0.160 ± 0.27	-0.322 ± 1.65
		900-1000	56.68 ± 50.48	0.257 ± 0.35	-0.440 ± 1.86	43.79 ± 49.08	0.154 ± 0.28	-1.089 ± 2.11

Dusk/dawn	Botswana	**0-100**	76.71 ± 34.34	0.048 ± 0.15	0.053 ± 1.32	79.60 ± 26.02	0.163 ± 0.03	-0.878 ± 2.18
		100-200	123.84 ± 35.98	0.118 ± 0.22	0.401 ± 1.18	16.46 ± 28.87	0.071 ± 0.15	0.973 ± 1.47
		200-300	70.69 ± 57.12	0.079 ± 0.15	-0.687 ± 1.32	39.34 ± 33.27	0.121 ± 0.22	-0.262 ± 1.35
		300-400	90.79 ± 48.49	0.117 ± 0.19	-0.402 ± 1.19	13.44 ± 43.89	0.133 ± 0.43	-0.070 ± 1.09
		400-500	125.31 ± 51.26	0.169 ± 0.20	-1.092 ± 1.09	10.83 ± 39.96	0.103 ± 0.18	-2.849 ± 1.64
		500-600	45.55 ± 52.24	0.073 ± 0.21	-0.137 ± 1.10	29.50 ± 0.10	0.064 ± 0.01	-0.280 ± 1.06
		600-700	22.16 ± 37.07	0.075 ± 0.20	-0.229 ± 1.21	22.89 37.56	0.054 ± 0.14	0.124 ± 1.43
		700-800	56.44 ± 49.32	0.114 ± 0.18	0.307 ± 1.12	31.77 ± 42.21	0.150 ± 0.36	-0.250 ± 1.91
		800-900	46.08 ± 33.59	0.080 ± 0.19	-0.222 ± 1.25	18.41 ± 10.20	0.032 ± 0.05	-0.579 ± 1.34
		900-1000	86.99 ± 41.31	0.115 ± 0.19	-0.474 ± 1.33	15.39 43.24	0.234 ± 0.50	1.541 ± 1.87

(b)

Period	**Region**	**Core Use Area**	**Conspecific**			**Competitor**		
			Activity	**Speed (m/s)**	**Tortuosity**	**Activity**	**Speed (m/s)**	**Tortuosity**
Nocturnal	Namibia	**Inside**	36.73 ± 40.62	0.205 ± 0.25	-0.056 ± 1.99	36.60 ± 42.69	0.183 ± 0.26	0.055 ± 1.91
		Outside	35.78 ± 41.07	0.192 ± 0.25	0.138 ± 1.87	34.41 ± 40.46	0.186 ± 0.25	0.059 ± 1.90
	Botswana	**Inside**	41.08 ± 32.77	0.178 ± 0.21	0.113 ± 2.88	28.52 ± 39.35	0.152 ± 0.22	0.032 ± 2.41
		Outside	31.50 ± 36.45	0.146 ± 0.23	-0.123 ± 2.33	27.55 ± 34.61	0.141 ± 0.22	-0.222 ± 2.43
Dusk/dawn	Namibia	**Inside**	37.21 ± 47.90	0.226 ± 0.32	-0.369 ± 2.63	37.89 ± 50.69	0.217 ± 0.33	0.073 ± 2.37
		Outside	34.45 ± 48.82	0.200 ± 0.31	0.088 ± 2.34	33.80 ± 47.92	0.204 ± 0.31	0.029 ± 2.51
	Botswana	**Inside**	33.52 ± 41.75	0.155 ± 0.25	0.203 ± 1.39	34.29 ± 50.88	0.165 ± 0.28	0.282 ± 1.79
		Outside	37.16 ± 46.29	0.173 ± 0.30	0.097 ± 1.66	30.66 ± 43.43	0.157 ± 0.28	0.263 ± 1.62

Table S3.5a. Akaike information criterion (AIC) for population level base and interaction model selection results for dry and wet season resource selection functions (RSFs) during the (i) 24-hour and (ii) nocturnal periods (18h00-6h00 and 17h00-8h00) fit to 11 lions in the Etosha National Park, Namibia and to 6 lions in the Chobe National Park and Linyanti Conservancy, Botswana. Due to correlations between the interaction variables distance to competitor/conspecific and competitor/conspecific probability, those variables were interchanged within the models to see which variable best-predicted lion resource selection. The covariates within the model, the type of model whether interaction or base, the Akaike (AIC) values, the Akaike difference (ΔAIC), and Akaike weight (ω_i) are presented.

(i)

Name	Model Covariates	Model Type	AIC	ΔAIC	ω_i
Etosha Dry season	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	23383.00	0.00	1.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb	interaction	30418.13	7035.13	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp + d_cmp	interaction	38347.39	14964.39	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cmp	interaction	38539.21	15156.21	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb	base	39568.73	16185.73	0.0000
Etosha Wet season	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	16679.40	0.00	1.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cnsp_prb	interaction	22113.57	5434.17	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb	interaction	32896.91	16217.52	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp + d_cmp	interaction	37364.58	20685.18	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cmp	interaction	37999.66	21320.26	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp	interaction	38401.51	21722.11	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb	base	39125.92	22446.53	0.0000
Chobe/ Linyanti Dry season	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb*	interaction	17486.50	0.00	1.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cnsp_prb	interaction	25852.39	8365.89	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cmp	interaction	26396.40	8909.91	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp + d_cmp	interaction	26399.41	8912.91	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp	interaction	26471.54	8985.05	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds	base	26486.69	9000.19	0.0000
Chobe/ Linyanti Wet season	*elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb + cnsp_prb*	interaction	36263.14	0.00	1.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cnsp_prb	interaction	36569.51	306.37	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb	interaction	36611.85	348.71	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds	base	36895.86	632.71	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cmp	interaction	36897.07	633.93	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp	interaction	36899.32	636.18	0.0000
	elvtn + xhr_day + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp + d_cmp	interaction	36900.55	637.41	0.0000

(ii)

Name	Model Covariates	Model Type	AIC	ΔAIC	ω_i
Etosha Dry season	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	94028.27	0.00	1.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cnsp_prb	interaction	129112.75	35084.49	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb	interaction	132914.66	38886.39	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp + d_cmp	interaction	167305.25	73276.98	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cmp	interaction	168093.83	74065.57	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp	interaction	170946.41	76918.14	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb	base	171875.13	77846.86	0.0000
Etosha Wet season	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb + cnsp_prb*	interaction	70001.08	0.00	1.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cnsp_prb	interaction	91476.01	21474.94	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + cmp_prb	interaction	151253.97	81252.89	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp + d_cmp	interaction	169286.18	99285.11	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cnsp	interaction	172575.73	102574.66	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb + d_cmp	interaction	172800.07	102798.99	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + athrx_prb	base	175896.65	105895.57	0.0000
Chobe/ Linyanti Dry season	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb + cnsp_prb*	interaction	28430.30	0.00	1.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb	interaction	66866.92	38436.61	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cnsp_prb	interaction	112051.57	83621.27	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp + d_cmp	interaction	114358.85	85928.54	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cmp	interaction	114374.44	85944.14	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp	interaction	114619.26	86188.95	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds	base	114721.72	86291.41	0.0000
Chobe/ Linyanti Wet season	*elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb + cnsp_prb*	interaction	166865.63	0.00	1.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cnsp_prb	interaction	168107.32	1241.69	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + cmp_prb	interaction	168913.96	2048.33	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp	interaction	169517.70	2652.07	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cnsp + d_cmp	interaction	169521.11	2655.48	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds	base	169689.55	2823.92	0.0000
	elvtn + xhr_night + ndvi + lndcvr + d_anthr + d_ssnwtr + d_rds + d_cmp	interaction	169693.27	2827.64	0.0000

Table S3.5b. Akaike information criterion (AIC) for population level base and interaction model selection results for dry and wet season step selection functions (SSFs) of (i) nocturnal periods (18h00 – 6h00 and 17h00 – 8h00), and (ii) dusk/dawn periods (19h00-21h00 and 4h00-6h00) fit to 11 lions in the Etosha National Park, Namibia and to 6 lions in the Chobe National Park and Linyanti Conservancy, Botswana. Due to correlations between the interaction variables distance to competitor/conspecific and competitor/conspecific probability, those variables were interchanged within the models to see which variable best-predicted lion step selection. The covariates within the model, the type of model whether interaction or base, the Akaike (AIC) values, the Akaike difference (ΔAIC), and Akaike weight (ω_i) are presented.

(i)

Name	Variables	Model Type	AIC	ΔAIC	ω_i
Etosha Dry season	*elvtn + d_anthr + d_ssnwtr + d_rds + d_crcs + moon_ill + cmp_prb + cnsp_prb*	interaction	271777.34	0.00	1.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + d_crcs + moon_ill + d_cmp + d_cnsp	interaction	272923.64	1146.29	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + d_crcs + moon_ill + d_cnsp	interaction	272923.88	1146.54	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + d_crcs + moon_ill + d_cmp	interaction	272925.65	1148.31	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + d_crcs + moon_ill	base	272928.19	1150.84	0.0000
Etosha Wet season	*elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cmp_prb + cnsp_prb*	interaction	288053.93	0.00	0.6972
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + d_cmp + d_cnsp	interaction	288055.61	1.68	0.3008
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cmp_prb	interaction	288065.66	11.73	0.0020
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill	base	288073.86	19.92	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + d_cmp	interaction	288076.31	22.38	0.0000
Chobe/ Linyanti Dry season	*elvtn + d_anthr + d_prmwtr + d_rds + temp + cmp_prb + cnsp_prb*	interaction	106099.74	0.00	1.0000
	elvtn + d_anthr + d_prmwtr + d_rds + temp + cmp_prb	interaction	106141.73	41.99	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + temp + d_cmp + d_cnsp	interaction	122985.42	16885.69	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + temp + d_cmp	interaction	122994.50	16894.76	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + temp + cnsp_prb	interaction	122996.81	16897.07	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + temp	base	122999.53	16899.80	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + temp + d_cnsp	interaction	122999.56	16899.82	0.0000
Chobe/ Linyanti Wet season	*elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cmp_prb + cnsp_prb*	interaction	182157.51	0.00	1.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cmp_prb	interaction	182214.78	57.27	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + d_cmp + d_cnsp	interaction	182246.16	88.65	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cnsp_prb	interaction	182247.25	89.74	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + d_cmp	interaction	182247.85	90.34	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + d_cnsp	interaction	182248.78	91.26	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill	base	182252.03	94.52	0.0000

(ii)

Name	**Variables**	**Model Type**	**AIC**	**ΔAIC**	**ω_i**
Etosha Dry season	*elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cmp_prb + cnsp_prb*	interaction	540581.24	0.00	1.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cmp_prb	interaction	541289.94	708.70	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + cnsp_prb	interaction	541558.57	977.33	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + d_cmp + d_cnsp	interaction	542904.54	2323.30	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + d_cnsp	interaction	542910.66	2329.42	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill + d_cmp	interaction	542924.67	2343.43	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + moon_ill	base	542939.67	2358.43	0.0000
Etosha Wet season	*elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + cmp_prb + cnsp_prb*	interaction	567843.20	0.00	1.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + cnsp_prb	interaction	567894.29	51.09	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + d_cmp + d_cnsp	interaction	570753.00	2909.80	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + d_cnsp	interaction	570775.35	2932.15	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + cmp_prb	interaction	570790.82	2947.62	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp + d_cmp	interaction	570811.95	2968.75	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + athrx_prb + temp	base	570826.37	2983.17	0.0000
Chobe/ Linyanti Dry season	*elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cmp_prb + cnsp_prb*	interaction	211079.32	0.00	1.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cmp_prb	interaction	211117.11	37.79	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + cnsp_prb	interaction	238320.34	27241.01	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + d_cmp + d_cnsp	interaction	238331.04	27251.71	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + d_cnsp	interaction	238335.50	27256.18	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill	base	238336.37	27257.04	0.0000
	elvtn + d_anthr + d_prmwtr + d_rds + moon_ill + d_cmp	interaction	238336.46	27257.14	0.0000
Chobe/ Linyanti Wet season	*elvtn + d_anthr + d_ssnwtr + d_rds + temp + cmp_prb + cnsp_prb*	interaction	371617.52	0.00	1.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + temp + d_cmp + d_cnsp	interaction	371708.81	91.29	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + temp + d_cnsp	interaction	371724.98	107.46	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + temp + cmp_prb	interaction	371789.21	171.70	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + temp + cnsp_prb	interaction	371823.91	206.39	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + temp + d_cmp	interaction	371830.21	212.69	0.0000
	elvtn + d_anthr + d_ssnwtr + d_rds + temp	base	371849.67	232.15	0.0000

Table S3.6a. Coefficients (β), standard errors (SE), Wald statistics (*Z*), and probability values (*P*) of variables from best population level resource selection function (RSF) models after backwards stepwise selection. Models were fit to lions during the 24-hour and nocturnal periods (18h00-6h00 and 17h00-8h00) of the dry and wet seasons in the (i) Etosha National Park, Namibia; (ii) Chobe National Park and Linyanti Conservancy; and (iii) NG32 concession in the Okavango Delta, Botswana, 2013-2017.

(i)

		Dry season				Wet season			
Region	**Variable**	**β**	**SE**	***Z***	***P***	**β**	**SE**	***Z***	***P***
24-hour	*elvtn*	13.592	3.060	4.442	**<0.001**	27.666	4.580	6.040	**<0.001**
	xhr_day	0.175	0.176	0.992	0.321	0.130	0.150	0.863	0.388
	ndvi	-1.525	0.053	-28.95	**<0.001**	-2.967	1.404	-2.113	**<0.05**
	woodland	4.760	3.606	1.320	0.187	1.280	1.387	0.922	0.356
	grassland	-2.814	1.476	-1.907	0.057	1.956	0.170	11.487	**<0.001**
	shrub	-1.298	0.356	-3.649	**<0.001**	-	-	-	-
	savanna_grass	-17.000	1229.47	-0.014	0.989	0.275	0.836	0.329	0.743
	crop	8.844	2.705	3.270	**<0.01**	-14.723	83.849	-0.176	0.861
	veget_wet	-5.223	15.748	-0.332	0.740	10.102	4.309	2.345	**<0.05**
	salt_pan	5.266	2.711	1.942	0.052	-	-	-	-
	settlement	-	-	-	-	6.596	1.338	4.929	**<0.001**
	d_anthr	-4.856	3.989	-1.217	0.224	-2.746	4.241	-0.647	0.517
	d_ssnwtr	-2.036	1.144	-1.781	0.075	-0.251	1.110	-0.226	0.821
	d_rds	-0.536	0.727	-0.737	0.461	-0.592	0.976	-0.607	0.544
	anthrx_prb	30.966	6.140	5.043	**<0.001**	8.960	2.466	3.633	**<0.001**
	sex	-	-	-	-	-1.019	690.213	-0.001	0.999
	grp_size	-57.278	219.528	-0.261	0.794	-	-	-	-
	cmp_prb	-101.79	17.793	-5.721	**<0.001**	-0.141	5.287	-0.027	0.979
	cnsp_prb	5.438	3.560	1.527	0.127	-16.646	9.177	-1.814	0.070
Nocturnal (18h00-6h00)	*elvtn*	12.391	3.456	3.585	**<0.001**	20.104	2.620	7.673	**<0.001**
	xhr_night	0.074	0.026	2.867	**<0.01**	0.088	0.135	0.651	0.515
	ndvi	-0.220	0.874	-0.252	0.801	-1.466	0.846	-1.734	0.083
	woodland	0.577	0.744	0.775	0.438	10.936	35.078	0.312	0.755
	grassland	6.663	3.754	1.775	0.076	13.241	35.099	0.377	0.706
	shrub	-1.108	0.616	-1.798	0.072	10.204	35.071	0.291	0.771
	savanna_grass	-	-	-	-	10.030	35.072	0.286	0.775
	crop	-	-	-	-	4.012	35.679	0.112	0.911
	veget_wet	7.297	3.933	1.856	0.064	17.163	35.175	0.488	0.626
	salt_pan	-	-	-	-	9.727	35.107	0.277	0.782
	settlement	6.971	3.593	1.940	0.052	14.158	35.116	0.403	0.687
	d_anthr	-5.101	2.838	-1.797	0.072	-1.771	2.886	-0.614	0.539
	d_ssnwtr	-1.934	0.881	-2.194	**<0.05**	-0.655	0.558	-1.173	0.241
	d_rds	-0.807	0.435	-1.857	0.063	-	-	-	-
	anthrx_prb	26.458	7.148	3.702	**<0.001**	6.746	1.679	4.019	**<0.001**
	sex	-	-	-	-	-1.100	690.026	-0.002	0.999
	cmp_prb	-43.731	52.745	-0.829	0.407	1.559	4.079	0.382	0.702
	cnsp_prb	3.540	19.157	0.185	0.853	-17.692	9.087	-1.947	0.052

Land cover variables are in reference to forested land cover.

(ii)

		Dry season				Wet season			
Region	**Variable**	**β**	**SE**	***Z***	***P***	**β**	**SE**	***Z***	***P***
24-hour	*elvtn*	-1.132	1.048	-1.081	0.280	13.480	5.420	2.487	**<0.05**
	xhr_day	-0.031	0.077	-0.401	0.688	-	-	-	-
	ndvi	0.760	0.421	1.803	0.071	-0.263	0.184	-1.428	0.153
	sp_forest	0.662	1.097	0.604	0.546	-	-	-	-
	woodland	-	-	-	-	2.082	0.459	4.537	**<0.001**
	clsd_grass	2.646	0.771	3.434	**<0.001**	0.918	0.136	6.739	**<0.001**
	opn_grass	2.116	0.481	4.401	**<0.001**	0.691	0.301	2.293	**<0.05**
	clsd_shrub	2.076	0.684	3.036	**<0.01**	-	-	-	-
	opn_shrub	-0.286	1.239	-0.230	0.818	1.877	0.655	2.865	**<0.01**
	crop	0.822	1.434	0.573	0.567	2.414	0.572	4.223	**<0.001**
	wetland	0.704	1.062	0.663	0.507	-	-	-	-
	floodplain	1.357	1.846	0.735	0.462	2.376	0.331	7.171	**<0.001**
	d_anthr	8.282	2.809	2.949	**<0.01**	0.280	0.468	0.599	0.549
	d_ssnwtr	2.321	1.960	1.184	0.236	-1.127	0.883	-1.276	0.202
	d_rds	-1.695	0.875	-1.937	0.053	-0.608	0.123	-4.956	**<0.001**
	age	53.308	347.849	0.153	0.878	-	-	-	-
	bc_score	-	-	-	-	-0.001	475.500	0.000	1.000
	cmp_prb	-67.843	18.932	-3.584	**<0.001**	0.887	1.093	0.811	0.417
	cnsp_prb	18.620	4.978	3.741	**<0.001**	0.823	0.527	1.561	0.119
Nocturnal (18h00-6h00) and (17h00-8h00)	*elvtn*	7.023	3.223	2.179	**<0.05**	11.801	4.826	2.445	**<0.05**
	xhr_night	0.163	0.096	1.695	0.090	0.045	0.020	2.268	**<0.05**
	ndvi	0.698	0.279	2.501	**<0.05**	-0.347	0.182	-1.905	0.057
	sp_forest	1.427	0.803	1.777	0.076	-0.010	0.219	-0.047	0.962
	woodland	-8.679	4.389	-1.977	**<0.05**	-	-	-	-
	clsd_grass	1.739	0.473	3.673	**<0.001**	1.945	0.573	3.396	**<0.001**
	opn_grass	1.922	0.632	3.042	**<0.01**	0.779	0.161	4.836	**<0.001**
	clsd_shrub	3.050	0.986	3.094	**<0.01**	0.822	0.254	3.230	**<0.01**
	crop	-0.842	1.607	-0.524	0.600	1.634	0.571	2.863	**<0.01**
	wetland	-0.103	1.617	-0.064	0.949	2.143	0.351	6.097	**<0.001**
	floodplain	1.821	0.520	3.504	**<0.001**	-2.436	0.583	-4.180	**<0.001**
	settlement	2.877	1.085	2.651	**<0.01**	1.369	0.392	3.492	**<0.001**
	d_anthr	4.038	2.468	1.636	0.102	0.118	0.375	0.314	0.754
	d_ssnwtr	-13.342	4.156	-3.210	**<0.01**	-0.893	0.805	-1.109	0.267
	d_rds	-0.756	0.553	-1.366	0.172	-0.578	0.154	-3.761	**<0.001**
	age	96.338	425.582	0.226	0.821	-	-	-	-
	cmp_prb	-106.64	26.665	-3.999	**<0.001**	0.647	0.885	0.731	0.465
	cnsp_prb	19.684	7.131	2.761	**<0.01**	0.719	0.554	1.297	0.195

Land cover variables are in reference to forested land cover.

(iii)

		Dry season				Wet season			
Period	**Variable**	**β**	**SE**	***Z***	***P***	**β**	**SE**	***Z***	***P***
24-hour	*elvtn*	6.510	0.075	86.93	**<0.001**	7.840	0.142	55.150	**<0.001**
	xhr_day	0.051	0.115	0.44	0.656	-0.174	0.106	-1.64	0.100
	ndvi	-	-	-	-	-0.724	0.162	-4.46	**<0.001**
	precip_mnth	-0.141	0.026	-5.34	**<0.001**	-	-	-	-
	sp_forest	-0.990	1.373	-0.72	0.471	-0.911	1.113	-0.82	0.413
	woodland	1.934	0.522	3.7	**<0.001**	2.882	0.563	5.12	**<0.001**
	clsd_grass	-0.111	0.831	-0.13	0.894	-0.196	0.804	-0.24	0.807
	clsd_shrub	0.759	0.284	2.68	**<0.01**	-0.169	0.111	-1.53	0.127
	opn_shrub	-0.330	0.104	-3.17	**<0.01**	-0.198	0.253	-0.78	0.434
	crop	1.485	0.876	1.7	0.090	0.749	1.544	0.49	0.627
	wetland	-1.279	0.218	-5.87	**<0.001**	-0.611	0.138	-4.42	**<0.001**
	d_ssnwtr	1.772	0.295	6.01	**<0.001**	2.060	0.536	3.85	**<0.001**
Nocturnal (17h00-8h00)	*elvtn*	6.278	0.113	55.4	**<0.001**	7.900	0.041	191.14	**<0.001**
	xhr_night	0.029	0.022	1.31	0.189	0.072	0.016	4.51	**<0.001**
	ndvi	-0.563	0.250	-2.25	**<0.05**	-0.771	0.200	-3.85	**<0.001**
	sp_forest	0.405	1.092	0.37	0.711	0.316	1.281	0.25	0.805
	woodland	2.614	0.424	6.17	**<0.001**	3.256	0.362	8.99	**<0.001**
	clsd_grass	0.530	1.119	0.47	0.636	0.830	0.910	0.91	0.362
	opn_grass	1.132	0.341	3.32	**<0.001**	1.131	0.243	4.65	**<0.001**
	clsd_shrub	1.528	0.403	3.79	**<0.001**	1.215	0.238	5.1	**<0.001**
	opn_shrub	0.946	0.343	2.76	**<0.01**	1.058	0.371	2.85	**<0.01**
	crop	2.404	0.909	2.65	**<0.01**	2.601	1.127	2.31	**<0.05**
	wetland	-0.956	0.352	-2.71	**<0.01**	0.727	0.250	2.9	**<0.01**
	d_ssnwtr	1.659	0.321	5.16	**<0.001**	2.083	0.569	3.66	**<0.001**

Land cover variables are in reference to forested land cover.

Table S3.6b. Coefficients (β), standard errors (SE), Wald statistics (*Z*), and probability values (*P*) of all variables from best population level step selection function (SSF) models after backwards stepwise selection. Models were fit to lions during (i) nocturnal periods (18h00 – 6h00 and 17h00 – 8h00) and (ii) dusk/dawn periods (19h00 – 21h00 and 4h00 – 6h00) of the dry and wet seasons in the Etosha National Park, Namibia; the Chobe National Park and Linyanti Conservancy, and the NG32 concession in the Okavango Delta, Botswana, 2013-2017.

(i)

		Dry season				Wet season			
Region	**Variable**	**β**	**SE**	***Z***	***P***	**β**	**SE**	***Z***	***P***
Etosha	*elvtn*	8.007	0.318	25.164	**<0.001**	7.939	0.443	17.938	**<0.001**
	d_anthr	-7.164	2.270	-3.156	**<0.01**	1.347	1.337	1.008	0.314
	d_ssnwtr	-	-	-	-	-2.855	0.426	-6.699	**<0.001**
	d_crcs	-15.791	4.741	-3.331	**<0.001**	-	-	-	-
	moon_ill	-1.124	7.616	-0.148	0.883	-	-	-	-
	cmp_prb	-11.135	5.709	-1.950	0.051	-1.164	1.790	-0.650	0.516
	cnsp_prb	-7.637	6.594	-1.158	0.247	-12.016	6.413	-1.874	0.061
Chobe/ Linyanti	*elvtn*	1.291	0.361	3.576	**<0.001**	7.639	1.816	4.207	**<0.001**
	d_anthr	2.538	0.926	2.742	**<0.01**	0.245	0.084	2.934	**<0.01**
	d_prmwtr	-0.953	0.926	-1.029	0.303	-2.517	0.839	-2.998	**<0.01**
	d_rds	-0.717	0.238	-3.010	**<0.01**	-0.681	0.253	-2.688	**<0.01**
	cmp_prb	-15.415	4.785	-3.222	**<0.01**	-0.789	0.890	-0.886	0.375
	cnsp_prb	5.990	1.798	3.331	**<0.001**	0.985	0.713	1.381	0.167
NG32	*d_prmwtr*	-15.310	797.920	-0.019	0.985	-12.270	760.090	-0.016	0.987

(ii)

		Dry season				Wet season			
Region	**Variable**	**β**	**SE**	***Z***	***P***	**β**	**SE**	***Z***	***P***
Etosha	*elvtn*	8.633	1.364	6.329	**<0.001**	8.302	0.677	12.267	**<0.001**
	d_anthr	-0.760	3.024	-0.251	0.802	-0.165	1.884	-0.087	0.930
	d_ssnwtr	-	-	-	-	-1.444	0.605	-2.389	**<0.05**
	d_rds	-1.227	0.689	-1.782	0.075	-0.755	0.618	-1.221	0.222
	anthrx_prb	14.413	5.298	2.721	**<0.01**	1.497	1.268	1.181	0.238
	temp	-2.622	5.493	-0.477	0.633	2.145	5.364	0.400	0.689
	cmp_prb	-7.907	3.749	-2.109	**<0.05**	-0.569	2.399	-0.237	0.813
	cnsp_prb	-11.062	8.525	-1.298	0.194	-8.815	5.315	-1.659	0.097
Chobe/ Linyanti	*elvtn*	2.688	0.285	9.442	**<0.001**	8.648	1.377	6.279	**<0.001**
	d_anthr	-	-	-	-	1.170	0.901	1.299	0.194
	d_prmwtr	-1.890	1.556	-1.214	0.225	-	-	-	-
	d_ssnwtr	-	-	-	-	-2.269	1.014	-2.238	**<0.05**
	d_rds	-1.009	0.427	-2.364	**<0.05**	-1.226	0.449	-2.732	**<0.01**
	moon_ill	-2.304	6.906	-0.334	0.739	-	-	-	-
	cmp_prb	-18.578	5.584	-3.327	**<0.001**	-1.799	1.145	-1.571	0.116
	cnsp_prb	7.409	2.214	3.347	**<0.001**	1.772	1.003	1.766	0.077
NG32	*d_prmwtr*	-18.830	379.450	-0.050	0.960	-16.850	383.080	-0.044	0.965

Land cover variables are in reference to forested land cover.

CHAPTER FOUR

Relative movement and spatiotemporal ecology of inter- and intraspecific lion and spotted hyena dyads

4.1. Abstract

Background: Interference competition among sympatric carnivores can potentially influence species viability through population reduction or extinction, and has important implications for the structure and function of large carnivore communities. Carnivores may mitigate the risk of competition through fine-scaled spatial or temporal separation that subsequently affects predator interactions and community dynamics. Simultaneous telemetry records of sympatric carnivores allows for an in-depth analysis of individual space use patterns and association metrics. Together with the application of a novel method in analyzing the types of interactions from fine-scaled movement data, quantifying spatiotemporal separation among predator species provides insight into understanding the dynamic interactions between co-existing carnivores.

Methods: We analyzed relocation data of GPS satellite collars from 17 lions (*Panthera leo*) and 14 spotted hyenas (*Crocuta crocuta*) over four-years, across two distinct ecosystems. Data were used to investigate lion and hyena space-use patterns and fine-scale movement of intra- and interspecific dyads. We applied a novel method to characterize the relative movement of these dyads and T-LoCoH (Time-Local Convex Hull) to study species range overlaps from an interactions perspective.

Results: Spatial overlaps among hetero- and conspecific competitors occurred at the edge of home ranges, within 2-5 km of water-points, and within >0.5-1 km along roads, and were indicative of joint, contemporaneous space-use. Temporally overlapping hulls within jointly used areas demonstrated the presence of interactions within the home ranges and core areas of dyads, across seasons and reserves. Lions spent more time together at closer distances with conspecifics than they did with hyenas. Hyenas were found in close proximity with conspecific competitors for short time durations, but spent more long time durations with heterospecific competitors. At distances <5 km to interspecific competitors, hyenas mostly demonstrated avoidance behaviour, whereas lions either moved in the direction of hyenas, or showed random movements. Among intraspecific pairs, lion dyads demonstrated a high occurrence of coordinated movements, whereas hyenas mostly avoided each other at close distances, with some individuals tracking one another at large distances.

Conclusions: Dynamic interactions among sympatric lions and spotted hyenas illuminates how hyenas effectively reduce their potential of interactions with lions by utilizing spatiotemporal partitioning strategies and local reactive avoidance behaviours within shared space use areas. Insight into the drivers shaping the spatiotemporal patterns enabling species co-existence between apex predators is essential in understanding the behavioural choices made by members of a guild that subsequently affects population dynamics and community structure of multi-species food networks. Knowledge of such processes can contribute towards informed management strategies for the effective conservation of such predators and systems.

4.2. Introduction

Interactions among apex mammalian predators can have profound impacts on community structure and population dynamics (Palomares & Caro 1999, Linnell & Strand 2000, Caro & Stoner 2003), potentially increasing the ecological influence of a discrete carnivore species (Terborgh et al. 1999, Hebblewhite et al. 2005). Interspecific competition occurs through either exploitative or interference mechanisms. Exploitative competition is an indirect negative effect in which one species depletes a resource before the other species can access it, and has featured prominently in ecological theory (MacArthur & Levins 1964, 1967, Simberloff 1982, Roughgarden 1983, Holt & Polis 1997). Interference competition is a direct form of competition that occurs when one species denies or restricts the other species' access to a resource (Miller 1967, Schoener 1983, Vance 1984). Among carnivores, interference competition can involve harassment (Lehmann et al. 2017), kleptoparasitism (Balme et al. 2017), direct killing or intraguild predation (Palomares & Caro 1999), and results in reductions in one species' density (Berger & Gese 2007), shifts in habitat use (Nelson et al. 2007), spatial or temporal avoidance (Ramesh et al. 2012), and/or exclusion from certain habitats or regions (Tannerfeldt et al. 2002). Carnivores are also able to mitigate the perceived risk of competition or injury from other carnivores by adjusting their behaviours in response to the perceived presence of competitors (Hayward & Slotow 2009, Broekhuis et al. 2013, Vanak et al. 2013, Haswell et al. 2018). Behavioural modifications such as increased vigilance or decreased rest are other flexible strategies carnivores employ to decrease the risk of competition or injury (Switalski 2003, Andersen et al. 2016). In addition, predators sometimes confer benefits to other predators through the provision of scavenging opportunities (Mattisson et al. 2011), or in releasing a prey's monopoly on a limiting resource (Ripple et al. 2014a), thereby facilitating coexistence among predator species (Sivy et al. 2017, O'Malley et al. 2018).

In many ecosystems, mobile predators of a guild have the ability to adjust their movement decisions to avoid spatial and temporal proximity with one another. Individual and group space-use decisions govern the level of spatial overlap among and between predator species, subsequently affecting predator interactions and community dynamics. As such, there has been an increasing focus on spatiotemporal partitioning among sympatric predators (Ramesh et al. 2012, Lovari et al. 2013, Petrov et al. 2016, Swanson et al. 2016, Karanth et al. 2017, Manlick et al. 2017, de Satgé et al. 2017, Mumma et al. 2017, Hearn et al. 2018), including avoidance of apex predators by cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*) (Durant 2000, Darnell et al. 2014, Swanson et al. 2014, 2016, Dröge et al. 2017), yet few have quantified the effects of such species interactions on the behavioural responses (i.e. movement characteristics) of sympatrically competing lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Moleón et al. 2014). Thus, much more is known about the space-use decisions of either predator, whereas there is relatively little known about the behavioural ecology of their *joint* space use. Understanding interactions among large carnivore species where carnivore overlaps may be extensive has implications for the regulation of prey and species persistence (Terborgh et al. 1999, Ripple et al. 2014a). Such information may prove crucial to protected area management and the development of informed conservation strategies in light of a changing climate and ongoing land-use constraints (Riggio et al. 2013, Ripple et al. 2014b, Tuqa et al. 2014).

The African lion and the spotted hyena, two of Africa's largest predators, continue to co-exist within protected areas despite a high degree of overlap in their habitat use (Périquet et al.

2015a), temporal activity budgets (Hayward & Slotow 2009), and diet (Hayward & Kerley 2008). Despite highly coordinated movements among lions within the same pride, the spatiotemporal patterns of lion ranges from different prides reveals small to minimal overlaps among female lion territories, with negligible to zero overlap among male lion territories (Loveridge et al. 2009, Kittle et al. 2016, Yiu et al. 2017, Zehnder et al. 2018), indicating avoidance behaviour among different prides. Spotted hyena clan territories are largely exclusive, and clans avoid each other temporally in areas of interclan overlap (Tilson & Henschel 1986, Mills 1990). Territoriality in hyenas results in relatively little overlap between neighbouring clans (Henschel & Skinner 1991, Boydston et al. 2001) because of interclan competition (Smith et al. 2008). Thus, potentially, mitigation of *intra*specific competition within lions and spotted hyenas facilitates coexistence between them. However, there still remains a gap in our knowledge of the spatiotemporal dynamics of lion and spotted hyena interactions. Specifically, the prevalence of spatiotemporal separation has yet to be quantified among lion and hyena interactions.

Understanding the conditions under which coexistence occurs when species exhibit spatial overlap and exploit similar resources is a challenge. Sympatrically occurring carnivores with dietary overlaps appear to mitigate competition through fine-scaled behavioural adjustments that result in the spatiotemporal partitioning of one species' range use in response to the presence of the competitor species (Brook et al. 2012, Soto & Palomares 2015, Petrov et al. 2016, Monterroso et al. 2016, Bianchi et al. 2016, Dröge et al. 2017, Herrera et al. 2018, Mueller et al. 2018, Sogbohossou et al. 2018, Rich et al. 2018). Thus, studies should incorporate an analysis of both the space use patterns and the intra- and interspecific interactions of the competing species (Ritchie et al. 2009). Two species can utilize the same resources but may be distributed at different locations and never interact directly (Darmon et al. 2012), or may exhibit temporal heterogeneity in their use of the shared resources (Edwards et al. 2015). As temporal differences in the use of resources were shown to facilitate coexistence of other large carnivore species (Karanth & Sunquist 2000), it becomes prudent to use a method of measuring movement patterns that detect temporal and spatial differences between the two species.

In this study, we aimed to evaluate the joint space use, movement and proximity characteristics of two sympatrically occurring and competing predator species under varying seasonal conditions. We first analyzed the temporal patterns of spatial overlap between lions and spotted hyenas to assess the extent of contemporaneous interactions between the two species. We then tested for significant differences among time-matched hulls against an equal subset of randomly paired hulls. Finally, we applied a novel method (Vissat et al. 2021) to quantify the effects of such species interactions on the movement characteristics of lions and spotted hyenas, as well as investigate whether these interactions were primarily influenced by interference competition from heterospecific or conspecific competitors of different social groups. We expected that intraspecific competitors would result in relatively more avoidance behavioural responses than interspecific competitors. We also expected that lions would elicit strong behavioural responses in spotted hyenas, and that hyenas would combine spatial avoidance with localized avoidance behaviours in locations of contemporaneous spatiotemporal overlaps with lions. Specifically, we expected that spotted hyenas would respond to lions reactively by adjusting their movements to avoid encounters with lions, and to actively move away from such potential encounters.

4.3. Methods

4.3.1. Study areas

This research was conducted within two areas of southern Africa (Fig. 4.1): the Etosha National Park, a fenced protected area in northern Namibia, the Chobe National Park, an unfenced protected area in northeastern Botswana, and adjacent to this, the Linyanti Conservancy, a community managed wildlife area within the Chobe Enclave. The study area represented a subset of each of the parks, encompassing a region of 17,500km^2 and focused on the lion and spotted hyena populations in the Okaukeujo and Halali regions (Etosha), and along the riparian zone of the Chobe and Linyanti rivers, hereafter Chobe.

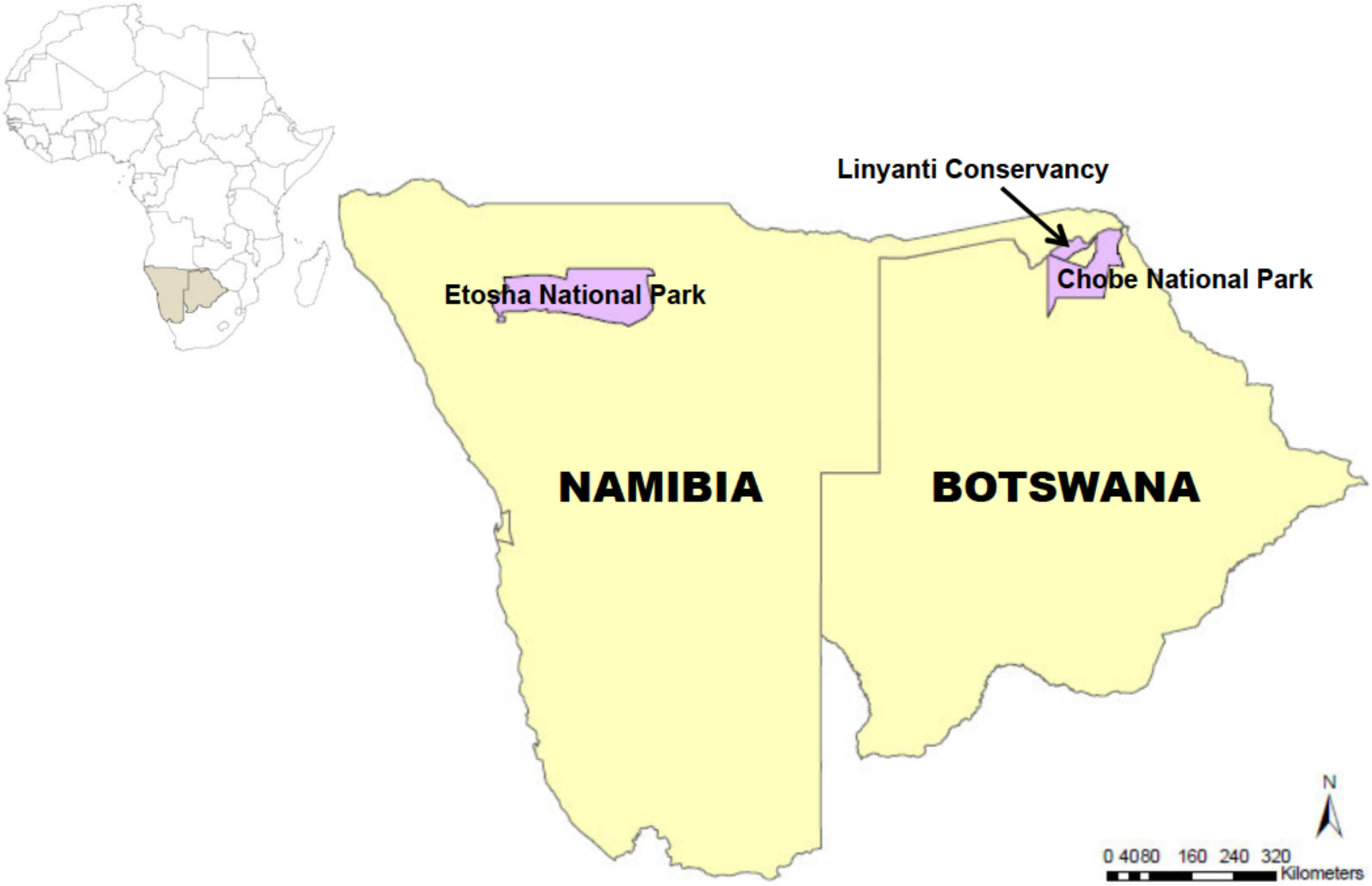


Figure 4.1. Location of the study areas. The map of the African continent shows the countries of Namibia and Botswana shaded, and the protected areas within these countries where the study was conducted. Maps were generated with ArcGIS (ESRI ArcMap v.10.0).

4.3.2. Data collection

Global Positioning System (GPS) satellite collars with dual-axis accelerometers (IridiumTrackM, Lotek Wireless Inc., Newmarket, Ontario, Canada) were fitted to 17 adult lions (13 females and 4 males) and 14 adult spotted hyenas (10 females and 4 males) and set to record fixes every 30 min from 18h00 – 6h00 or 17h00 – 8h00, and every 5 min for two hours after sunset and before sunrise, with two fixes during the day at 10h00 and 14h00 respectively (Hayward & Slotow 2009). See Supplementary Table S4.1 for a summary of the data collected for all collared individuals, and the number of tracking days over the tracking period for each individual. Collared animals were located using satellite uploads of GPS locations, and, when necessary, radio-tracked from a vehicle using a handheld 3-element Yagi antenna (Lotek), and a custom built vehicular-mounted 5-element antenna, with a SRX 600 telemetry receiver. Satellite data were monitored on a daily basis for each individual to ensure no mortality, and individuals with locations accessible by the road network prior to sundown were selected for continuous follows during the night for the ground-truthing of acceleration data. Animals chosen for collaring were identified to belong to separate groups (see supplementary materials to methods in Chapter 2 for details), with females favored as they represented natal breeding group members, and because males have higher likelihoods of dispersal. Thus, all known groups within the study area included a collared individual, and the ranges of these selected species groups overlapped extensively with the study area. All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018), and all Geographic Information System (GIS) applications were conducted in ArcGIS (ESRI ArcMap v.10.0, Redlands, CA, USA).

4.3.3. Spatially and temporally overlapping hulls

We constructed seasonal utilization distributions (UDs) for each individual using *a*-LoCoH (adaptive Local Convex Hull) method in the "*T-LoCoH*" (time local convex hulls) R package (Lyons et al. 2013). The T-LoCoH methods itself facilitates the identification of regularly revisited sites (Getz et al. 2007). We used the 95% and 50% UDs to respectively represent the home ranges and core use areas of individuals. We used the intersection function from the "*rgeos*" R package to compute the areas of overlap between neighbouring individuals' ranges.

For each of the overlapping ranges between a lion and spotted hyena pair (pair of individuals - dyad forthwith), we computed the hull metrics for spatially, and then temporally, overlapping hulls for each dyad. Spatially overlapping hulls are hulls that intersect irrespective of time, and the number of intersecting hulls provides a coarse measure of shared used space without regard to time (Lyons 2012). Temporally overlapping hulls require that the overlap of hulls occur contemporaneously. Since hulls are composed of the hull parent point and nearest neighbours identified by the time-scaled distance (TSD), and are unique to each individual, a measure of the temporal lag time between joint space-use can be derived from the minimum time difference of the hull parent points for each individual (Lyons 2012). Hulls that have no temporally overlapping counterpart are assigned a value of NA (missing value) (Lyons 2012). Thus, it is possible for spatially overlapping hulls (the number of intersecting hulls) and temporally overlapping hulls (minimum time difference between hull parent points) to differ in that the hulls overlap spatially but not temporally, and to differ between individuals within a dyad.

As we were interested in lion-hyena interactions on a fine scale, we focused our hull metric analyses during the periods of dusk and dawn, as this was the period when sampling intervals were every 5 min, and when lions and spotted hyenas were most active. Using the "*T-locoh.dev*" R package, we extracted the frequency of intersecting hulls, and the minimum time lag between spatially overlapping hulls, for each dyad. For temporally overlapping hulls, we used a maximum time interval of 2.5 min to compute the mean centroid distances, and tested for equal means between time-matched and randomly paired centroid distances. We used the Welch Two Sample *t*-test ("*stats*" R package) to test whether the distribution of time-matched centroid distances were significantly different from a null model of no interaction, using an equal number of randomly paired hulls. In addition, we used two-sample Kolmogorov-Smirnov tests ("*stats*" R package) to test whether time-matched and randomly paired centroid distances came from the same distribution.

We assessed the frequency of spatial overlaps between dyads on the map, and determined whether spatial overlaps occurred within the center of either individual's home range, or at the edge of home ranges. We checked with the chi-square test to determine whether increased spatial overlaps between dyads occurred more often at the edge of ranges or inside of home ranges. We further related the intensity of spatially overlapping hulls between lions and hyenas to the distance from water and roads, two landscape features known to influence the space use patterns of both species (Abade et al. 2014, Kushata et al. 2018, Vitale et al. 2020, Périquet et al. 2021). We focused on high incidences of spatial overlaps between dyads, and assigned them into distance bins of 25 m, 50 m, 100 m, 200 m, 500 m, 1 km, and 2 km from the nearest water and road. We then assessed with the mixed effects analysis of variance (ANOVA) on whether lions and hyenas had increased frequencies of high spatial overlaps at closer distances to water and roads.

4.3.4. Frequency of time-matched distances

The distances between collared individuals were obtained to analyze for interactive effects. We developed a temporally aligned matrix for each individual that overlapped in their collaring periods. For each sampling record of collar overlap, we measured the minimum Euclidean distance of that individual to all other collared individuals, at all locations, over the same time period. For each individual, we calculated the percentage frequency occurrences of time-matched distances between the individual to any heterospecific or conspecific competitor, in five frequency bins between distances of 5 km, 1 km, 200 m, 100 m, 50 m, and 10 m. We used the *t*-test to compare the frequencies that lions and hyenas were at to competitors at different distances. We determined whether lions or spotted hyenas occurred at closer distances more often to each other (heterospecific competitors) than with one another among their own species (conspecific competitors) with the chi-square test.

4.3.5. Consecutive time points

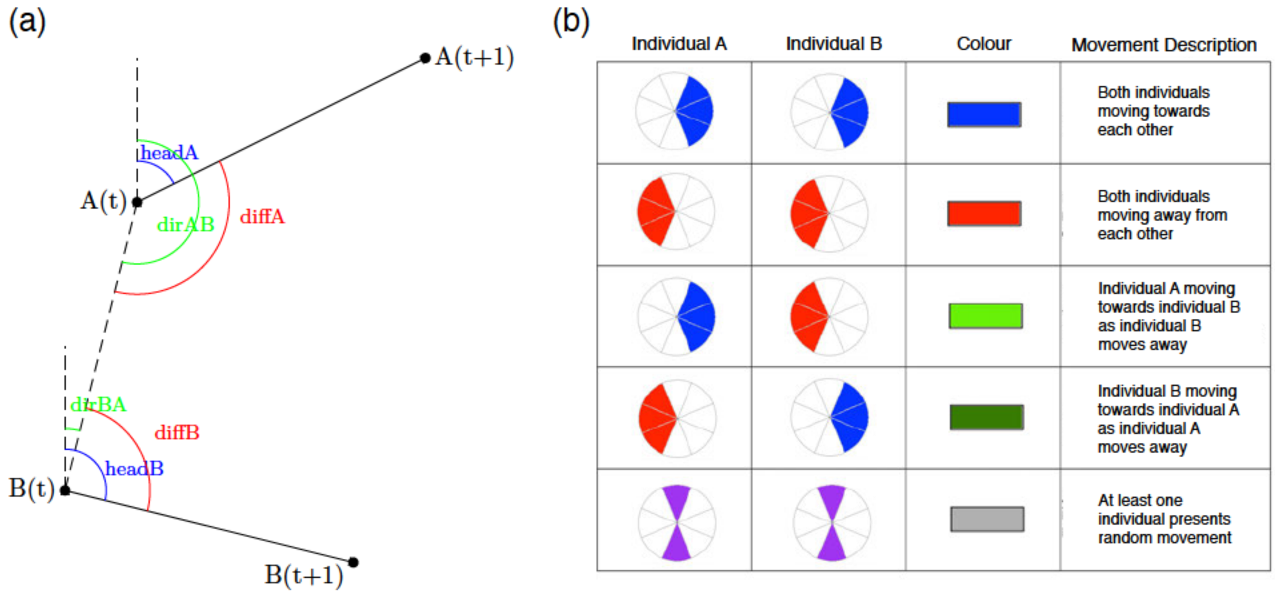
In addition, we ascertained the length of time individuals spent with either competitors or conspecifics. We used the *distm* function from the "*geosphere*" R package to calculate the distance for each time-matched point in the movement path for each dyad. We then calculated the number of consecutive time points (indicating a longer duration together) for which the individuals were at a distance below a given value (2 km, 1 km, 500 m, 200 m, 100 m). We again used the t-test to determine whether either lions or spotted hyenas occurred at closer distances more often to heterospecific or conspecific competitors, during consecutive time points.

4.3.6. Movement responses of individuals

As we were interested in the movement interactions between species on a finer scale, we focused our analyses on individuals with bursts of data obtained from 5 min sampling intervals. These consisted of 13 lions (10 females and 3 males from Namibia, with 3 females from Botswana) and 8 spotted hyenas (6 females and 1 male from Namibia, with 1 female from Botswana). We examined the distribution of the mean step lengths for each burst of data for all lions and hyenas together, and assessed the mean step lengths for each individual. We further subdivided the bursts into their respective morning (4h00-6h00) and evening (19h00-21h00) periods to assess individual mean step length for each of the two periods.

We then analyzed the movement behaviour of pairs of individuals, using approach and retreat behaviours as a means of identifying the type of interaction occurring between individuals. This method is described elsewhere (Vissat et al. 2021); briefly dyad pairs were identified from the 5 min sampling intervals representing lion-lion, hyena-hyena, lion-hyena interactions with minimum distance less than or equal to 5 km. We first computed the absolute heading and direction of each individual towards the other within the pair. We defined as *absolute heading* at time *t* the angle between the North direction and the vector between the position of the individual at time *t* and at time *t* + 1. These angles are shown in blue in Figure 4.2a. We defined as *direction towards the other*, the angle between the North direction and the vector between the position at time *t* of the considered individual and the position at time *t* of the other individual, shown in green in Figure 4.2a. We used the bearing function from the "*geosphere*" R package to calculate these angles.

For each detected dyad (A,B), we evaluated the difference between the absolute heading and the direction of each individual towards the other animal (shown in red in Figure 4.2a). We divided a circle (which consists of all possible angles of a turn) into eight sections and established that if the absolute value of the difference were either below 67.5 or above 292.5 degrees, then individual A is said to be moving *towards* individual B. However, if the absolute value lies between 112.5 and 247.5 degrees, then individual A is said to be moving *away* from individual B (Fig. 4.2b). Subsequently, any value that falls in between these two sections is orthogonal and deemed to be of random movements in relation to the other individual. Individuals were coded as moving towards, away, or randomly relative to each other. Note, we checked that this analysis was not sensitive to random movements. In one analysis we considered just the towards and away segments, and checked if the results changed when using all the segments including the random ones, and the results did not change.



Individual A	Individual B	Colour	Movement Description
		🟦	Both individuals moving towards each other
		🟥	Both individuals moving away from each other
		🟩	Individual A moving towards individual B as individual B moves away
		🟩	Individual B moving towards individual A as individual A moves away
		⬜	At least one individual presents random movement

Figure 4.2. A description of the relative-motion method in using approach and retreat behaviours to identify the type of interaction occurring between individuals. (a) Absolute heading of individual A and B (angles shown in blue, see text for details). Direction towards the other individual (angles shown in green, see text for details), and the difference between these two angles (red) for individual A and B. (b) Legend for barplots depicting the simultaneous movement behaviours of both individuals A and B in the dyad. The blue represents movements towards, red is movements away, and purple random movements.

From these bursts of activity during dusk and dawn periods, we counted the number of movements towards (blue) and away (red) from the other individual. We designated nine distance intervals of 0<50 m, 50<100 m, 100<200 m, 200<500 m, 500 m<1 km, 1<2 km, 2<3 km, 3<5 km, and 5<10 km, and grouped the counts for each individual when at a particular distance in a given interval. We computed the 95% confidence interval of approach (towards) and retreat (away) movements from the other individual in the dyad, for each of the distance intervals available for that dyad. Using the "*binom*" R package (Dorai-Raj 2014), we calculated the confidence interval for each distance bin, taking the proportion of movement towards (blue) the other individual over the total number of towards/away movements calculated for that dyad. We expected this value to be equal to 0.5 for random movement. If the calculated 95% confidence interval did not include this value, we conclude that there was a statistically significant difference between individual movements from random movements. For certain pairs, where individuals spent some time at close distances to each other (i.e. < 15 m and < 100 m) and we had sufficient data, we assessed, using the same statistical analysis, whether individuals exhibited different behaviours at these two close distances (effectively adjacent (0-15 m), or nearby (15-100 m)).

We plotted the distribution of towards, away, and random movements for each individual in the pair, and grouped them accordingly to the distances among the individuals in the pair. We then calculated the ratio between the towards movements and the sum of towards and away movements. Values close to 0 implied movement mostly away from the other individual, while values close to 1 implied movement mostly towards the other individual. Values close to 0.5 represented a similar number of movements both towards and away from the other individual, which we defined as random movements.

4.3.7. Movement responses of dyads

For given dyads (A,B), we repeated the analysis to evaluate simultaneous movement behaviours in which two individuals moved at the same time to come closer or further apart or one approaches as the other moves away. For each time point during that period of 5 min sampling intervals, we assign one of five different types of simultaneous movements (Fig. 4.2b). We repeated the statistical analysis as above, excluding the random (orthogonal) movements, and we evaluated whether or not the proportion of the four different movement behaviour types was significantly different from random (Fig. 4.2b). Thus, when there is random movement, we expected this proportion to be equal to 0.25 for each movement type. Again, we plotted the distribution of the different movement types, and grouped them according to the distances between the individuals in the pair. Finally, we presented the simultaneous behaviour over time for the dyad at distances below 10 km, with each point coloured to the corresponding simultaneous movement type. We indicate cases where individual movements or the pair's movement types differed significantly from random movements with an asterisk (Tables S4.2.1-4, Supplementary materials). For each dyad, we illustrated, with the ratio and distribution plots, which individual was demonstrating movements towards or away from the other, for a given distance interval. In addition, distance over time plots revealed incidences of simultaneous approach/retreat behaviours exhibited by the pair throughout the study period.

4.4. Results

4.4.1. Data Collection

We retrieved 57% of all possible relocations while collars were deployed, due to the loss of collars from individuals that were killed, or for which we were unable to retrieve the collar (*n* = 3 lions and 6 hyenas). These data (*n* = 349,163) from the two study areas comprised of 55% lion and 45% spotted hyena relocations (Table S4.1, Supplementary materials). Collared lions were sometimes observed together in both Etosha (51% of fixes within ≤50 m to the other) and Chobe (6% of fixes within ≤50 m to the other), while only female collared hyenas occurred together in Etosha and Chobe (1% and 2% of fixes within ≤50 m to the other, respectively). Of the collared lions observed together within ≤50 m in Etosha, 65% were of female-female pairs, and 35% were of male-female pairs. However, in Chobe nearly all of the pairs were male-female, with 1% female-female.

4.4.2. Spatially and temporally overlapping hulls

We found a high degree of spatial overlap between lions and spotted hyenas in their home ranges and core areas across the two ecosystems. Lions and hyenas shared more of their home ranges than they did their core areas, with core area overlaps being at most a quarter of the entire overlap in their home ranges. The frequencies of overlapping hulls within an individual's home range indicate the areas of spatial overlaps or shared space-use with a competitor (Figs. 4.3a-b). Areas of high spatial overlaps typically occurred at the edge of individual ranges (Table 4.1; and see Appendix S4.1). Increased spatial overlaps among lions and hyenas were found to differ as a result of the distances from roads (Etosha F = 10.76, Chobe F = 3.87, $p < 0.001$; Fig. 4.3) and water points in Etosha (F = 24.70, $p < 0.0001$; Fig. 4.3) or the river in Chobe (F = 3.11,

$p < 0.01$; Fig. 4.3). Lions had greater intensity of spatial overlaps than hyenas within 50 m from the river in Chobe during the dry season ($F = 3.65$, $p < 0.01$; Fig. 4.3), while hyenas had a greater intensity of spatial overlaps than lions at further distances from the river (2 km) in both seasons ($F = 13.72$, $p < 0.001$; Fig. 4.3). However, in Etosha during the dry season, spotted hyenas had greater intensity of spatial overlaps than lions within 200 m from water points up to 2 km ($F = 3.55$, $p < 0.01$; Fig. 4.3).

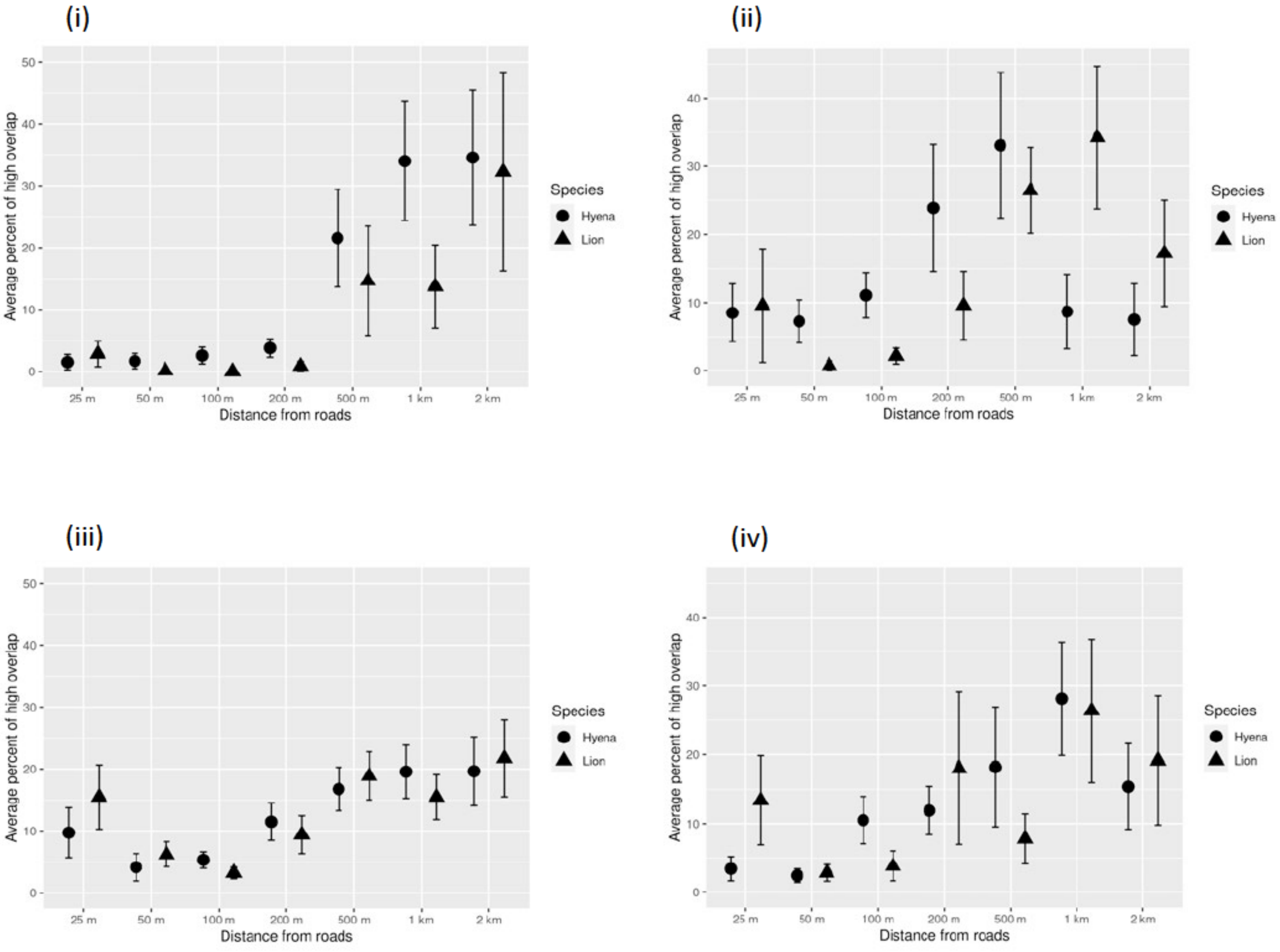


Figure 4.3.a. Increased intensity of spatially overlapping hulls for each of lions and spotted hyenas at distance intervals from roads. Dry season (i, iii) and wet season (ii, iv) of spatially overlapping hulls for lion and hyena dyads from the Etosha National Park, Namibia (i, ii) and the Chobe National Park and Linyanti Conservancy, Botswana (iii, iv).

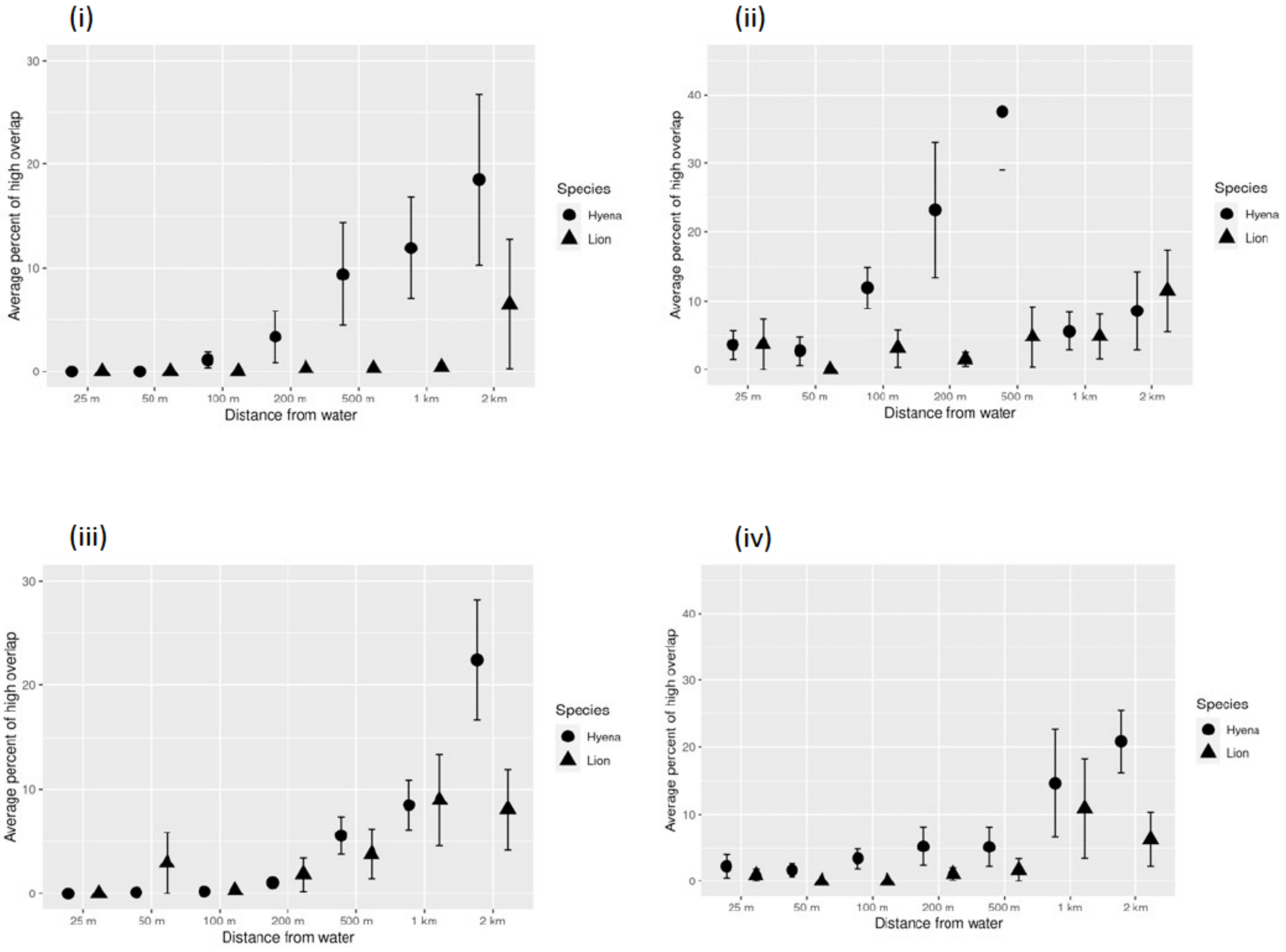


Figure 4.3.b. Increased intensity of spatially overlapping hulls for each of lions and spotted hyenas at distance intervals from water points in Etosha and the river in Chobe. Dry season (i, iii) and wet season (ii, iv) of spatially overlapping hulls for lion and hyena dyads from the Etosha National Park, Namibia (i, ii) and the Chobe National Park and Linyanti Conservancy, Botswana (iii, iv).

Analyses of dyads' hull association metrics are presented in Appendix S4.1-3 (Supplementary materials). With the minimum time lag separated into different periods of 0, >0-15 mins, >15 mins-1 h, >1-2, >2-12, >12-24, and >24 h, the majority of the minimum time between overlapping hulls for nearly all dyads occurred at >12-24 and >24 h (Figs. 4.4c-d). Hulls with a minimum time lag of 0 min occurred for several lion-hyena dyads from each of the dry and wet seasons in Etosha and Chobe, and are indicative of joint space-use at the same times (see Appendix S4.2, Supplementary materials for more details).

Interactions between lion and spotted hyena dyads were identified from the temporally overlapping hulls within these joint space-use areas (Figs. 4.4e-f). There was significant interaction (Welch Two Sample *t*-test $p < 0.05$) in the temporally overlapping hulls among the home ranges (95% range) for most lion-hyena dyads in Etosha, and for at least half of the lion-hyena dyads in Chobe for each season (Table 4.1, and see Appendix S4.3, Supplementary materials). Similarly, there was significant interaction ($p < 0.05$) in the temporally overlapping hulls within core areas (50% core use area) for the majority of the lion-hyena dyads in each season for both Etosha, and for at least half of the lion-hyena dyads in Chobe (Table 4.1). Overall, Etosha dyads had higher occurrences of interactions between lions and spotted hyenas both in home ranges and core areas, than did Chobe dyads (Table 4.1).

Additionally, there were significant differences in the distributions of time-matched versus randomly paired centroid distances for all dyads (two-sample Kolmogorov-Smirnov test $p < 0.05$). Histograms of the significant temporal overlapping dyads ($n = 74$) revealed similar occurrences of right-skewed (44.6%) and normal (43.2%) distributions, with few left-skewed (12.2%) distributions. Although normally distributed dyads indicate neither a magnetic or repulsive effect, right-skewed dyads (e.g., NU-33865 & GO-33869; SU-33868 & SA-33872 in Appendix S4.3) indicate that these individuals remained closer together during time-matched observations, whereas left-skewed dyads (e.g., OJ-33867 & SA-33872; KB-36717 & KW-33871 in Appendix S4.3) were further apart than random pairing.

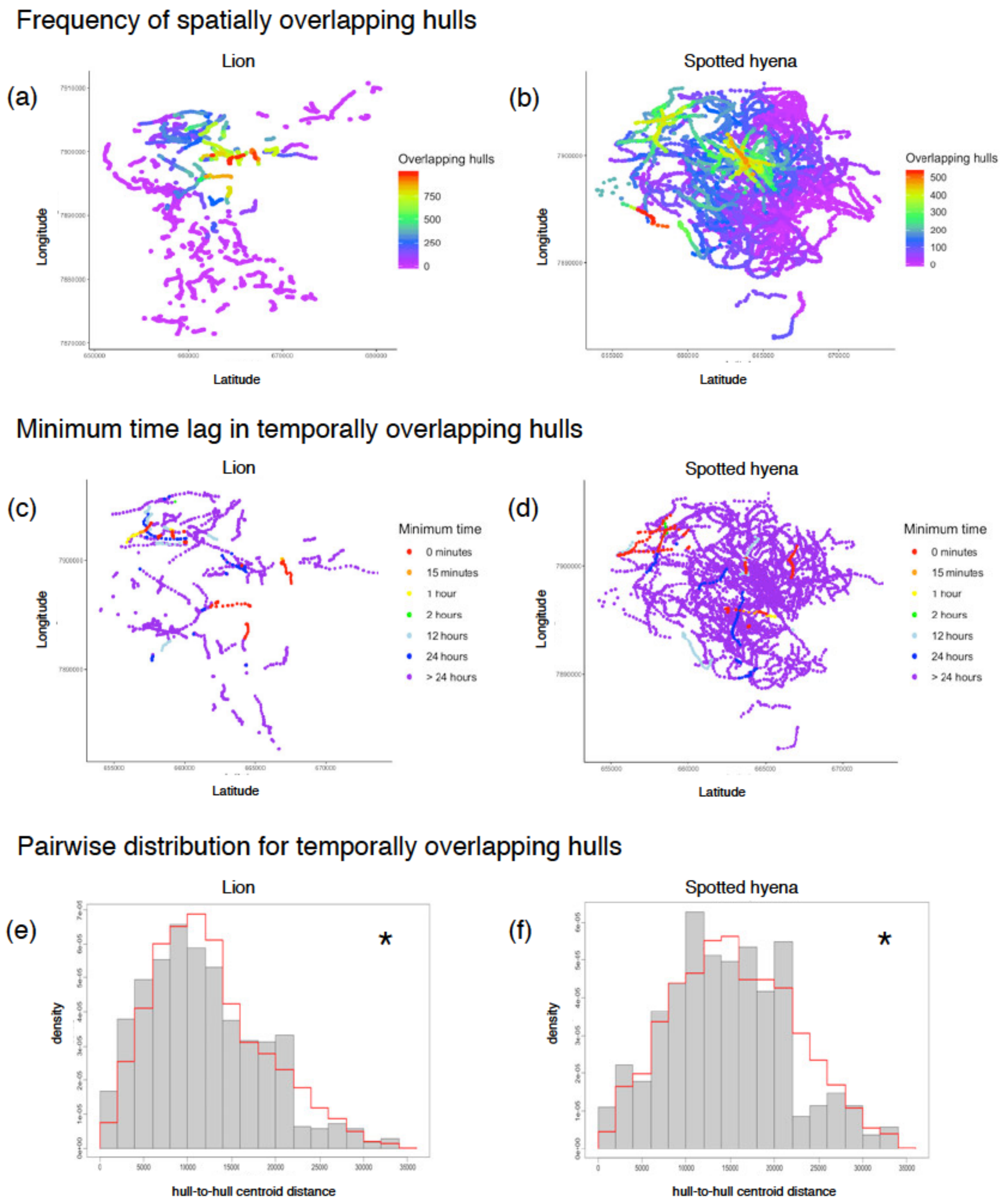


Figure 4.4. Hull association metrics of a single lion (NU-33865) and spotted hyena (GO-33869) dyad from Etosha, Namibia. Overlapping hulls for the individual in the dyad are shown for the lion (a, c) and the hyena (b, d). Plots depict the frequency of (a, b), and minimum time lag (c, d) in spatially overlapping hulls for the dyad. In (a, b), red colours indicate the greatest number of overlapping hulls, and purple the least. In (c, d), purple colours indicate a time lag of >24 h between overlapping hulls, and red colours indicate when the dyad occurred in the same area at the same time. Histograms show the pairwise distribution of the mean centroid distance for temporally overlapping hulls in the home range (e), and core area overlap (f) between the lion-hyena dyad. The red line is the histogram envelope from an equivalent number of randomly matched pairs of hulls, and represents the null model of no interaction. An asterisk denotes significance ($p < 0.05$).

Table 4.1. (i) Chi-square results on the frequencies of spatially overlapping hulls between individuals from dyads (see *Appendix S4.1* for all dyads). Spatially overlapping hulls either occurred within the center of the individual's home range or at the edges of their home range. (ii) Percent frequencies of significant interactions observed in temporally overlapping hulls among home ranges (95%) and core use areas (50%) of lion and spotted hyena dyads ($n = 50$) for each season from the Etosha National Park, Namibia and the Chobe National Park and Linyanti Conservancy, Botswana (see *Appendix S4.3* for all dyads). (iii) Chi-square results on the frequencies of significant interactions from (ii). An asterisk denotes significance at the alpha level with * < 0.05, ** < 0.01, *** < 0.005, and **** < 0.001.

(i)

Region	**Center**	**Edge**	**Significance**
ENP ($n = 60$)	18	42	***
CNP ($n = 40$)	6	34	****

(ii)

	Region	**Overall (%)**	**Dry season (%)**	**Wet season (%)**
Home ranges	Etosha ($n = 8$ dry, 22 wet)	87	63	96
	Chobe ($n = 8$ dry, 12 wet)	60	50	67
Core use areas	Etosha ($n = 8$ dry, 22 wet)	80	75	82
	Chobe ($n = 8$ dry, 12 wet)	60	50	67

(iii)

	Region	**Season**	**Frequency**	**Significance**
Home ranges	ENP	overall	26	****
		dry	5	
		wet	21	****
	CNP	overall	12	
		dry	4	
		wet	8	
Core use areas	ENP	overall	24	***
		dry	6	
		wet	18	
	CNP	overall	12	
		dry	4	
		wet	8	

4.4.3. Frequency of time-matched distances

Of 1,155,488 records of distances between collared individuals that overlapped in time, 46.7% occurred between conspecifics (26.1% for lions and 20.6% for spotted hyenas), and 53.3% occurred between lions and spotted hyenas (competitors). From these data, we extracted all measured records between two collared individuals that occurred at a distance of ≤5 km (*n* = 34,682). Overall, predators were at distances of ≤5 km to competitors and conspecifics with nearly equal frequency (51% and 49%; $x^2 = 0.071$, df = 1, $p > 0.05$; Fig. 4.5). Etosha lions occurred at distances of ≤5 km with each other more often than Chobe lions did ($x^2 = 39.69$, df = 1, $p < 0.001$), while Chobe hyenas were at distances of ≤5 km with each other more often than Etosha hyenas were ($x^2 = 8.29$, df = 1, $p < 0.005$). Etosha lions occurred more often with competitors at further distances (1-5 km), and with conspecifics at closer distances (0-50 m), whereas hyenas occurred at distances of <5 km with competitors more often than with conspecifics (Fig. 4.5, and Table S4.3, Supplementary materials). However, hyenas in Chobe occurred more often with conspecifics than they did with competitors at distances of 200 m-1 km (Fig. 4.5, and Table S4.3, Supplementary materials). In addition, lions and hyenas tended to be at further distances to competitors than to conspecifics, although this was not significant in all cases (Table S4.3, Supplementary materials).

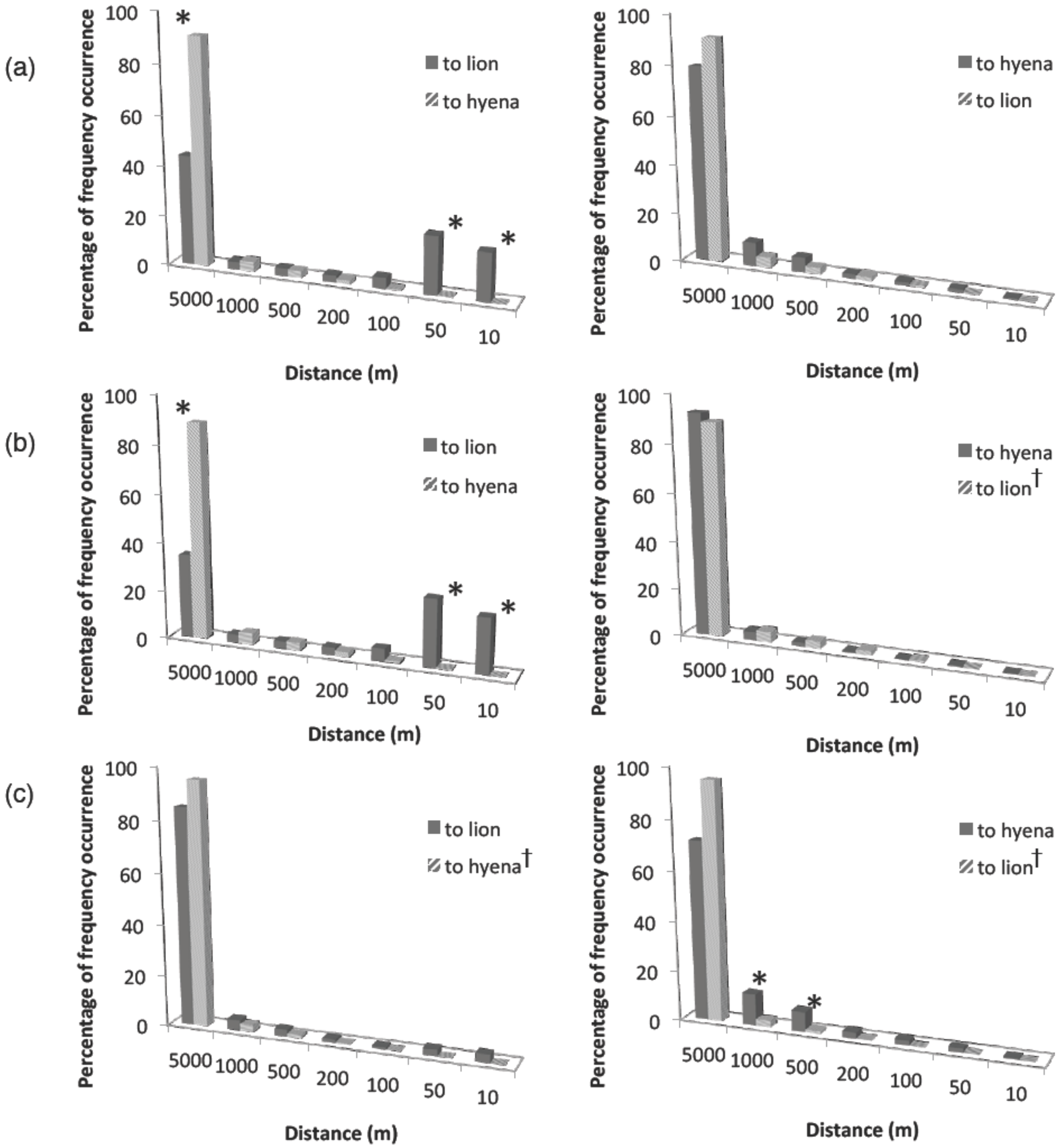


Figure 4.5. Percent frequency occurrence of time-matched distances from lions (left side plots) and spotted hyenas (right side plots) to collared individuals at distance intervals of 0-10 m, >10-50 m, >50-100 m, >100-200 m, >200-500 m, >500-1000 m, and >1-5 km. Dark grey bars reflect frequency of distances to conspecifics, and hatched bars frequency of distances to competitors. (a) Overall percentage frequency occurrence, (b) Etosha animals, and (c) Chobe/Linyanti animals. Asterisks denotes the significant difference between competing groups for that interval; and a dagger indicates which competing group has the greater percent frequency occurrence between 0-5 km. Statistical results are presented in Table S4.3 (Supplementary materials).

4.4.4. Consecutive time points

During consecutive time points (which indicates a longer duration of time together), there were significantly more instances of lion-lion dyads at distance intervals of 0-100 m, 100-200 m, 200-500 m, and 500-1000 m than there were of lion-hyena dyads, indicating that lions spent more time together at these distances than they did with hyenas (Fig. 4.6). In addition, intraspecific dyads had more instances (85%) of being together for consecutive time points than interspecific dyads (15%). Lion dyads consistently presented higher values for both the "11-30" and ">30" consecutive time point groups, indicating that they spent more time together at these distances than they did with hyenas, and more than hyenas did (Table S4.4, Supplementary materials). However, despite higher frequencies of hyenas spending more time together than they did with competitors at shorter consecutive intervals (i.e. "1" and "2" groups indicating 5-10 mins), there were more occurrences of lion-hyena dyads at greater consecutive time points (">30" group), indicating a longer time interval of at least 300 consecutive minutes for lion-hyena dyads at distances between 0-2 km.

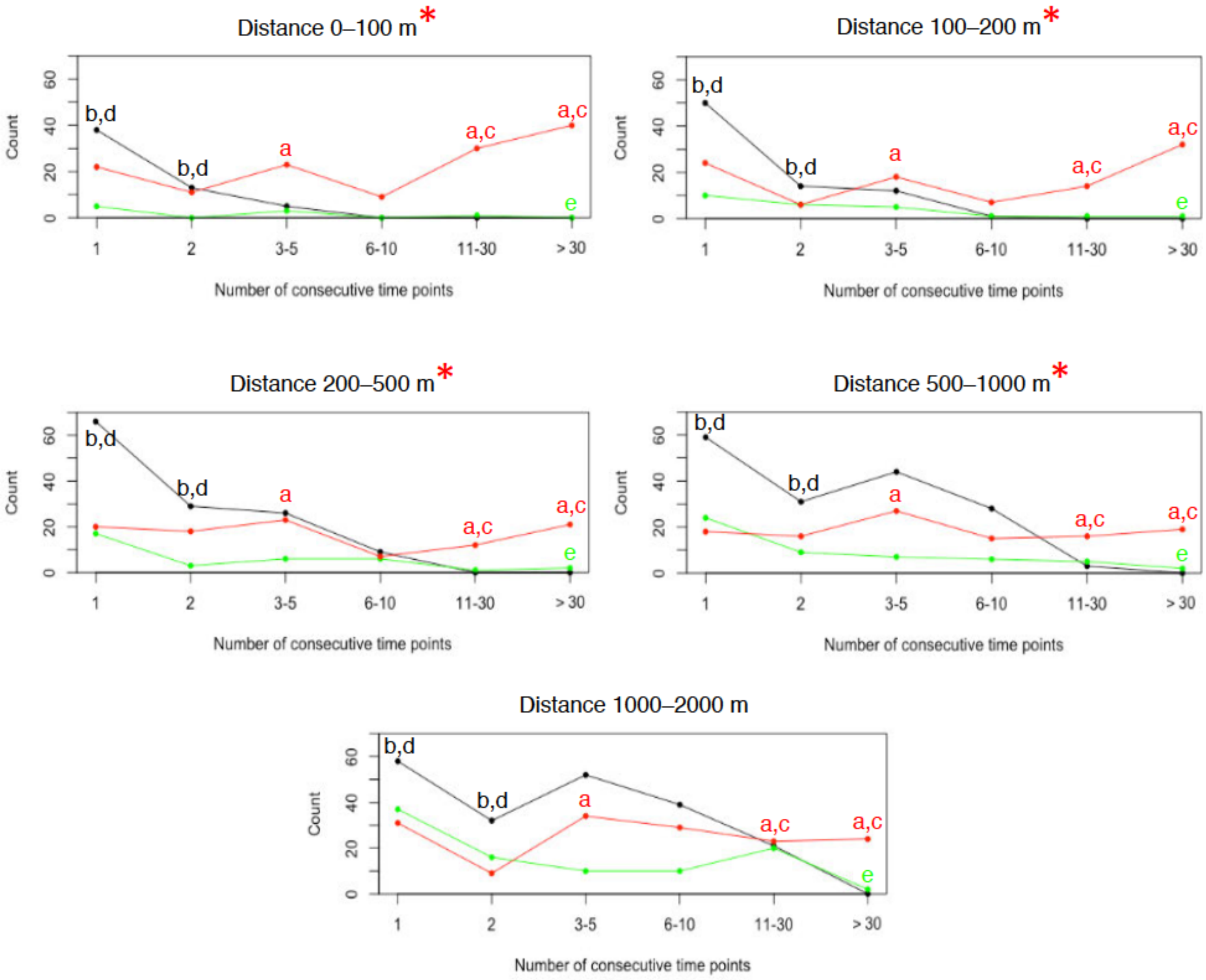


Figure 4.6. Number of consecutive time points (indicating longer time duration) for which pairs of lion-lion (red), hyena-hyena (black), and lion-hyena (green) dyads were at distances of 0-100, >100-200, >200-500, >500-1000, or >1000-2000 m. Red asterisks at distance intervals indicates where the lion-lion dyad had significantly more consecutive time points contrasted to lion-hyena dyads. Letters indicate significance for the dyad at that time duration: lion-lion vs lion-hyena (a), hyena-hyena vs lion-hyena (b), lion-lion vs hyena-hyena (c), hyena-hyena vs lion-lion (d), lion-hyena vs hyena-hyena (e). Number of dyads: 9 lion-lion dyads; 4 hyena-hyena dyads; 10 lion-hyena dyads. T-tests statistical results are presented in Table S4.4, (Supplementary materials).

4.4.5. Movement responses of individuals and pairs from interspecific dyads

Among interspecific dyads (Table S4.2.1, Supplementary materials), spotted hyenas exhibited mostly retreat movements in response to lions, while lions had more approach movements towards hyenas (Table 4.2.i). During simultaneous pair movements, lions mostly tracked hyenas, and hyenas tracked lions more often than they either approached or moved away from each other simultaneously (Table 4.2.ii). Although the movement distribution ratios indicated variation among whether individuals in the dyad utilized approach or retreat behaviours at various distance intervals (Fig. 4.7; and see Appendix S4.4, Supplementary materials for additional pairs), hyenas exhibited significantly more retreat than they did approach or random movements towards the lion counterpart (Table 4.2.iii). Contrarily, lions did not significantly differ in their movements towards their hyena counterpart. At larger distance intervals of up to 5 and 10 km, more than half of the lion-hyena dyads presented a ratio close to 0.5 (67% and 70%, respectively), indicating mostly random movements. Conversely at distances of up to 5 km, 22% of the hyenas moved mostly away from lions.

Table 4.2. Chi-square statistical results for differences among movement types for each focal species (lion or spotted hyena) within a dyad (lion-hyena, lion-lion, or hyena-hyena), as obtained from the (i) individual or (ii) simultaneous movements (Table S4.2.1-4, Supplementary materials), and (iii) movement distribution ratios (Appendix S4.4-5, Supplementary materials). An asterisk denotes significance at the alpha level with * < 0.05, ** < 0.01, *** < 0.005, and **** < 0.001.

(i)

Dyad	Focal Species	Movement types	Percentage of cases		Significance
Lion-Hyena	Lion	towards	38%	$x^2 = 77.44$, df = 3, $p < 0.001$	****
		away	8%		
	Hyena	towards	0		
		away	54%		
Lion-Lion	Lion	towards	74%	$x^2 = 23.04$, df = 1, $p < 0.001$	****
		away	26%		
Hyena-Hyena	Hyena	towards	38%	$x^2 = 5.76$, df = 1, $p < 0.05$	*
		away	62%		

(ii)

Dyad	Movement types	Percentage of cases		Significance
Lion-Hyena	Lion → ←Hyena	12%	$x^2 = 53.20$, df = 3, $p < 0.001$	****
	← Lion Hyena →	6%		
	Lion → Hyena →	53%		
	Hyena → Lion →	29%		
Lion-Lion	Lion → ← Lion	7%	$x^2 = 47.54$, df = 2, $p < 0.001$	****
	← Lion Lion →	30%		
	Lion → Lion →	63%		
Hyena-Hyena	Hyena → ←Hyena	22%	$x^2 = 23.12$, df = 2, $p < 0.001$	****
	← Hyena Hyena →	22%		
	Hyena → Hyena →	56%		

(iii)

Dyad	Focal Species	Percentage of cases *Movement types*				Significance
		approach	*retreat*	*random*		
Lion-Hyena	Lion	35%	25%	40%	$x^2 = 3.50$, df = 2, $p > 0.05$	****
	Hyena	14%	57%	29%	$x^2 = 28.58$, df = 2, $p < 0.001$	
Lion-Lion	Lion	34%	32%	34%	$x^2 = 0.08$, df = 2, $p > 0.05$	
Hyena-Hyena	Hyena	32%	32%	36%	$x^2 = 0.32$, df = 2, $p > 0.05$	

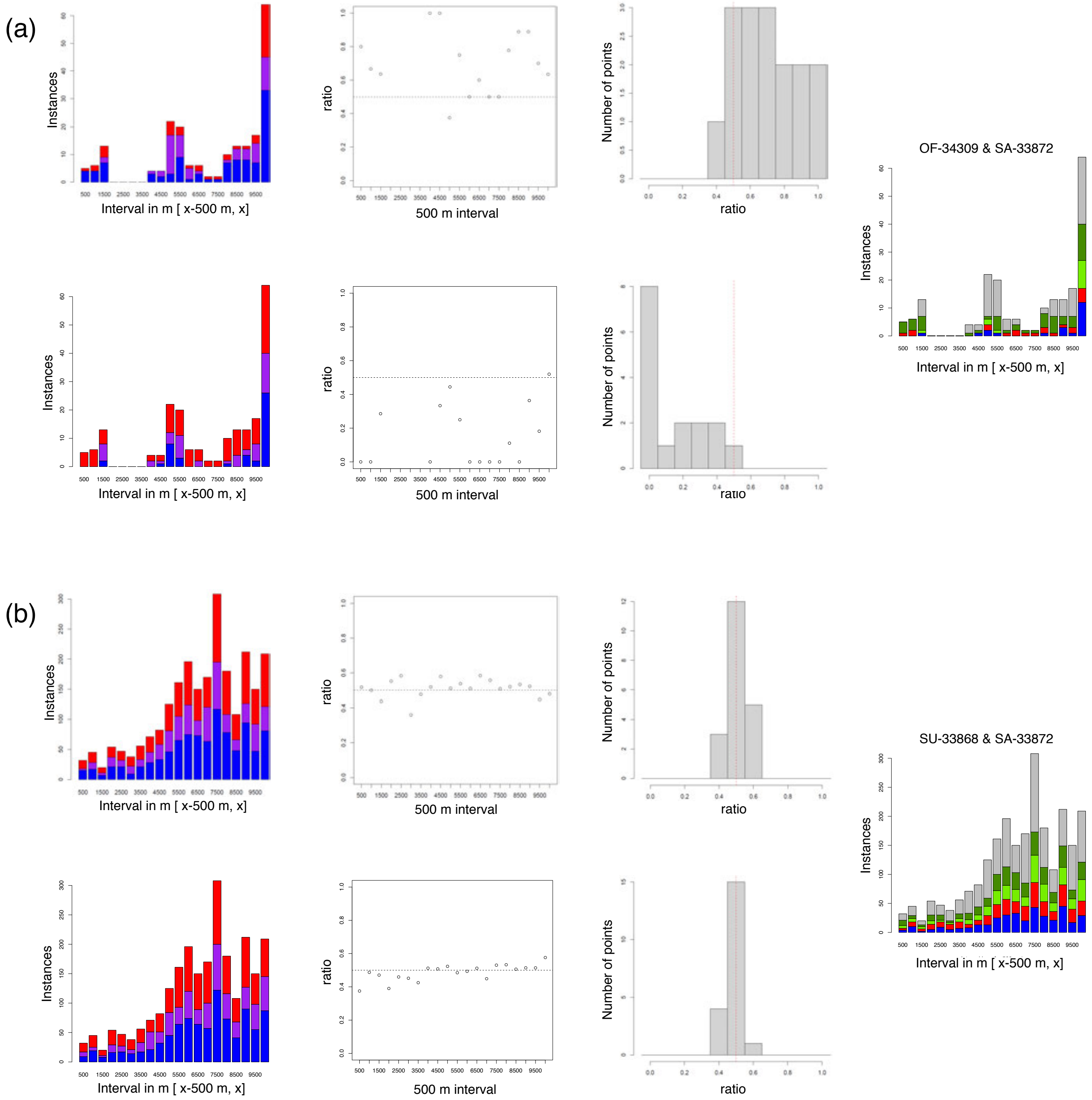


Figure 4.7. Movement distribution and ratio plots for lion and spotted hyena dyads from Etosha, Namibia. Panels on the far left indicate the difference in the heading of one individual towards the other individual, while panels on the far right indicate the dyad's simultaneous movement types at distance intervals from 0-10 km. Panels second from the left indicate the ratio of the blue/(blue + red) areas for the individual, and panels second from the right indicate the distribution for the ratio. Upper three panels in both figures (a, b) represent the movements of the lion towards the hyena in the dyad, and the lower three panels represent the movements of the hyena towards the lion in the dyad. In (a), the lion moves mostly towards the hyena while the hyena moves mostly away, and in (b) both the lion and the hyena demonstrate mostly random movements towards each other.

4.4.6. Movement responses of individuals and pairs from intraspecific dyads

Individual movements from intraspecific dyads differed between species (Table S4.2.2-3, Supplementary materials), in that lions exhibited mainly approach movements towards conspecifics, with spotted hyenas demonstrating mostly retreat movements (Table 4.2.i). However, both lions and spotted hyenas tracked their conspecific counterpart (i.e., following synchronously as the other individual moves) more often than they approached or moved away from each other simultaneously (Table 4.2.ii). At distances of 3-5 km, lions either tracked or moved away from their counterpart lion, whereas at larger distances of 5-10 km, Etosha lions continued to track their counterpart, with Chobe lions exhibiting mostly avoidance movements. Conversely, spotted hyenas demonstrated mostly avoidance movements towards their counterpart hyena at distances of 1-3 km, despite tracking them at distances of 2-10 km.

Furthermore, at close distances of 0-500 m, Etosha lions display highly coordinated movements in which they either moved in the same direction or tracked one another for extended periods. Since three lion dyads were observed to move together for a significant amount of time, we repeated the analysis while looking at the heading difference for both individuals at distances below 100 m and distances below 15 m (Table S4.2.4; Supplementary materials). This analysis indicated a ratio above 0.5 at distances below 100 m, suggesting that these dyads tended to move in the same direction when close to each other. In dyads that consisted of mating pairs, we found that the females tended to move more towards the males when at closer distances (up to 15 m) when she would present herself to be receptive for mating. At further distances (between 15 m and 100 m), the female moved mostly away from the male, whereas the males moved mostly towards the females, presumably in anticipation of the next mating opportunity.

The movement distribution ratios revealed no occurrences of hyena dyads occurring at distances below 2 km, while lion dyads were observed to occur at distances as low as 15 m (Appendix S4.5, Supplementary materials). Both lion and hyena movements were nearly equally distributed among approach, retreat, and random movements towards their conspecific counterpart in the dyad (Table 4.2.iii). However, most of the lion and spotted hyena individuals exhibited random movements (89% and 63%, respectively) at larger distance intervals up to 10km, although retreat movements were demonstrated in 25% of the hyena individuals. In addition, hyenas approached conspecifics more (33%) than they retreated (17%), with half of their movements random (50%; $x^2 = 16.34$, df = 2, $p < 0.001$) at shorter distances of up to 5 km. Contrarily, lions did not differ between random and retreat movements towards conspecifics at distances up to 5 km.

4.5. Discussion

Ecological niches, as a competition-centered property of species' impacts on the environment (Sales et al. 2021), are partitioned both in space and time (Schoener 1974, Hassell et al. 1994), and sympatric guild members have been documented to utilize spatiotemporal separation to facilitate co-existence in the same space (Fedriani et al. 1999, Linnell & Strand 2000, Albrecht & Gotelli 2001, Redfern et al. 2006, Valeix et al. 2007, Ritchie et al. 2009, Darmon et al. 2012). Within Africa's large carnivore guild, carnivores mitigate the risk of dangerous interactions with dominant predators through spatial or temporal avoidance (Durant 1998, Hayward & Slotow 2009, Vanak et al. 2013, Edwards et al. 2015, Ramesh et al. 2017). Our results demonstrate that lions and spotted hyenas behaviourally mediate the potential for interference competition by adjusting their space-use and activity patterns, and movement behaviours in different ways that have implications for co-existence.

Our findings indicate that lions and spotted hyenas utilize either minimal overlaps among core areas or a large lag time of 12-24 and >24 h within shared space-use, as a spatiotemporal strategy to allow the two species to co-exist within the same areas without encountering one another. However, spatially fixed resources such as permanent water points or large carcasses that cannot be carried away (i.e. elephants *Loxodonta africana*), requires that carnivores use a different mechanism to avoid directly encountering one another at these locations. Similar to Atwood et al. (2011) who recorded dominant carnivore species at nearly all of the artificial water points, lions and spotted hyenas were observed at all of the permanent water points in Etosha, providing limited opportunity for spatial resource partitioning to occur. Thus, the degree of partitioning may be associated with the differences in the densities of spatially fixed resources. Edwards et al. (2015) found higher levels of temporal partitioning between free-ranging carnivores, including brown hyenas (*Hyaena brunnea*) and leopards (*Panthera pardus*) on farms with lower densities of water points.

Notwithstanding the spatiotemporal partitioning strategies observed in this study, lions and spotted hyenas persisted in tracking one another and sometimes for extended periods. Although the type of interaction (whether remaining closer together or further apart than random) differed among pairs, the results of this study provides empirical evidence for the presence and occurrence of important interactions among lions and spotted hyenas. Other studies have documented competitive interactions between lions and spotted hyenas (Cooper 1991, Honer et al. 2002, Trinkel & Kastberger 2005, Lehmann et al. 2017, Périquet et al. 2021), including induced changes in one species' behaviour according to the density and distribution of the other (Watts & Holekamp 2008, Watts et al. 2010, Périquet et al. 2015b, 2016, Kushata et al. 2018); however, data, such as we present, on direct interactions between lions and hyenas are rare. In a review of lion-hyena interactions, Périquet et al. (2015a) identified costs and benefits to both species through exploitation and interference competition, scavenging opportunities, and differences in prey selection, while acknowledging a lack of studies using telemetry data on both species simultaneously to examine spatiotemporal avoidance. A recent study in the Serengeti which deployed tracking collars simultaneously on both lions and spotted hyenas, found lions to be strongly positively associated with areas of high hyena utilization (Kittle et al. 2016). To our knowledge, this present study is the first of its kind to use a fine scale sampling method of GPS and acceleration data on the two species simultaneously to allow for an analysis of the direct effects of the two species on one another.

In addition to interspecific interactions, our results indicated a prevalence of intraspecific interactions among lions. Lion prides in both Etosha and Chobe exhibited a fission-fusion social system; however, Etosha lion pairs were at closer distances more frequently than Chobe lions. In both ecosystems, lions occurred at near distances more often, and spent more time together at closer distances with conspecifics than they did with competitors. These results correspond with Benhamou et al. (2014) who found a high degree of joint movement between lion dyads. Lions derive benefits from associating with conspecifics to attain access to high quality habitats and for territorial defense (Mosser & Packer 2009, Yiu et al. 2019), cooperative group hunting (Bailey et al. 2013), and to defend kills against kleptoparasitism from spotted hyenas (Cooper 1991). Our analysis revealed coordinated movements between conspecific pairs, and while both individuals of the pair tended to move towards each other, we were able to determine which individual of the pair was tracking the other. In addition to knowing who was tracking whom, our analysis was also able to illustrate the movement behaviours synonymous with mating between lion pairs.

In contrast, Chobe hyena clans were observed to exhibit more of a fission-fusion social system than was seen with the Etosha clans. Hyenas from different clans in Chobe were sometimes observed to share large carcasses, at times feeding together or within minutes of each other. Etosha clans occupied nearly exclusive territories that fluctuated seasonally with the migratory movements of prey species (see Chapter 2), and encounters among members of neighbouring clans were rare. These findings coincide with previous studies in Etosha (Trinkel et al. 2004, 2006), and are similar to hyena clan territories in the Serengeti which remain largely exclusive with frequent foraging trips outside territories to feed on migratory herbivores (Hofer & East 1993). On the rare occasions during this study when two individuals of different clans encountered one another, this was often followed by a sudden halt in movement, increased vigilance and acute sniffing of the air in the direction of the other, and either one or both individuals would almost always actively change direction to avoid each other or retreat in the direction they had just come. During night follows in Chobe, hyenas were sometimes observed to be startled by the unexpected appearance of each other (noted by the sudden jerk backwards and the rapidly departing speed of both individuals in opposite directions). It is potentially likely that hyenas exhibiting similar foraging strategies may unknowingly come close together in dense, riparian habitats, which would account for the increased frequency of shorter consecutive time points between hyena pairs observed in Chobe during this study.

The fission-fusion social structure observed in Chobe hyenas coincides with the “uninterrupted mosaic” of territories observed in hyenas from the Maasai Mara in Kenya (Boydston et al. 2001), and in the Savuti region of the Chobe National Park (Cooper 1989). Hyenas were found to scavenge more food from lions, and had higher food intake in areas of low lion densities relative to areas of higher lion densities (Watts & Holekamp 2008), and adjusted their grouping patterns in response to feeding competition (Smith et al. 2008). In contrast to a previous study in Etosha which never saw hyenas steal food from lions (Trinkel & Kastberger 2005), the hyenas in this study were observed to successfully appropriate food from female lions in both ecosystems. Thus, hyenas presumably derive benefits from conspecifics to both appropriate resources and for protection from lions.

Coexistence among species is possible when a trade-off occurs between exploitation and interference (Amarasekare 2002). Carnivore species that employ costly interference mechanisms (i.e. territoriality or resource guarding) are able to coexist with competitors provided that they also engage in interference mechanisms that confer a benefit to themselves (i.e. predation or kleptoparastism) (Amarasekare 2002). Our findings from the analysis of interspecific pair movements demonstrates that a majority of hyenas exhibit retreat behaviours away from lions while a third of lions present approach behaviours towards hyenas. This is in line with Vanak et al. (2013), which demonstrated lions to consistently move towards other carnivore species while they, in turn, moved away, although their study lacked data on spotted hyenas. Similarly, cheetahs avoided immediate risk by positioning themselves at larger distances from lions and hyenas (Broekhuis et al. 2013), despite this behaviour not being emulated by the hyenas in response to the lions in that study. Furthermore, lions and hyenas were found to actively track each other (Swanson et al. 2016), and hyenas appeared to lose more of their kills to lions although not in terms of biomass (Périquet et al. 2015a). As lions are significantly larger and stronger than hyenas, and the success of acquiring food from hyenas is largely dependent on the ratio of lions to hyenas (Cooper 1991, Honer et al. 2002), it follows that lions would likely approach hyenas at the prospect of encountering a feeding opportunity.

In addition, simultaneous interspecific pair movements demonstrated that a majority of hyenas exhibit retreat behaviours away from lions, as lions simultaneously followed or tracked hyenas. This behaviour persisted even at large distances of 1-10 km, which suggest that the strength of pairwise interactions is closely associated with the distance between the paired individuals. Kittle et al. (2016) suggested that the observed positive association between lions and spotted hyenas in his study resulted from one species tracking the other. Our results provide evidence towards this hypothesis, with long periods of interaction occurring between the two species (upwards of 300 consecutive minutes). Despite considerable variation among individual animals, more than half of the hyena individuals consistently show retreat behaviours away from lions. Similarly, cheetahs were observed to exhibit localized reactive avoidance to lions in the Serengeti (Swanson et al. 2016). However, lions rarely retreated and, instead, demonstrated mainly movements towards hyenas, as hyenas simultaneously moved away.

Alternatively, if both species interfere less with the other species than they do among themselves with the acquisition of resources, then the higher intensity of intraspecific competition relative to interspecific competition enables species coexistence (Vance 1984, Zemel & Lubin 1995). We also applied our analyses to intraspecific interactions between conspecific pairs. Our results indicated that both species differed in the utilization of approach and retreat movements towards conspecifics, with lions utilizing approach movements in nearly three quarters of cases, and hyenas retreating in more than half of the cases. However, lions were found to spend considerably more time together than hyenas did. Lions have been documented in other studies to have fission-fusion societies in which pride members form subgroups of various sizes (Schaller 1972). Larger prides were found to have a competitive advantage in intergroup competition for territory (McComb et al. 1994), and better able to defend against kleptoparasitism from other predators (Cooper 1991). Prides with more adult females were more likely to gain access to higher quality habitats and had increased reproductive success (Mosser & Packer 2009), and were able to better defend cubs against predation and infanticidal males (Grinnell & McComb 1996). Similarly, intraspecific interactions in a reintroduced population of lions resulted in shifts in the habitat selection among lion groups, relegating subordinate members to suboptimal habitats (Yiu et al. 2019). Thus, for the lions in our study, it is likely that the direct effect of intraspecific interactions exerted a stronger influence on lion movement behaviour than the indirect effect of interspecific interactions.

The opposite, however, is true for spotted hyenas. Our findings effectively demonstrated that, despite variation among individuals, lions actively tracked spotted hyenas across much of their shared ranges, while hyenas utilized local reactive avoidance behaviours in response to being in close proximity to lions. The active behavioural avoidance of lions by spotted hyenas demonstrated in this study is similar to the behaviours exhibited by cheetahs and wild dogs from other studies which have actively avoided lions (Cozzi et al. 2012, Broekhuis et al. 2013, Vanak et al. 2013, Swanson et al. 2016). In studies that examined the behavioural response of hyenas to lion calls, hyenas were found to vary their level of vigilance and responses to lion calls based on individual characteristics of risk-taking temperaments (Webster et al. 2010, Watts et al. 2010). In the Hwange National Park, spotted hyenas selected den sites and altered their patterns of den attendance, and shifted their foraging strategy from active predation to scavenging in response to the potential of competitive interactions with lions (Périquet et al. 2015b, 2016). Therefore, and as observed in this study, spotted hyenas have the capacity to behaviourally mediate their responses to a dynamic environment, including whether they choose to track, or to retreat from lions.

Measures of dynamic interactions have been proposed to allow researchers to quantify the type of interactions between dyads based on movement data (see Long et al. 2014, Joo et al. 2018 for a complete review). The majority of these approaches focuses on proximity (*Prox, Don, Cs, Iab*) which reflects the proportion of time the two individuals spent together and is generally given as a range of 0 to 1 (*Prox, HAI, LixnT, jPPA, CSEM*), or reflects the movement coordination within a range of -1 to 1 (*Cs, rV, DI*). Some of these metrics are either difficult to interpret (*Cs, DI*), requires a reference area (*HAI, LixnT*), or depend on a parameter with its underlying assumptions (*Prox, Cs, jPPA, CSEM, DI*). Benhamou et al. (2014) uses successive distances between lion individuals while moving to determine joint movements of a dyad. To our knowledge, previous measures of dynamic interaction do not illustrate following/leadership behaviour, or whether individuals exhibit approach/retreat behaviours. Here, we have used a reliable inferential framework for analyzing the movement interactions of paired individuals, to understand the dynamics of asymmetrical movement interactions.

The relative-motion method is a novel technique to analyze the movement behaviour of pairs of individuals, using approach and retreat behaviours as a means of identifying the type of interaction occurring between individuals. The application of this method allowed us to ascertain specific nuances of the animal's behaviour in relation to the other, so that we could test hypotheses related to how movement interactions are dictated by species that compete for the same resources, and how they are influenced by sex and social bonds within conspecifics. Movement interactions between pairs were restricted to individuals with joint space use to ensure that our analyses were focused on pairs with shared or overlapping ranges which potentially influence each other. Further, we restricted our analyses to pairs that consisted of simultaneous 5 min sampling data to determine the type of interactions between individuals at a fine scale.

Thus, movement interactions could reveal spatiotemporal avoidance when competing individuals encounter each other as they move across shared space-use areas. Animals that segregate their shared space use, or visit the same areas at different times, never meet, and our findings indicate that this is not the case for lions and spotted hyenas, which not only have shared space-use areas, but also often encounter one another within these jointly used areas. Consequently, knowledge of the nuances that which individuals are utilizing approach or retreat behaviours to their counterpart is essential in understanding the dynamic interactions between pairs.

Further to the mechanism of large-scale spatiotemporal partitioning exhibited by sympatric lions and spotted hyenas to occupy the same area at different times, we conclude that fine scale temporal partitioning of activity periods, and reactive local avoidance employed by hyenas, acts as the main mechanisms to allow for the co-existence of the two species. Specifically, spotted hyenas minimize the potential for interference competition by behaviourally adjusting their movements to effectively avoid encountering lions. Understanding the space-use patterns and movement characteristics of sympatric predators on a fine-scale provides insight into the dynamic interactions between co-existing species (Benhamou et al. 2014, Long et al. 2014, Miller 2015, Gurarie et al. 2016, Michelot et al. 2016, Edelhoff et al. 2016, Joo et al. 2018). Such dynamic interactions between individuals can reveal how behaviour choices are made by predators and scavengers of a guild, and has profound implications for the management strategies for both species (Zemel & Lubin 1995, Wilson & Wolkovich 2011, Moleón et al. 2014). In light of a changing global climate and increasing land-use pressures, factors influencing the spatial and temporal constraints imposed by predator movements can inform future area and configuration requirements of co-existing large predators (Gurd et al. 2001, Riggio et al. 2013, Ripple et al. 2014b, Tuqa et al. 2014, Zielinski et al. 2017), which ultimately may prove vital towards the conservation of multi-trophic communities and the maintenance of ecosystem function.

4.6. Conclusions

We have provided evidence for the presence of detailed interactions between lions and spotted hyenas within their home ranges where they overlap spatially and temporally. Areas of overlap among individuals typically occurred at the edge of individual ranges, within 2-5 km of water points, and within >0.5-1 km along roads. Although the majority of the minimum time lag between spatially overlapping hulls among lion and spotted hyena dyads was 12-24 and >24 h, there were several incidences of overlapping hulls without any time lag which indicates the occurrence of a shared space use at the same times. Lions and spotted hyenas evidently interacted within these jointly-used areas, both across seasons and ecosystems. Furthermore, we have demonstrated a method to quantify the movement interactions between two or more simultaneously tracked animals, while employing approach and retreat behaviours as a means of identifying the type of interaction occurring between paired individuals. Within lion-hyena interactions, our findings revealed that lions are significantly more often tracking spotted hyenas while hyenas simultaneously utilize local reactive avoidance behaviours to reduce the probability of encountering or coming into close contact with lions. Thus, certain species mediate the potential effects of interspecific competition by utilizing localized habitat shifts, temporal shifts in activity periods, or behaviourally adjusting their trajectory in response to reducing the risk of potential interactions with a competitor. Quantifying these types of movement behaviour can be a useful indication of the type of interaction occurring in a dyad, and may prove essential to guide conservation efforts of certain species. Understanding how apex predators move across the landscape in response to interactions with competitors will ultimately affect the maintenance of diverse and functional ecosystems in the face of increasing climatic variability and dwindling wild lands.

4.7. References

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4.8. Supplementary materials

Supplementary Table S4.1. Summary of data collection records of the collared animals in this study. Asterisks denotes unretrieved data from the collars. Study regions: ENP = Etosha National Park, Namibia; CNP = Chobe National Park, Botswana; LC = Linyanti Conservancy, Botswana.

	INDIVIDUAL	SEX	REGION	TRACKING DAYS	GPS LOCATIONS	ACTIVITY RECORDS	TRACKING PERIOD
LION	OK-33863	F	ENP	121	5643	44010	11 Oct 2013 – 9 Feb 2014
	RE-33864	F	ENP	166	9875	60116	19 Oct 2013 – 3 April 2014
	NU-33865	F	ENP	368	24264	132362	21 Nov 2013 – 24 Nov 2014
	MO-33866	F	ENP	342	22966	123335	23 Nov 2013 – 31 Oct 2014
	OJ-33867	M	ENP	89	3962	32231	11 Oct 2013 – 8 Jan 2014
	SU-33868	M	ENP	234	13971	84276	25 Oct 2013 – 16 June 2014
	G1-33950	F	ENP	36	205	14828	5 Oct 2013 – 10 Nov 2013
	OM-34308	F	ENP	141	6586	51141	24 Sept 2013 – 12 Feb 2014
	LU-34308	F	ENP	212	14169	76401	28 March 2014 – 26 Oct 2014
	OF-34309	M	ENP	116	4441	41511	27 Sept 2013 – 21 Jan 2014
	G2-35678	F	ENP	178	11893	64089	1 May 2014 – 26 Oct 2014
	SW-33950	F	CNP	228	16129	82075	24 July 2015 – 8 March 2016
	AF-34308	F	LC	109	10914	39060	10 Oct 2015 – 27 Jan 2016
	BE-35678	F	LC	71	1377	*	29 Oct 2015 – 8 Jan 2016
	AM-36714	M	LC	638	15410	*	10 Oct 2015 – 9 July 2017
	KW-36716	F	CNP	367	20414	133470	18 June 2015 – 19 June 2016
	KB-36717	F	CNP	355	9128	*	26 June 2015 – 15 June 2016
SPOTTED HYENA	GO-33869	F	ENP	498	30126	179658	18 Oct 2013 – 28 Feb 2015
	TJ-33870	F	ENP	150	8841	53919	24 Oct 2013 – 23 March 2014
	NE-33871	F	ENP	346	22915	125182	5 Nov 2013 – 17 Oct 2014
	SA-33872	F	ENP	332	18315	128164	17 Oct 2013 – 14 Sept 2014
	AU-33873	F	ENP	464	28876	167264	5 Nov 2013 – 12 Feb 2015
	OM-33874	F	ENP	484	9719	*	7 Nov 2013 – 6 March 2015
	SU-33951	F	ENP	79	551	*	27 Oct 2013 – 14 Jan 2014
	OK-34310	M	ENP	3	12	1258	10 Oct 2013 – 13 Oct 2013
	WO-34310	M	ENP	130	8580	46750	18 June 2014 – 26 Oct 2014
	AR-33869	M	LC	60	1205	*	10 Nov 2015 – 9 Jan 2016
	IH-33870	F	CNP	461	7697	*	26 July 2015 – 29 Oct 2016
	KW-33871	F	CNP	159	2642	*	18 June 2015 – 24 Nov 2015
	RV-33873	M	LC	197	4049	*	9 Nov 2015 – 24 May 2016
	SR-34310	F	CNP	214	14288	76961	11 July 2015 – 10 Feb 2016

Supplementary Table S4.2.1. Calculated 95% confidence intervals of (a) movement towards the other individual over total number of towards/away movements and (b) four types of simultaneous movements over total movements between lion and spotted hyena individuals for each dyad. Males are underlined. An asterisk denotes significance between random and individual movements (a = 0.5, b = 0.25).

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SU-33868 & TJ-33870	SU-33868	0-50	3	2	0.0943	0.9916	
	TJ-33870		3	2	0.0943	0.9916	
	SU-33868	50-100	17	10	0.3292	0.8156	
	TJ-33870		18	9	0.2602	0.7398	
	SU-33868	100-200	24	14	0.3664	0.7789	
	TJ-33870		25	13	0.3131	0.722	
	SU-33868	200-500	48	22	0.3137	0.6083	
	TJ-33870		43	22	0.3546	0.6669	
	SU-33868	500-1000	21	5	0.0822	0.4717	*
	TJ-33870		18	10	0.3076	0.7847	
	SU-33868	1000-2000	84	42	0.3889	0.6111	
	TJ-33870		70	35	0.378	0.622	
	SU-33868	2000-3000	89	55	0.5089	0.719	*
	TJ-33870		81	34	0.3109	0.5346	
	SU-33868	3000-5000	291	138	0.4147	0.5333	
	TJ-33870		264	135	0.4493	0.5731	
	SU-33868	5000-10 000	1054	551	0.4921	0.5533	
	TJ-33870		1056	506	0.4487	0.5098	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SU-33868 & TJ-33870	0-50	2	0	A → ← B	0	0.8419	
			0	← A B →	0	0.8419	
			1	A → B →	0.0126	0.9874	
			1	← A ← B	0.0126	0.9874	
	50-100	16	3	A → ← B	0.0405	0.4565	
			2	← A B →	0.0155	0.3835	
			6	A → B →	0.1520	0.6457	
			5	← A ← B	0.1102	0.5866	
	100-200	18	4	A → ← B	0.0641	0.4764	
			3	← A B →	0.0358	0.4142	
			6	A → B →	0.1334	0.5901	
			5	← A ← B	0.0969	0.5348	
	200-500	35	7	A → ← B	0.0844	0.3694	
			9	← A B →	0.1249	0.4326	
			8	A → B →	0.1042	0.4014	
			11	← A ← B	0.1685	0.4929	
	500-1000	13	1	A → ← B	0.0019	0.3603	
			5	← A B →	0.1386	0.6842	
			0	A → B →	0	0.2471	*
			7	← A ← B	0.2513	0.8078	*
	1000-2000	56	10	A → ← B	0.0891	0.3040	
			9	← A B →	0.0762	0.2833	
			19	A → B →	0.2181	0.4781	
			18	← A ← B	0.2029	0.4596	
	2000-3000	71	20	A → ← B	0.1813	0.4010	
			16	← A B →	0.1346	0.3400	
			24	A → B →	0.2300	0.4601	
			11	← A ← B	0.0800	0.2603	
	3000-5000	196	54	A → ← B	0.2142	0.3437	
			54	← A B →	0.2142	0.3437	
			44	A → B →	0.1681	0.2894	
			44	← A ← B	0.1681	0.2894	
	5000-10 000	810	187	A → ← B	0.2023	0.2615	
			199	← A B →	0.2164	0.2768	
			225	A → B →	0.2472	0.3100	
			199	← A ← B	0.2164	0.2768	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SU-33868 & SA-33872	SU-33868	0-50	0	0	0	1	
	SA-33872		0	0	0	1	
	SU-33868	50-100	1	1	0.0250	1	
	SA-33872		1	1	0.0250	1	
	SU-33868	100-200	6	3	0.1181	0.8819	
	SA-33872		6	2	0.0433	0.7772	
	SU-33868	200-500	22	11	0.2822	0.7178	
	SA-33872		17	6	0.1421	0.6167	
	SU-33868	500-1000	34	17	0.3243	0.6757	
	SA-33872		39	19	0.3242	0.6522	
	SU-33868	1000-2000	54	28	0.3784	0.6566	
	SA-33872		58	24	0.2860	0.5507	
	SU-33868	2000-3000	61	30	0.3614	0.6230	
	SA-33872		68	31	0.3345	0.5812	
	SU-33868	3000-5000	245	128	0.4579	0.5864	
	SA-33872		230	115	0.4336	0.5664	
	SU-33868	5000-10 000	1430	741	0.4919	0.5444	
	SA-33872		1415	727	0.4874	0.5401	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SU-33868 & SA-33872	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	1	1	A → ← B	0.0250	1	
			0	← A B →	0	0.9750	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	100-200	6	1	A → ← B	0.0042	0.6412	
			2	← A B →	0.0433	0.7772	
			2	A → B →	0.0433	0.7772	
			1	← A ← B	0.0042	0.6412	
	200-500	14	2	A → ← B	0.0178	0.4281	
			1	← A B →	0.0018	0.3387	
			7	A → B →	0.2304	0.7696	
			4	← A ← B	0.0839	0.5810	
	500-1000	29	10	A → ← B	0.1794	0.5433	
			8	← A B →	0.1273	0.4724	
			5	A → B →	0.0585	0.3577	
			6	← A ← B	0.0799	0.3972	
	1000-2000	43	7	A → ← B	0.0681	0.3070	
			13	← A B →	0.1718	0.4613	
			13	A → B →	0.1718	0.4613	
			10	← A ← B	0.1176	0.3863	
	2000-3000	50	14	A → ← B	0.1623	0.4249	
			18	← A B →	0.2292	0.5081	
			12	A → B →	0.1306	0.3817	
			6	← A ← B	0.0453	0.2431	*
	3000-5000	168	41	A → ← B	0.1812	0.3162	
			41	← A B →	0.1812	0.3162	
			47	A → B →	0.2134	0.3541	
			39	← A ← B	0.1706	0.3034	
	5000-10 000	1098	291	A → ← B	0.2391	0.2922	
			263	← A B →	0.2146	0.2659	
			282	A → B →	0.2312	0.2838	
			262	← A ← B	0.2137	0.2650	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
RE-33864 & TJ-33870	RE-33864	0-50	0	0	0	1	
	TJ-33870		0	0	0	1	
	RE-33864	50-100	0	0	0	1	
	TJ-33870		0	0	0	1	
	RE-33864	100-200	0	0	0	1	
	TJ-33870		0	0	0	1	
	RE-33864	200-500	0	0	0	1	
	TJ-33870		0	0	0	1	
	RE-33864	500-1000	0	0	0	1	
	TJ-33870		0	0	0	1	
	RE-33864	1000-2000	12	4	0.0992	0.6511	
	TJ-33870		19	9	0.2445	0.7114	
	RE-33864	2000-3000	30	20	0.4719	0.8271	
	TJ-33870		25	10	0.2113	0.6133	
	RE-33864	3000-5000	128	54	0.3351	0.5123	
	TJ-33870		131	58	0.3561	0.5321	
	RE-33864	5000-10 000	1324	664	0.4742	0.5288	
	TJ-33870		1295	640	0.4666	0.5218	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
RE-33864 & TJ-33870	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	12	3	A → ← B	0.0549	0.5719	
			5	← A B →	0.1517	0.7233	
			1	A → B →	0.0021	0.3848	
			3	← A ← B	0.0549	0.5719	
	2000-3000	21	6	A → ← B	0.1128	0.5218	
			3	← A B →	0.0305	0.3634	
			10	A → B →	0.2571	0.7022	*
			2	← A ← B	0.0117	0.3038	
	3000-5000	99	21	A → ← B	0.1364	0.3058	
			30	← A B →	0.2147	0.4035	
			23	A → B →	0.1533	0.3279	
			25	← A ← B	0.1706	0.3498	
	5000-10 000	1001	248	A → ← B	0.2213	0.2757	
			243	← A B →	0.2165	0.2706	
			259	A → B →	0.2319	0.2871	
			251	← A ← B	0.2242	0.2788	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
RE-33864 & SA-33872	RE-33864	0-50	1	0	0	0.9750	
	SA-33872		1	0	0	0.9750	
	RE-33864	50-100	1	1	0.0250	1	
	SA-33872		0	0	0	1	
	RE-33864	100-200	3	1	0.0084	0.9057	
	SA-33872		4	2	0.0676	0.9324	
	RE-33864	200-500	14	8	0.2886	0.8234	
	SA-33872		12	6	0.2109	0.7891	
	RE-33864	500-1000	7	3	0.0990	0.8159	
	SA-33872		7	4	0.1841	0.9010	
	RE-33864	1000-2000	44	30	0.5242	0.8139	*
	SA-33872		44	15	0.2049	0.4992	*
	RE-33864	2000-3000	54	28	0.3784	0.6566	
	SA-33872		55	24	0.3030	0.5768	
	RE-33864	3000-5000	100	55	0.4473	0.6497	
	SA-33872		115	51	0.3509	0.5391	
	RE-33864	5000-10 000	562	299	0.4898	0.5739	
	SA-33872		552	252	0.4144	0.4991	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
RE-33864 & SA-33872	0-50	1	0	A → ← B	0	0.975	
			1	← A B →	0.0250	1	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	3	1	A → ← B	0.0084	0.9057	
			1	← A B →	0.0084	0.9057	
			0	A → B →	0	0.7076	
			1	← A ← B	0.0084	0.9057	
	200-500	10	4	A → ← B	0.1216	0.7376	
			2	← A B →	0.0252	0.5561	
			2	A → B →	0.0252	0.5561	
			2	← A ← B	0.0252	0.5561	
	500-1000	6	0	A → ← B	0	0.4593	
			1	← A B →	0.0042	0.6412	
			2	A → B →	0.0433	0.7772	
			3	← A ← B	0.1181	0.8819	
	1000-2000	35	10	A → ← B	0.1464	0.4630	
			5	← A B →	0.0481	0.3026	
			16	A → B →	0.2883	0.6335	*
			4	← A ← B	0.0320	0.2674	
	2000-3000	33	8	A → ← B	0.1109	0.4226	
			10	← A B →	0.1559	0.4871	
			10	A → B →	0.1559	0.4871	
			5	← A ← B	0.0511	0.3190	
	3000-5000	85	18	A → ← B	0.1306	0.3139	
			18	← A B →	0.1306	0.3139	
			26	A → B →	0.2105	0.4153	
			23	← A ← B	0.1799	0.3779	
	5000-10 000	426	102	A → ← B	0.1997	0.2829	
			115	← A B →	0.2283	0.3148	
			125	A → B →	0.2506	0.3392	*
			84	← A ← B	0.1604	0.2382	*

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
OF-34309 & SA-33872	OF-34309	0-50	0	0	0	1	
	SA-33872		0	0	0	1	
	OF-34309	50-100	0	0	0	1	
	SA-33872		0	0	0	1	
	OF-34309	100-200	0	0	0	1	
	SA-33872		0	0	0	1	
	OF-34309	200-500	5	4	0.2836	0.9949	
	SA-33872		5	0	0	0.5218	
	OF-34309	500-1000	6	4	0.2228	0.9567	
	SA-33872		6	0	0	0.4593	*
	OF-34309	1000-2000	11	7	0.3079	0.8907	
	SA-33872		7	2	0.0367	0.7096	
	OF-34309	2000-3000	0	0	0	1	
	SA-33872		0	0	0	1	
	OF-34309	3000-5000	13	8	0.3158	0.8614	
	SA-33872		23	9	0.1971	0.6146	
	OF-34309	5000-10 000	112	78	0.6024	0.7798	*
	SA-33872		116	36	0.2277	0.4029	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
OF-34309 & SA-33872	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	5	0	A → ← B	0	0.5218	
			1	← A B →	0.0051	0.7164	
			4	A → B →	0.2836	0.9949	*
			0	← A ← B	0	0.5218	
	500-1000	6	0	A → ← B	0	0.4593	
			2	← A B →	0.0433	0.7772	
			4	A → B →	0.2228	0.9567	
			0	← A ← B	0	0.4593	
	1000-2000	7	1	A → ← B	0.0036	0.5787	
			0	← A B →	0	0.4096	
			5	A → B →	0.2904	0.9633	*
			1	← A ← B	0.0036	0.5787	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	10	3	A → ← B	0.0667	0.6525	
			2	← A B →	0.0252	0.5561	
			3	A → B →	0.0667	0.6525	
			2	← A ← B	0.0252	0.5561	
	5000-10 000	86	18	A → ← B	0.1290	0.3105	
			16	← A B →	0.1102	0.2845	
			41	A → B →	0.3679	0.5873	*
			11	← A ← B	0.0656	0.2173	*

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
OK-33863 & SA-33872	OK-33863	0-50	0	0	0	1	
	SA-33872		0	0	0	1	
	OK-33863	50-100	0	0	0	1	
	SA-33872		0	0	0	1	
	OK-33863	100-200	0	0	0	1	
	SA-33872		0	0	0	1	
	OK-33863	200-500	0	0	0	1	
	SA-33872		0	0	0	1	
	OK-33863	500-1000	0	0	0	1	
	SA-33872		0	0	0	1	
	OK-33863	1000-2000	10	6	0.2624	0.8784	
	SA-33872		7	2	0.0367	0.7096	
	OK-33863	2000-3000	10	10	0.6915	1	*
	SA-33872		8	2	0.0319	0.6509	
	OK-33863	3000-5000	15	2	0.0166	0.4046	*
	SA-33872		11	4	0.1093	0.6921	
	OK-33863	5000-10 000	28	10	0.1864	0.5593	
	SA-33872		32	20	0.4369	0.7890	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
OK-33863 & SA-33872	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	6	1	A → ← B	0.0042	0.6412	
			1	← A B →	0.0042	0.6412	
			3	A → B →	0.1181	0.8819	
			1	← A ← B	0.0042	0.6412	
	2000-3000	8	2	A → ← B	0.0319	0.6509	
			0	← A B →	0	0.3694	
			6	A → B →	0.3491	0.9681	*
			0	← A ← B	0	0.3694	
	3000-5000	11	0	A → ← B	0	0.2849	
			7	← A B →	0.3079	0.8907	*
			0	A → B →	0	0.2849	
			4	← A ← B	0.1093	0.6921	
	5000-10 000	26	8	A → ← B	0.1433	0.5179	
			5	← A B →	0.0655	0.3935	
			2	A → B →	0.0095	0.2513	
			11	← A ← B	0.2335	0.6308	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
OM-34308 & SA-33872	OM-34308	0-50	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	50-100	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	100-200	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	200-500	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	500-1000	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	1000-2000	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	2000-3000	0	0	0	1	
	SA-33872		0	0	0	1	
	OM-34308	3000-5000	35	17	0.3138	0.6601	
	SA-33872		28	10	0.1864	0.5593	
	OM-34308	5000-10 000	168	77	0.3814	0.5368	
	SA-33872		167	96	0.4961	0.6509	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
OM-34308 & SA-33872	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	24	3	A → ← B	0.0266	0.3236	
			9	← A B →	0.1880	0.5941	
			8	A → B →	0.1563	0.5532	
			4	← A ← B	0.0474	0.3738	
	5000-10 000	130	42	A → ← B	0.2437	0.4107	
			35	← A B →	0.1952	0.3540	
			20	A → B →	0.9066	0.2276	*
			33	← A ← B	0.1816	0.3376	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
NU-33865 & SA-33872	NU-33865	0-50	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	50-100	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	100-200	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	200-500	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	500-1000	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	1000-2000	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	2000-3000	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	3000-5000	0	0	0	1	
	SA-33872		0	0	0	1	
	NU-33865	5000-10 000	86	37	0.3239	0.5415	
	SA-33872		90	29	0.2275	0.4290	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
NU-33865 & SA-33872	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	5000-10 000	72	10	A → ← B	0.0687	0.2406	*
			29	← A B →	0.2888	0.5250	*
			20	A → B →	0.1786	0.3959	
			13	← A ← B	0.0998	0.2889	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
KW-36716 & SR-34310	KW-36716	0-50	0	0	0	1	
	SR-34310		0	0	0	1	
	KW-36716	50-100	0	0	0	1	
	SR-34310		0	0	0	1	
	KW-36716	100-200	0	0	0	1	
	SR-34310		0	0	0	1	
	KW-36716	200-500	1	0	0	0.9750	
	SR-34310		1	0	0	0.9750	
	KW-36716	500-1000	9	4	0.1370	0.7880	
	SR-34310		10	6	0.2624	0.8784	
	KW-36716	1000-2000	10	6	0.2624	0.8784	
	SR-34310		15	6	0.1634	0.6771	
	KW-36716	2000-3000	79	34	0.3194	0.5467	
	SR-34310		83	42	0.3940	0.6176	
	KW-36716	3000-5000	187	97	0.4446	0.5922	
	SR-34310		204	85	0.3482	0.4876	*
	KW-36716	5000-10 000	1544	766	0.4709	0.5214	
	SR-34310		1473	691	0.4434	0.4950	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
KW-36716 & SR-34310	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	1	0	A → ← B	0	0.9750	
			1	← A B →	0.0250	1	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	500-1000	6	1	A → ← B	0.0042	0.6412	
			2	← A B →	0.0433	0.7772	
			1	A → B →	0.0042	0.6412	
			2	← A ← B	0.0433	0.7772	
	1000-2000	9	3	A → ← B	0.0749	0.7007	
			2	← A B →	0.0281	0.6001	
			2	A → B →	0.0281	0.6001	
			2	← A ← B	0.0281	0.6001	
	2000-3000	64	14	A → ← B	0.1251	0.3397	
			20	← A B →	0.2024	0.4406	
			14	A → B →	0.1251	0.3397	
			16	← A ← B	0.1502	0.3740	
	3000-5000	139	29	A → ← B	0.1444	0.2857	
			36	← A B →	0.1885	0.3401	
			41	A → B →	0.2207	0.3782	
			33	← A ← B	0.1694	0.3169	
	5000-10 000	1116	241	A → ← B	0.1921	0.2413	*
			294	← A B →	0.2378	0.2903	
			309	A → B →	0.2508	0.3041	*
			272	← A ← B	0.2188	0.2700	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SW-33950 & SR-34310	SW-33950	0-50	1	0	0	0.9750	
	SR-34310		1	0	0	0.9750	
	SW-33950	50-100	4	2	0.0676	0.9324	
	SR-34310		4	2	0.0676	0.9324	
	SW-33950	100-200	0	0	0	1	
	SR-34310		0	0	0	1	
	SW-33950	200-500	2	2	0.1581	1	
	SR-34310		2	0	0	0.8419	
	SW-33950	500-1000	23	12	0.3059	0.7318	
	SR-34310		19	7	0.1629	0.6164	
	SW-33950	1000-2000	104	60	0.4761	0.6732	
	SR-34310		99	46	0.3638	0.5677	
	SW-33950	2000-3000	141	71	0.4182	0.5888	
	SR-34310		152	78	0.4308	0.5950	
	SW-33950	3000-5000	614	288	0.4290	0.5094	
	SR-34310		633	306	0.4438	0.5231	
	SW-33950	5000-10 000	2010	1112	0.5312	0.5751	*
	SR-34310		2066	1032	0.4777	0.5213	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SW-33950 & SR-34310	0-50	1	0	A → ← B	0	0.9750	
			1	← A B →	0.0250	1	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	50-100	4	1	A → ← B	0.0063	0.8059	
			1	← A B →	0.0063	0.8059	
			1	A → B →	0.0063	0.8059	
			1	← A ← B	0.0063	0.8059	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	2	0	A → ← B	0	0.8419	
			0	← A B →	0	0.8419	
			2	A → B →	0.1581	1	
			0	← A ← B	0	0.8419	
	500-1000	16	1	A → ← B	0.0016	0.3023	
			4	← A B →	0.0727	0.5238	
			7	A → B →	0.1975	0.7012	
			4	← A ← B	0.0727	0.5238	
	1000-2000	84	23	A → ← B	0.1821	0.3820	
			18	← A B →	0.1322	0.3174	
			25	A → B →	0.2027	0.4073	
			18	← A ← B	0.1322	0.3174	
	2000-3000	108	27	A → ← B	0.1717	0.3425	
			26	← A B →	0.1637	0.3325	
			29	A → B →	0.1878	0.3624	
			26	← A ← B	0.1637	0.3325	
	3000-5000	456	101	A → ← B	0.1842	0.2624	
			125	← A B →	0.2337	0.3175	
			109	A → B →	0.2006	0.2809	
			121	← A ← B	0.2254	0.3084	
	5000-10 000	1528	413	A → ← B	0.2482	0.2933	
			351	← A B →	0.2088	0.2516	
			432	A → B →	0.2603	0.3060	*
			332	← A ← B	0.1968	0.2388	*

Supplementary Table S4.2.2. Calculated 95% confidence intervals of (a) movement towards the other individual over total number of towards/away movements and (b) four types of simultaneous movements over their total sum between lion individuals for each dyad. Males are underlined. An asterisk denotes significance between random and individual movements (a = 0.5, b = 0.25).

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
MO-33866 & NU-33865	MO-33866	0-50	2172	1305	0.5799	0.6215	*
	NU-33865		2201	1225	0.5355	0.5775	*
	MO-33866	50-100	154	95	0.5352	0.6940	*
	NU-33865		169	85	0.4252	0.5807	
	MO-33866	100-200	52	38	0.5898	0.8443	*
	NU-33865		50	29	0.4321	0.7181	
	MO-33866	200-500	54	34	0.4874	0.7571	
	NU-33865		45	25	0.4000	0.7036	
	MO-33866	500-1000	49	25	0.3634	0.6558	
	NU-33865		44	23	0.3669	0.6754	
	MO-33866	1000-2000	126	62	0.4019	0.5826	
	NU-33865		135	82	0.5197	0.6903	*
	MO-33866	2000-3000	136	76	0.4712	0.6438	
	NU-33865		135	85	0.5423	0.7111	*
	MO-33866	3000-5000	263	128	0.4248	0.5489	
	NU-33865		276	161	0.5227	0.6421	*
	MO-33866	5000-10 000	718	367	0.4739	0.5483	
	NU-33865		697	377	0.5031	0.5784	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
MO-33866 & NU-33865	0-50	1741	460	A → ← B	0.2436	0.2856	
			221	← A B →	0.1117	0.1435	*
			576	A → B →	0.3088	0.3535	*
			484	← A ← B	0.2571	0.2997	*
	50-100	134	36	A → ← B	0.1958	0.3520	
			21	← A B →	0.0997	0.2295	*
			48	A → B →	0.2773	0.4456	*
			29	← A ← B	0.1500	0.2958	
	100-200	42	14	A → ← B	0.1957	0.4955	
			3	← A B →	0.0150	0.1948	*
			15	A → B →	0.2155	0.5197	
			10	← A ← B	0.1205	0.3945	
	200-500	41	13	A → ← B	0.1808	0.4809	
			7	← A B →	0.0715	0.3206	
			11	A → B →	0.1422	0.4294	
			10	← A ← B	0.1236	0.4030	
	500-1000	36	10	A → ← B	0.1420	0.4519	
			8	← A B →	0.1012	0.3915	
			8	A → B →	0.1012	0.3915	
			10	← A ← B	0.1420	0.4519	
	1000-2000	106	38	A → ← B	0.2677	0.4574	*
			27	← A B →	0.1751	0.3486	
			10	A → B →	0.0462	0.1667	*
			31	← A ← B	0.2081	0.3887	
	2000-3000	102	33	A → ← B	0.2342	0.4234	
			14	← A B →	0.0771	0.2196	*
			24	A → B →	0.1569	0.3296	
			31	← A ← B	0.2167	0.4029	
	3000-5000	204	57	A → ← B	0.2190	0.3464	
			43	← A B →	0.1569	0.2732	
			43	A → B →	0.1569	0.2732	
			61	← A ← B	0.2371	0.3669	
	5000-10 000	549	153	A → ← B	0.2416	0.3182	
			124	← A B →	0.1915	0.2632	
			125	A → B →	0.1932	0.2651	
			147	← A ← B	0.2311	0.3069	

(a)

Dyad	**Individual**	**Distance Interval (m)**	**Total**	**Towards**	**Lower CI**	**Upper CI**	**Significance**
OJ-33867 & OK-33863	OJ-33867	0-50	116	73	0.5347	0.7171	*
	OK-33863		118	67	0.4734	0.6587	
	OJ-33867	50-100	29	24	0.6423	0.9415	*
	OK-33863		24	4	0.0474	0.3738	*
	OJ-33867	100-200	19	17	0.6686	0.9870	*
	OK-33863		20	6	0.1189	0.5428	
	OJ-33867	200-500	51	33	0.5007	0.7757	*
	OK-33863		56	27	0.3466	0.6197	
	OJ-33867	500-1000	35	22	0.4492	0.7853	
	OK-33863		29	14	0.2945	0.6747	
	OJ-33867	1000-2000	87	51	0.4755	0.6908	
	OK-33863		90	43	0.3713	0.5857	
	OJ-33867	2000-3000	145	76	0.4396	0.6076	
	OK-33863		159	86	0.4601	0.6201	
	OJ-33867	3000-5000	108	59	0.4476	0.6424	
	OK-33863		105	65	0.5191	0.7121	*
	OJ-33867	5000-10 000	331	170	0.4583	0.5686	
	OK-33863		317	158	0.4420	0.5548	

(b)

Dyad	**Distance Interval (m)**	**Total**	**Count**	**Type**	**Lower CI**	**Upper CI**	**Significance**
OJ-33867 & OK-33863	0-50	102	25	A → ← B	0.1653	0.3402	
			5	← A B →	0.0161	0.1107	*
			39	A → B →	0.2879	0.4839	*
			33	← A ← B	0.2342	0.4234	
	50-100	22	2	A → ← B	0.0112	0.2916	
			2	← A B →	0.0112	0.2916	
			17	A → B →	0.5463	0.9218	*
			1	← A ← B	0.0012	0.2284	*
	100-200	17	3	A → ← B	0.0380	0.4343	
			0	← A B →	0	0.1951	*
			13	A → B →	0.5010	0.9319	*
			1	← A ← B	0.0015	0.2869	
	200-500	42	10	A → ← B	0.1205	0.3945	
			5	← A B →	0.0398	0.2563	
			18	A → B →	0.2772	0.5904	*
			9	← A ← B	0.1030	0.3681	
	500-1000	24	8	A → ← B	0.1563	0.5532	
			4	← A B →	0.0474	0.3738	
			8	A → B →	0.1563	0.5532	
			4	← A ← B	0.0474	0.3738	
	1000-2000	76	24	A → ← B	0.2139	0.4325	
			18	← A B →	0.1468	0.3482	
			22	A → B →	0.1911	0.4049	
			12	← A ← B	0.0843	0.2596	
	2000-3000	118	32	A → ← B	0.1935	0.3608	
			27	← A B →	0.1565	0.3152	
			29	A → B →	0.1712	0.3335	
			30	← A ← B	0.1786	0.3426	
	3000-5000	91	28	A → ← B	0.2151	0.4132	
			17	← A B →	0.1128	0.2822	
			21	A → B →	0.1489	0.3309	
			25	← A ← B	0.1863	0.3783	
	5000-10 000	251	66	A → ← B	0.2096	0.3220	
			59	← A B →	0.1840	0.2925	
			65	A → B →	0.2059	0.3178	
			61	← A ← B	0.1913	0.3009	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SU-33868 & RE-33864	SU-33868	0-50	1020	678	0.6348	0.6937	*
	RE-33864		1030	485	0.44	0.5019	
	SU-33868	50-100	206	173	0.7824	0.8871	*
	RE-33864		203	36	0.1274	0.237	*
	SU-33868	100-200	163	151	0.8749	0.9614	*
	RE-33864		164	23	0.091	0.203	*
	SU-33868	200-500	112	95	0.7681	0.909	*
	RE-33864		100	20	0.1267	0.2918	*
	SU-33868	500-1000	109	68	0.526	0.7148	*
	RE-33864		110	42	0.2908	0.4793	*
	SU-33868	1000-2000	180	106	0.5133	0.6615	*
	RE-33864		200	71	0.2888	0.4256	*
	SU-33868	2000-3000	157	90	0.4919	0.6517	
	RE-33864		181	68	0.3049	0.4506	*
	SU-33868	3000-5000	478	244	0.4647	0.5561	
	RE-33864		478	235	0.4459	0.5374	
	SU-33868	5000-10 000	1268	642	0.4784	0.5342	
	RE-33864		1250	641	0.4847	0.5409	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SU-33868 & RE-33864	0-50	841	211	A → ← B	0.2219	0.2816	
			106	← A B →	0.1044	0.1504	*
			356	A → B →	0.3896	0.4575	*
			168	← A ← B	0.1732	0.2284	*
	50-100	188	13	A → ← B	0.0373	0.1153	*
			10	← A B →	0.0258	0.0956	*
			147	A → B →	0.7160	0.8387	*
			18	← A ← B	0.0577	0.1471	*
	100-200	152	14	A → ← B	0.0513	0.1497	*
			7	← A B →	0.0187	0.0926	*
			126	A → B →	0.7595	0.8851	*
			5	← A ← B	0.0108	0.0751	*
	200-500	93	14	A → ← B	0.0848	0.2397	*
			11	← A B →	0.0605	0.2018	*
			64	A → B →	0.5837	0.7802	*
			4	← A ← B	0.0118	0.1065	*
	500-1000	89	20	A → ← B	0.1430	0.3255	
			18	← A B →	0.1245	0.3007	
			38	A → B →	0.3226	0.5363	*
			13	← A ← B	0.0801	0.2368	*
	1000-2000	139	24	A → ← B	0.1139	0.2459	*
			31	← A B →	0.1568	0.3014	
			62	A → B →	0.3618	0.5327	*
			22	← A ← B	0.1019	0.2298	*
	2000-3000	130	24	A → ← B	0.1220	0.2621	
			30	← A B →	0.1614	0.3128	
			53	A → B →	0.3224	0.4973	*
			23	← A ← B	0.1156	0.2535	
	3000-5000	350	90	A → ← B	0.2122	0.3063	
			97	← A B →	0.2309	0.3272	
			82	A → B →	0.1909	0.2822	
			81	← A ← B	0.1883	0.2792	
	5000-10 000	956	245	A → ← B	0.2289	0.2852	
			241	← A B →	0.2248	0.2809	
			233	A → B →	0.2168	0.2722	
			237	← A ← B	0.2208	0.2766	

(a)

Dyad	**Individual**	**Distance Interval (m)**	**Total**	**Towards**	**Lower CI**	**Upper CI**	**Significance**
SU-33868 & MO-33866	SU-33868	0-50	24	12	0.2912	0.7088	
	MO-33866		27	15	0.3533	0.7452	
	SU-33868	50-100	1	0	0	0.9750	
	MO-33866		1	0	0	0.9750	
	SU-33868	100-200	1	0	0	0.9750	
	MO-33866		1	0	0	0.9750	
	SU-33868	200-500	1	1	0.0250	1	
	MO-33866		1	0	0	0.9750	
	SU-33868	500-1000	8	3	0.0852	0.7551	
	MO-33866		8	1	0.0032	0.5265	
	SU-33868	1000-2000	21	9	0.2182	0.6598	
	MO-33866		22	13	0.3635	0.7929	
	SU-33868	2000-3000	52	31	0.4510	0.7299	
	MO-33866		51	23	0.3113	0.5966	
	SU-33868	3000-5000	56	39	0.5590	0.8122	*
	MO-33866		56	31	0.4147	0.6866	
	SU-33868	5000-10 000	321	184	0.5171	0.6280	*
	MO-33866		320	151	0.4161	0.5282	

(b)

Dyad	**Distance Interval (m)**	**Total**	**Count**	**Type**	**Lower CI**	**Upper CI**	**Significance**
SU-33868 & MO-33866	0-50	22	8	A → ← B	0.1720	0.5934	
			7	← A B →	0.1386	0.5487	
			3	A → B →	0.0291	0.3491	
			4	← A ← B	0.0519	0.4028	
	50-100	1	0	A → ← B	0	0.9750	
			1	← A B →	0.0250	1	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	100-200	1	0	A → ← B	0	0.9750	
			1	← A B →	0.0250	1	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	7	0	A → ← B	0	0.4096	
			4	← A B →	0.1841	0.9010	
			2	A → B →	0.0367	0.7096	
			1	← A ← B	0.0036	0.5787	
	1000-2000	16	4	A → ← B	0.0727	0.5238	
			3	← A B →	0.0405	0.4565	
			3	A → B →	0.0405	0.4565	
			6	← A ← B	0.1520	0.6457	
	2000-3000	43	15	A → ← B	0.2101	0.5093	
			12	← A B →	0.1533	0.4367	
			11	A → B →	0.1352	0.4117	
			5	← A ← B	0.0389	0.2508	
	3000-5000	47	18	A → ← B	0.2451	0.5362	
			7	← A B →	0.0620	0.2831	
			16	A → B →	0.2086	0.4931	
			6	← A ← B	0.0483	0.2574	
	5000-10 000	254	58	A → ← B	0.1782	0.2850	
			57	← A B →	0.1746	0.2808	
			78	A → B →	0.2509	0.3678	*
			61	← A ← B	0.1890	0.2975	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
G2-35678 & LU-34308	G2-35678	0-50	0	0	0	1	
	LU-34308		0	0	0	1	
	G2-35678	50-100	0	0	0	1	
	LU-34308		0	0	0	1	
	G2-35678	100-200	0	0	0	1	
	LU-34308		0	0	0	1	
	G2-35678	200-500	0	0	0	1	
	LU-34308		0	0	0	1	
	G2-35678	500-1000	0	0	0	1	
	LU-34308		0	0	0	1	
	G2-35678	1000-2000	6	4	0.2228	0.9567	
	LU-34308		6	2	0.0433	0.7772	
	G2-35678	2000-3000	71	36	0.3856	0.6278	
	LU-34308		81	38	0.3573	0.5833	
	G2-35678	3000-5000	138	76	0.4638	0.6354	
	LU-34308		163	71	0.3582	0.5154	
	G2-35678	5000-10 000	1533	818	0.5083	0.5588	*
	LU-34308		1539	771	0.4757	0.5263	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
G2-35678 & LU-34308	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	5	1	A → ← B	0.0051	0.7164	
			2	← A B →	0.0527	0.8534	
			2	A → B →	0.0527	0.8534	
			0	← A ← B	0	0.5218	
	2000-3000	51	10	A → ← B	0.0982	0.3312	
			12	← A B →	0.1279	0.3749	
			17	A → B →	0.2076	0.4792	
			12	← A ← B	0.1279	0.3749	
	3000-5000	113	26	A → ← B	0.1561	0.3187	
			28	← A B →	0.1714	0.3378	
			38	A → B →	0.2501	0.4312	*
			21	← A ← B	0.1189	0.2699	
	5000-10 000	1178	330	A → ← B	0.2546	0.3067	*
			280	← A B →	0.2136	0.2631	
			315	A → B →	0.2423	0.2937	
			253	← A ← B	0.1916	0.2393	*

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
OF-34309 & OM-34308	OF-34309	0-50	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	50-100	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	100-200	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	200-500	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	500-1000	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	1000-2000	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	2000-3000	0	0	0	1	
	OM-34308		0	0	0	1	
	OF-34309	3000-5000	20	9	0.2306	0.6847	
	OM-34308		27	13	0.2867	0.6805	
	OF-34309	5000-10 000	150	78	0.4370	0.6022	
	OM-34308		134	50	0.2912	0.4608	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
OF-34309 & OM-34308	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	18	5	A → ← B	0.0969	0.5348	
			6	← A B →	0.1334	0.5901	
			3	A → B →	0.0358	0.4142	
			4	← A ← B	0.0641	0.4764	
	5000-10 000	103	23	A → ← B	0.1471	0.3160	
			37	← A B →	0.2670	0.4597	*
			27	A → B →	0.1804	0.3580	
			16	← A ← B	0.0915	0.2400	*

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
MO-33866 & RE-33864	MO-33866	0-50	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	50-100	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	100-200	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	200-500	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	500-1000	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	1000-2000	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	2000-3000	0	0	0	1	
	RE-33864		0	0	0	1	
	MO-33866	3000-5000	2	0	0	0.8419	
	RE-33864		1	0	0	0.9750	
	MO-33866	5000-10 000	463	235	0.4610	0.5540	
	RE-33864		461	223	0.4373	0.5304	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
MO-33866 & RE-33864	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	1	0	A → ← B	0	0.9750	
			1	← A B →	0.0250	1	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	5000-10 000	353	87	A → ← B	0.2024	0.2948	
			90	← A B →	0.2103	0.3038	
			95	A → B →	0.2235	0.3186	
			81	← A ← B	0.1866	0.2769	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SU-33868 & NU-33865	SU-33868	0-50	0	0	0	1	
	NU-33865		0	0	0	1	
	SU-33868	50-100	0	0	0	1	
	NU-33865		0	0	0	1	
	SU-33868	100-200	0	0	0	1	
	NU-33865		0	0	0	1	
	SU-33868	200-500	0	0	0	1	
	NU-33865		0	0	0	1	
	SU-33868	500-1000	0	0	0	1	
	NU-33865		0	0	0	1	
	SU-33868	1000-2000	0	0	0	1	
	NU-33865		0	0	0	1	
	SU-33868	2000-3000	15	8	0.2659	0.7873	
	NU-33865		17	6	0.1421	0.6167	
	SU-33868	3000-5000	0	0	0	0	
	NU-33865		0	0	0	0	
	SU-33868	5000-10 000	157	75	0.3975	0.5588	
	NU-33865		155	85	0.4665	0.6283	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SU-33868 & NU-33865	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	13	3	A → ← B	0.0504	0.5381	
			3	← A B →	0.0504	0.5381	
			4	A → B →	0.0909	0.6143	
			3	← A ← B	0.0504	0.5381	
	3000-5000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	5000-10 000	119	31	A → ← B	0.1844	0.3489	
			27	← A B →	0.1552	0.3127	
			26	A → B →	0.1480	0.3035	
			35	← A ← B	0.2142	0.3846	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
KW-36716 & SW-33950	KW-36716	0-50	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	50-100	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	100-200	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	200-500	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	500-1000	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	1000-2000	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	2000-3000	0	0	0	1	
	SW-33950		0	0	0	1	
	KW-36716	3000-5000	13	5	0.1386	0.6842	
	SW-33950		18	4	0.0641	0.4764	*
	KW-36716	5000-10 000	828	382	0.4270	0.4960	*
	SW-33950		877	430	0.4567	0.5239	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
KW-36716 & SW-33950	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	12	0	A → ← B	0	0.2646	
			4	← A B →	0.0992	0.6511	
			5	A → B →	0.1517	0.7233	
			3	← A ← B	0.0549	0.5719	
	5000-10 000	631	147	A → ← B	0.2005	0.2679	
			174	← A B →	0.2412	0.3124	
			144	A → B →	0.1960	0.2630	
			166	← A ← B	0.2291	0.2993	

Supplementary Table S4.2.3. Calculated 95% confidence intervals of (a) movement towards the other individual over total number of towards/away movements and (b) four types of simultaneous movements over their total sum between spotted hyena individuals for each dyad. Males are underlined. An asterisk denotes significance between random and individual movements (a = 0.5, b = 0.25).

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SA-33872 & NE-33871	SA-33872	0-50	0	0	0	1	
	NE-33871		0	0	0	1	
	SA-33872	50-100	0	0	0	1	
	NE-33871		0	0	0	1	
	SA-33872	100-200	0	0	0	1	
	NE-33871		0	0	0	1	
	SA-33872	200-500	0	0	0	1	
	NE-33871		0	0	0	1	
	SA-33872	500-1000	0	0	0	1	
	NE-33871		0	0	0	1	
	SA-33872	1000-2000	6	0	0	0.4593	*
	NE-33871		7	1	0.0036	0.5787	
	SA-33872	2000-3000	37	10	0.1379	0.4412	*
	NE-33871		40	23	0.4089	0.7296	
	SA-33872	3000-5000	108	41	0.2880	0.4781	*
	NE-33871		118	53	0.3575	0.5434	
	SA-33872	5000-10 000	810	350	0.3977	0.4670	*
	NE-33871		767	445	0.5444	0.6154	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SA-33872 & NE-33871	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	4	0	A → ← B	0	0.6024	
			4	← A B →	0.3976	1	*
			0	A → B →	0	0.6024	
			0	← A ← B	0	0.6024	
	2000-3000	28	1	A → ← B	0.0009	0.1835	*
			7	← A B →	0.1069	0.4487	
			5	A → B →	0.0606	0.3689	
			15	← A ← B	0.3387	0.7249	*
	3000-5000	81	14	A → ← B	0.0978	0.2730	
			23	← A B →	0.1893	0.3950	
			17	A → B →	0.1273	0.3146	
			27	← A ← B	0.2324	0.4468	
	5000-10 000	580	133	A → ← B	0.1957	0.2657	
			148	← A B →	0.2202	0.2927	
			101	A → B →	0.1441	0.2075	*
			198	← A ← B	0.3028	0.3816	*

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
GO-33869 & TJ-33870	GO-33869	0-50	0	0	0	1	
	TJ-33870		0	0	0	1	
	GO-33869	50-100	0	0	0	1	
	TJ-33870		0	0	0	1	
	GO-33869	100-200	0	0	0	1	
	TJ-33870		0	0	0	1	
	GO-33869	200-500	0	0	0	1	
	TJ-33870		0	0	0	1	
	GO-33869	500-1000	0	0	0	1	
	TJ-33870		0	0	0	1	
	GO-33869	1000-2000	1	1	0.0250	1	
	TJ-33870		1	1	0.0250	1	
	GO-33869	2000-3000	5	3	0.1466	0.9473	
	TJ-33870		6	5	0.3588	0.9958	
	GO-33869	3000-5000	80	50	0.5096	0.7308	*
	TJ-33870		80	33	0.3035	0.5282	
	GO-33869	5000-10 000	555	272	0.4477	0.5325	
	TJ-33870		524	273	0.4773	0.5645	

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
GO-33869 & TJ-33870	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	1	1	A → ← B	0.0250	1	
			0	← A B →	0	0.9750	
			0	A → B →	0	0.9750	
			0	← A ← B	0	0.9750	
	2000-3000	4	1	A → ← B	0.0063	0.8059	
			0	← A B →	0	0.6024	
			1	A → B →	0.0063	0.8059	
			2	← A ← B	0.0676	0.9324	
	3000-5000	60	17	A → ← B	0.1745	0.4144	
			17	← A B →	0.1745	0.4144	
			21	A → B →	0.2313	0.4840	
			5	← A ← B	0.0276	0.1839	*
	5000-10 000	401	94	A → ← B	0.1938	0.2790	
			96	← A B →	0.1984	0.2843	
			102	A → B →	0.2124	0.3000	
			109	← A ← B	0.2289	0.3182	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
SA-33872 & TJ-33870	SA-33872	0-50	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	50-100	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	100-200	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	200-500	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	500-1000	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	1000-2000	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	2000-3000	0	0	0	1	
	TJ-33870		0	0	0	1	
	SA-33872	3000-5000	4	3	0.1941	0.9937	
	TJ-33870		7	5	0.2904	0.9633	
	SA-33872	5000-10 000	102	30	0.2080	0.3925	*
	TJ-33870		94	36	0.2846	0.4890	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
SA-33872 & TJ-33870	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	3	2	A → ← B	0.0943	0.9916	
			1	← A B →	0.0084	0.9057	
			0	A → B →	0	0.7076	
			0	← A ← B	0	0.7076	
	5000-10 000	78	8	A → ← B	0.0453	0.1921	*
			34	← A B →	0.3239	0.5530	*
			14	A → B →	0.1017	0.2828	
			22	← A ← B	0.1859	0.3953	

(a)

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
NE-33871 & WO-34310	NE-33871	0-50	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	50-100	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	100-200	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	200-500	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	500-1000	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	1000-2000	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	2000-3000	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	3000-5000	0	0	0	1	
	WO-34310		0	0	0	1	
	NE-33871	5000-10 000	48	19	0.2577	0.5473	
	WO-34310		39	28	0.5513	0.8500	*

(b)

Dyad	Distance Interval (m)	Total	Count	Type	Lower CI	Upper CI	Significance
NE-33871 & WO-34310	0-50	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	50-100	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	100-200	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	200-500	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	500-1000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	1000-2000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	2000-3000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	3000-5000	0	0	A → ← B	0	1	
			0	← A B →	0	1	
			0	A → B →	0	1	
			0	← A ← B	0	1	
	5000-10 000	33	13	A → ← B	0.2291	0.5786	
			7	← A B →	0.0898	0.3891	
			2	A → B →	0.0074	0.2023	*
			11	← A ← B	0.1796	0.5183	

Supplementary Table S4.2.4. Calculated 95% confidence intervals of movement towards the other individual over total number of towards/away movements between lion individuals for each dyad with extended time together at very close distances. Males in the dyad are underlined. An asterisk denotes significance between random (0.5) and individual movements.

Dyad	Individual	Distance Interval (m)	Total	Towards	Lower CI	Upper CI	Significance
MO-33866 & NU-33865	MO-33866	0 – 15	1345	794	0.5635	0.6168	*
	NU-33865		1369	769	0.535	0.5882	*
	MO-33866	15 – 100	981	606	0.5865	0.6483	*
	NU-33865		1001	541	0.509	0.5717	*
OJ-33867 & OK-33863	OJ-33867	0 – 15	95	54	0.4628	0.6697	
	OK-33863		94	60	0.5327	0.7349	*
	OJ-33867	15 – 100	50	43	0.7326	0.9418	*
	OK-33863		48	11	0.1203	0.3731	*
SU-33868 & RE-33864	SU-33868	0 – 15	604	371	0.5741	0.6532	*
	RE-33864		632	344	0.5046	0.5836	*
	SU-33868	15 – 100	622	480	0.7367	0.8041	*
	RE-33864		601	177	0.2583	0.3327	*

Supplementary Table S4.3. Statistical results for the percent frequency occurrence of, and average distance in meters to, the nearest conspecific and competitor for each bin of distance intervals, to accompany Figure 4.4 in the main text. An asterisk denotes significance at the alpha level with * < 0.05, ** < 0.01, *** < 0.005, and **** < 0.001.

Region & Species	**Distance Interval (m)**	**Conspecific** *Percent frequency occurrence / Average distance to (m)*	**Competitor** *Percent frequency occurrence / Average distance to (m)*		**Significance**
Etosha Lion	*0 – 5000*	*47%*	*53%*	*$x^2 = 0.35$, df = 1, $p > 0.05$*	
	1000 – 5000	35% 3396 ± 688	89% 3560 ± 450	$x^2 = 23.85$, df = 1, $p < 0.001$ $t = -0.66$, df = 11, $p > 0.05$	****
	500 – 1000	3% 730 ± 54	5% 763 ± 62	$x^2 = 0.30$, df = 1, $p > 0.05$ $t = -1.08$, df = 5, $p > 0.05$	
	200 – 500	3% 327 ± 17	3% 376 ± 38	$x^2 = 0.01$, df = 1, $p > 0.05$ $t = -3.86$, df = 12, $p < 0.005$	***
	100 – 200	3% 156 ± 26	2% 154 ± 18	$x^2 = 0.27$, df = 1, $p > 0.05$ $t = 0.11$, df = 4, $p > 0.05$	
	50 – 100	5% 69 ± 3	1% 80 ± 11	$x^2 = 3.29$, df = 1, $p > 0.05$ $t = -3.07$, df = 11, $p < 0.05$	*
	10 – 50	28% 27 ± 6	0.3% 32 ± 8	$x^2 = 27.12$, df = 1, $p < 0.001$ $t = -1.28$, df = 8, $p > 0.05$	****
	0 – 10	23% 6 ± 3	0.01% 8	$x^2 = 22.84$, df = 1, $p < 0.001$ t = N/A	****
Chobe Lion	*0 – 5000*	*37%*	*63%*	*$x^2 = 7.08$, df = 1, $p < 0.01$*	**
	1000 – 5000	85% 3315 ± 781	95% 3730 ± 407	$x^2 = 0.61$, df = 1, $p > 0.05$ $t = -1.22$, df = 6, $p > 0.05$	
	500 – 1000	4% 785 ± 92	3% 823 ± 94	$x^2 = 0.29$, df = 1, $p > 0.05$ $t = -0.74$, df = 9, $p > 0.05$	
	200 – 500	3% 307 ± 49	1% 334 ± 32	$x^2 = 0.49$, df = 1, $p > 0.05$ $t = -1.08$, df = 7, $p > 0.05$	
	100 – 200	1% 152 ± 13	0.4% 148 ± 10	$x^2 = 0.55$, df = 1, $p > 0.05$ $t = 0.51$, df = 5, $p > 0.05$	
	50 – 100	1% 71 ± 14	0.2% 77 ± 15	$x^2 = 0.55$, df = 1, $p > 0.05$ $t = -0.72$, df = 4, $p > 0.05$	
	10 – 50	3% 34 ± 9	0.4% 33 ± 2	$x^2 = 2.55$, df = 1, $p > 0.05$ $t = 0.33$, df = 2, $p > 0.05$	
	0 – 10	3% 6 ± 2	0 NA	$x^2 = 3.24$, df = 1, $p > 0.05$ t = N/A	
Etosha Hyena	*0 – 5000*	*6%*	*94%*	*$x^2 = 76.53$, df = 1, $p < 0.001$*	****
	1000 – 5000	92.5% 3502 ± 343	89% 3560 ± 450	$x^2 = 0.07$, df = 1, $p > 0.05$ $t = -0.37$, df = 13, $p > 0.05$	
	500 – 1000	3.9% 804 ± 121	4.7% 763 ± 62	$x^2 = 0.09$, df = 1, $p > 0.05$ $t = 0.78$, df = 6, $p > 0.05$	
	200 – 500	1.8% 339 ± 48	3.2% 376 ± 38	$x^2 = 0.40$, df = 1, $p > 0.05$ $t = -1.56$, df = 6, $p > 0.05$	
	100 – 200	0.7% 158 ± 20	1.9% 154 ± 18	$x^2 = 0.61$, df = 1, $p > 0.05$ $t = 0.29$, df = 5, $p > 0.05$	
	50 – 100	0.3% 65 ± 4	0.8% 80 ± 11	$x^2 = 0.19$, df = 1, $p > 0.05$ $t = -3.37$, df = 4, $p < 0.05$	*

	10 – 50	0.6% 27 ± 13	0.3% 32 ± 8	$x^2 = 0.12$, df = 1, $p > 0.05$ $t = -0.64$, df = 4, $p > 0.05$	
	0 – 10	0.2% 3	0.01% 8	$x^2 = 0.21$, df = 1, $p > 0.05$ t = N/A	
Chobe Hyena	*0 – 5000*	*26%*	*74%*	$x^2 = 23.37$, *df = 1*, $p < 0.001$	****
	1000 – 5000	71.8% 2842 ± 1192	95.3% 3730 ± 407	$x^2 = 3.31$, df = 1, $p > 0.05$ t = -7.24, df = 13, $p < 0.001$	 ****
	500 – 1000	12.8% 749 ± 142	2.8% 823 ± 94	$x^2 = 6.43$, df = 1, $p < 0.05$ $t = -2.28$, df = 10, $p < 0.05$	* *
	200 – 500	8.3% 341 ± 87	1.2% 334 ± 32	$x^2 = 5.28$, df = 1, $p < 0.05$ $t = 0.49$, df = 9, $p > 0.05$	*
	100 – 200	2.6% 150 ± 30	0.4% 148 ± 10	$x^2 = 1.59$, df = 1, $p > 0.05$ $t = 0.26$, df = 16, $p > 0.05$	
	50 – 100	2.2% 68 ± 14	0.2% 77 ± 15	$x^2 = 1.66$, df = 1, $p > 0.05$ $t = -1.09$, df = 4, $p > 0.05$	
	10 – 50	1.7% 26 ± 12	0.1% 33 ± 2	$x^2 = 1.57$, df = 1, $p > 0.05$ $t = -2.50$, df = 12, $p < 0.05$	 *
	0 – 10	0.6% 6	0 NA	$x^2 = 0.63$, df = 1, $p > 0.05$ t = N/A	

Supplementary Table S4.4. Statistical results of consecutive time points among dyads (indicating longer time duration), to accompany Figure 4.5 in the main text. T-tests comparing dyads with consecutive time points at various distance intervals (a), and the frequency occurrences of dyads for different consecutive time points (b). An asterisk denotes significance at the alpha level with * < 0.05, ** < 0.01, *** < 0.005, and **** < 0.001.

(a)

Dyads	Distance Intervals (m)		Significance
LN-LN vs LN-HY	0-100	t = 4.31, df = 5, p < 0.01	**
	100-200	t = 2.94, df = 6, p < 0.05	*
	200-500	t = 3.19, df = 10, p < 0.01	**
	500-1000	t = 2.65, df = 8, p < 0.05	*
	1000-2000	t = 1.50, df = 9, p = 0.167	
HY-HY vs LN-HY	0-100	t = 1.27, df = 5, p = 0.257	
	100-200	t = 1.10, df = 5, p = 0.317	
	200-500	t = 1.51, df = 6, p = 0.186	
	500-1000	t = 1.89, df = 6, p = 0.107	
	1000-2000	t = 1.79, df = 8, p = 0.112	
LN-LN vs HY-HY	0-100	t = 1.70, df = 9, p = 0.121	
	100-200	t = 0.45, df = 8, p = 0.665	
	200-500	t = -0.46, df = 6, p = 0.663	
	500-1000	t = -0.94, df = 5, p = 0.386	
	1000-2000	t = -0.92, df = 7, p = 0.388	

(b)

Dyads	Consecutive Time Points		Significance
LN-LN vs LN-HY	1	t = 0.73, df = 5, p = 0.497	
	2	t = 1.47, df = 8, p = 0.180	
	3-5	t = 6.47, df = 6, p < 0.001	****
	6-10	t = 1.93, df = 6, p = 0.106	
	11-30	t = 2.70, df = 8, p < 0.05	*
	>30	t = 6.60, df = 4, p < 0.005	***
HY-HY vs LN-HY	1	t = 4.83, df = 8, p < 0.005	***
	2	t = 3.37, df = 7, p < 0.05	*
	3-5	t = 2.38, df = 4, p = 0.074	
	6-10	t = 1.36, df = 5, p = 0.240	
	11-30	t = -0.15, df = 8, p = 0.888	
	>30	t = -3.50, df = 4, p < 0.05	*
LN-LN vs HY-HY	1	t = -5.91, df = 6, p < 0.005	***
	2	t = -2.47, df = 6, p < 0.05	*
	3-5	t = -0.30, df = 5, p = 0.778	
	6-10	t = 0.23, df = 6, p = 0.828	
	11-30	t = 2.70, df = 8, p < 0.05	*
	>30	t = 6.99, df = 4, p < 0.005	***

CHAPTER FIVE

Summary and conclusions

My aim in undertaking this study was to assess the spatiotemporal and movement ecology of lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), with a lens on the role that interspecific interactions between the two species potentially has in driving the space use patterns of both predators. Specifically, my objective was to effectively quantify the presence and prevalence of such interactions, and to determine the effects of these interactions on lion and hyena ecology and behaviour. In addition to demonstrating the underlying factors that shape the spatiotemporal patterns of the two species, I particularly wanted to ascertain whether interspecific interactions between lions and hyenas significantly influenced the movement decisions of these apex predators over the landscape. I also investigated whether these patterns persisted across different ecosystems by analyzing lion and hyena movements from semi-arid and mesic extremes of their environment. This allowed me to substantiate that the effects of such interactions among lions and spotted hyenas were conventional, and not a result of different environmental characteristics. Although I decidedly focused my analyses on both lions and spotted hyenas for this study, the application of these methods could be applied to other multi-species communities where carnivores co-exist, and potentially interact. In this chapter, I summarize the key findings of my study and discuss their implications in the context of carnivore conservation. In addition, I identify limitations and gaps in this study and propose areas for potential future research.

5.1. Synthesis of key results

Despite being often positively associated with one another (Périquet et al. 2015, Kittle et al. 2016), lions and spotted hyenas mediate the potential for interference competition through subtle differences in temporal activity (Chapter 2), fine-scale habitat use differentiation (Chapters 2 and 3), and localized reactive-avoidance behaviours (Chapter 4). In Chapter 2, although both lions and hyenas were mainly active during nocturnal periods in this study, there were temporal shifts in activity between lions and hyenas in which periods of heightened activity were dominated by one species during different time periods of the night, lending support towards a temporal partitioning strategy (Edwards et al. 2015, Herrera et al. 2018, Hearn et al. 2018). In addition, spotted hyenas moved at higher activity, travelled faster and further than lions, and focused their foraging and hunting efforts during periods of sufficient light conditions. Coexistence between lions and hyenas may further be facilitated by such differences in movement characteristics which can be attributed to the hunting strategies of the two species, resulting in fine-scale habitat separation (Preisser et al. 2007, Milleret et al. 2018). Lion core use areas were anchored by water sources, whereas hyenas had increased recursivity to locations far from water, suggesting that hyenas are either relegated to suboptimal habitats (Loveridge et al. 2017) or choosing to avoid detection by lions (Périquet et al. 2016, Kushata et al. 2018). Although lions and hyenas did not respond to inter- and intraspecific interactions equally among heterogeneous and homogeneous environments, such interactions were consistently selected as the most important factor after time of day and land cover categories that explained the time-use patterns of both predators. Hyenas and female lions chose to remain longer in areas of low competitor probabilities and at far distances to competitors, presumably as a result of the perceived risk of competition (Vanak et al. 2013, Swanson et al. 2016). However, male lions had longer durations in areas of high competitor probabilities, potentially seeking to increase the likelihood of encountering hyenas so as to benefit from them through kleptoparasitism (Höner et al. 2005, Watts & Holekamp 2009).

In Chapter 3, Lion space-use patterns across arid and mesic environments reveal the influences of habitat characteristics and competitive interactions with competitors (spotted hyenas) on lion habitat selection and movement. Lion ranges and movement patterns differed across seasons and as a function of environmental heterogeneity among protected areas. Lions exhibited longer steps and increased activity in drier environments, but had more tortuous paths in wetland areas. Lion core areas were larger in arid systems than they were in mesic systems, and had larger ranges in the wet season except in the Okavango Delta (Kotze et al. 2018). Although lions in mesic environments (Chobe) shared more of their home ranges than they did in arid environments (Etosha), intra- and interspecific interactions influenced lion habitat selection and movements during the dry season. Lions used areas within their home range with a lower probability of spotted hyenas in both ecosystems, and used steps further away from high hyena probabilities, probably as a localized avoidance mechanism (Périquet et al. 2021). Conversely, lions from Chobe used areas with a higher probability of conspecifics, and were often within <5 km to conspecifics in Etosha, likely as a result of the gregarious sociality of lion pride networks in which they form and maintain subgroups (Mosser & Packer 2009, Mbizah et al. 2020). In addition to inter- and intraspecific interactions, lions in Etosha were more likely to move closer to water and anthropogenic features, and towards anthrax areas with a high probability of site-attracted foragers. Similarly, Chobe lions were also more likely to move closer to water and roads, but avoided areas close to anthropogenic features. However, lions from the Okavango

Delta consistently used areas that were further from seasonal water sources. Interestingly, while interaction variables consistently improved all resource selection function (RSF) and step selection function (SSF) models for the Etosha and Chobe groups, I did not have any measures of interactions for the Okavango group, and as a result the SSF models failed to return any significant predictors for the Okavango group.

In Chapter 4, spatial overlaps among heterospecific and conspecific competitors occurred at the edge of home ranges, within 2-5 km of water-points, and within >0.5-1 km along roads, and were indicative of joint, contemporaneous space-use. Temporally overlapping hulls within jointly used areas demonstrated the presence of interactions within the home ranges and core areas of dyads (Lyons 2012). Although the majority of the minimum time lag between spatially overlapping hulls among lion and spotted hyena dyads was 12-24 and >24 h, there were several incidences of overlapping hulls without any time lag which indicates the occurrence of a shared space use at the same times. Lions and spotted hyenas evidently interacted within these jointly used areas, both across seasons and ecosystems. Dynamic interactions among sympatric lions and spotted hyenas illuminates how hyenas effectively reduce their potential of interactions with lions by utilizing spatiotemporal partitioning strategies and local reactive avoidance behaviours within shared space use areas. Lions and spotted hyenas utilize minimal overlaps among core use areas and large lag times of 12-24 and >24 h within shared space-use, as a spatiotemporal strategy to allow the two species to co-exist within the same areas without encountering one another (Broekhuis et al. 2013, Swanson et al. 2016). Movement analyses among interspecific dyads indicated that the majority of hyenas exhibited retreat behaviours away from lions while a third of lions presented approach behaviours towards hyenas. Additionally, simultaneous movements also demonstrated that hyenas exhibited retreat behaviours away from lions, as lions simultaneously followed or tracked hyenas. Despite these behaviours, the two species persisted in tracking one another, and at times for extended periods of upwards of 300 consecutive minutes. Among intraspecific pairs, lion dyads demonstrated a high occurrence of coordinated movements, whereas hyenas mostly avoided each other at close distances, with some individuals tracking one another at large distances. Lion prides exhibited a fission-fusion social system; with lion dyads occurring at closer distances more frequently in Etosha than in Chobe. Lions also occurred at near distances more often, and spent more time together at closer distances with conspecifics than they did with competitors (Mosser & Packer 2009, Kotze et al. 2018, Mbizah et al. 2020). Contrarily, hyenas from Chobe exhibited more of a fission-fusion social system than was observed in the Etosha clans, which were largely territorial (Cooper 1989, Boydston et al. 2001, Trinkel et al. 2004, 2006).

5.2. Implications of this study for conservation

Our results have implications for the conservation of large carnivores in substantiating the potential effects of interference competition on lion and spotted hyena spatial patterns and movements. These findings supplement the growing body of evidence that demonstrates coexistence among carnivores is facilitated by fine-scale behavioural mechanisms (Chapters 2 and 4) in addition to spatial and temporal partitioning (Chapters 2-4). As large carnivores are becoming increasingly constrained to protected areas (Riggio et al. 2013, Ripple et al. 2014), it is important to note that lions and spotted hyenas do not respond to inter- and intraspecific interactions equally among heterogeneous and homogeneous environments. Specifically, the movement decisions and behavioural responses of lions and spotted hyenas are adaptable across different systems, and are likely a result of several factors, including hunting strategies (Chapter

2), habitat complexity (Chapters 2 and 3), and the active avoidance of intraspecific and heterospecific competitors (Chapter 4).

These findings of a seasonal effect on lion habitat selection and movement responses, to select for areas with low probabilities of competitors (Chapter 3), has important ramifications in light of the global trend towards a warmer world. The impacts of climate change has been linked to a decrease in lion densities through the reduction of prey biomass (Ogutu & Dublin 2004, Trinkel 2013), and shifts in lion ranges (Tuqa et al. 2014). With increases in temperatures and droughts brought on by climatic variability, the influences of inter- and intraspecific interactions on lion movements and habitat selection are likely to be amplified (Parmesan & Yohe 2003, Chen et al. 2011, Tuqa et al. 2014, Lenoir & Svenning 2015, Wiens 2016). Restricted to protected areas which are becoming increasingly fragmented, such effects may potentially drive lions outside reserve boundaries and into human dominated landscapes resulting in escalated conflicts, which poses a challenge for lion conservation (Kissui 2008, Creel et al. 2013, Di Minin et al. 2016, 2021, Weise et al. 2018).

The potential for interaction with spotted hyenas during the dry season drives lions to select for areas with low hyena probabilities, and to select for steps further away from high hyena probabilities (Chapters 2 and 3). These findings have implications for the conservation planning and reserve design of lions, to not only ensure that different environmental characteristics are incorporated within lion habitats, but also that such habitats allow for movements that may mitigate the effects of inter- and intraspecific interactions on lion space use patterns (Trinkel & Kastberger 2005, Yiu et al. 2019, Périquet et al. 2021). The conservation of lions has long relied on designated, demarcated protected areas which reduces the potential for lion interaction with humans. However, it ignores not only the potential effects of environmental and landscape changes that may occur as a result of climatic variability (Trinkel 2013, Tuqa et al. 2014), but also discounts the effects of competitive interactions both among lions and with other sympatric predators, which may impose a greater influence on lion behaviour than the environment alone (Kotze et al. 2018, Périquet et al. 2021).

Therefore, and ideally, the maintenance of large enough protected areas or the linking of several smaller reserves with the use of wildlife corridors away from the pressures of anthropogenic influences, is a conservation priority for lions who share their ranges with spotted hyenas. However as wild lands become increasingly fragmented and interspersed with human activities, strong resistance is likely to ensue when attempting to establish wildlife corridors for the protection of carnivores. Thus, limiting the types and amounts of human activities seasonally, or during periods of droughts, will become a crucially important tool for reducing the impacts on wildlife, especially when carnivores move outside of protected areas into human-use landscapes where the potential for conflict with humans becomes amplified (Woodroffe & Frank 2005, Ogutu et al. 2005, Di Minin et al. 2016). As certain species appear to mediate the potential effects of interspecific competition by adjusting their movements in response to reducing the risk of potential interactions with a competitor, quantifying these types of movement behaviour can be a useful indication of the type of interaction occurring in a dyad (Chapter 4), and can help guide conservation efforts of certain species.

Understanding how apex predators move across the landscape in response to interactions with competitors will ultimately affect the maintenance of diverse and functional ecosystems in the face of increasing climatic variability and dwindling wild lands. Patterns of recursion and locations of extended stays within the home ranges of apex predators are influenced by the probability of and proximity to competitors and conspecifics (Chapter 2), and can be used to inform management strategies for the maintenance of carnivore communities. Carnivore movements resulting from competitive interactions may translate into movements away from such immediate risk into different areas of potential conflicts (i.e., with humans in human-dominated landscapes) which may compromise conservation actions. Thus, it may become prudent to identify certain locales of potential hotspots of conflict between carnivores (i.e., at water points during dry periods), and to provide potential areas of refugia within such locations, or alternatively to supplement such resources at an increased density in areas away from humans. Wildlife managers will need to account for not only environmental heterogeneity, but also take into consideration the influences of competitive interactions that can impact carnivore movement behaviour, when designing and managing protected areas, and in constructing wildlife corridors when linking smaller reserves into larger conservation areas. Consequently, we encourage conservation practitioners to recognize the importance of the potential effects of inter- and intraspecific interactions among apex predators in managing diverse, ecological communities.

5.3. Implications of this study for biological understanding

My work in this study has enhanced our understanding of the behavioural ecology of apex predators. Identifying and quantifying the types of interactions that occur between two individuals within a dyad reveals the effects that the movements of one individual has on the other (Chapter 4). With this method, I demonstrated that interactions between lions and spotted hyenas are prevalent, and also significantly influenced the movement responses of each other more than had been previously recorded. Thus, it is likely that in other multi-species communities where an individual’s range overlaps with others, such individuals presumably interact; and the application of this method may provide an understanding of the effects that these species have on each other, both among their own group, and across groups.

As certain carnivore species are able to mediate the potential for competition by modifying their spatiotemporal patterns, carnivores are able to co-exist with other predator species by habitat use differentiation on a fine-scale. Carnivores select to use and move through habitats as a result of habitat characteristics that facilitate movements (Roever et al. 2010, Bender et al. 2017), to increase the likelihood of obtaining resources (Hopcraft et al. 2005, Preisser et al. 2007), and to decrease detection by competitors (Beier 2010). In addition to fine-scale habitat use differentiation, carnivores utilize localized reactive-avoidance behaviours (Broekhuis et al. 2013, Swanson et al. 2016), and have the ability to alter their responses in a dynamic environment, including choosing whether to track, follow, or retreat from competitors. As a result, complete exclusion or total segregation among sympatric carnivore species is likely alleviated by the localized movement responses and fine-scale separation, facilitating co-existence between carnivores. This however, requires that carnivores have ample space to do this. In light of the global decline of available habitats for carnivore conservation, the potential effects of competitive interactions may drive carnivores outside of protected areas and into human-dominated landscapes (Di Minin et al. 2016, 2021, Weise et al. 2018), which poses a challenge for the maintenance of natural multi-predator systems.

5.4. Limitations of the study and gaps

As this study depended on obtaining extensive relocation records across two species, when collars experienced structural failures, this resulted in gaps in the data in which some collars failed while others continued to operate. This meant that our relocation records had full continuous tracking days for some individuals and not for others. Such gaps in the data make it difficult to obtain information on a continuous basis when looking for occasions of proximity encounters across species for analyses of interactions. Although missing relocations may be imputed with continuous-time movement modelling (ctmm, Calabrese et al. 2016) to estimate the movement paths, unless there is a short time interval between actual fixes, such imputed data increases the likelihood of inaccurate measures when analyzing imputed data across two individuals. Thus, while we included the missing data in this study which had ctmm applied for range analysis of home ranges and core areas, they were not included for analyses of interactions. In addition to gaps in the data from collar failures, there was also a significant loss of collars from Botswana individuals (*n* = 7) because of mortalities of some individuals and delays in retrievals after collar batteries had been depleted. As the collars were programmed to upload every third fix to conserve batteries for long-term data collection, this significantly reduced the amount of data for Botswana individuals for interaction analyses, which are reflected in the small numbers of lion and hyena dyads from Chobe.

Although we focused our study on the effects of potential competitive interactions on the spatiotemporal ecology of lions and spotted hyenas, our analyses of lion and hyena space use patterns would have been made more robust had we integrated the density and distribution of prey as a driver of predator movement. Despite using normalized difference vegetation index (NDVI) as a proxy for potential prey resources, our results were ambiguous in finding that landscape use by lions and hyenas were both positively and negatively correlated with NDVI. Presumably, predators prioritize finding food over avoiding competitors during periods when prey are dispersed and harder to find (i.e., during the wet season), whereas during the dry season when prey are clustered around key resources such as water holes, the importance of competitors becomes an influential driver of predator movement patterns. Thus, future studies analyzing the effects of competitive interactions among carnivores would do well to include prey data collected at similar sampling frequencies, difficult as this may be.

Analyses of interactions require that at least two individuals overlap in their ranges. Since I did not have any data on spotted hyenas in the Okavango Delta, I was unable to apply the relative-motion method on the data from the lions I had collared in the region. Further to this, while we had collared one individual in each group to ensure that any potential interactions with other collared individuals would be from unfamiliar conspecifics to account for intraspecific competition, the seasonal fission-fusion networks of both lion and spotted hyena groups resulted in changes in the compositions of prides and clans over time. Thus, it becomes difficult to ascertain whether effects of intraspecific interactions among conspecifics stemmed from familiar or unfamiliar conspecifics, unless such encounters or interactions were actually observed in the field. It therefore becomes possible that intraspecific competition between prides or clans is what facilitates coexistence between them, and future studies could further investigate this. Moreover, I assumed for the purpose of this study that all heterospecific competitors were treated equally. It is possible that knowledge of certain or familiar individuals across different species groups may potentially attenuate (or exacerbate) such interactive effects as Watts et al. (Watts et al. 2010) found the responses of spotted hyenas to lion to reflect individual differences in behaviours. Thus, future studies may benefit from investigating the differences in movement responses towards familiar and unfamiliar competitors.

Another limitation of this study is in the amount of analyses undertaken during this study. In analyzing the data for this study, the number of comparisons increased exponentially with assessing two different species (lions vs hyenas) from two different ecosystems (Etosha vs

Chobe or Botswana), across different seasons (wet vs dry), time periods (night vs day), and sampling frequencies (nocturnal vs dusk/dawn or 24 h). Therefore the statistical modelling approach was subjected to multiple testing, which increases the probability of type 1 errors. Multiple testing corrections such as the Bonferroni adjustment have been proposed in the statistical literature (Chen et al. 2017), although this was not conducted here due to the conservative nature of such corrections. Instead, we aimed to limit comparisons between groups and inspected supporting data from other studies to validate the results of our study. Future studies should strive to collect a large enough amount of data that would allow for breaking up the data into separate analyses, or to apply the multiple testing corrections.

5.5. Future research

The application of current advances in the relative-motion method presents an interesting and exciting avenue for future research, especially with the capacity for higher resolution data loggers. This method enables us to determine the type of interaction occurring among individuals of a dyad, and allows us to know whom is following or tracking whom. Such an application may also be applied towards members of entire groups in understanding how collective group movements influence the movement decisions of individuals. These findings could then be linked to the hierarchical status of individuals living among social groups, or applied towards entire community networks in where movements of apex predators may have important effects on the structure and function of multi-species communities.

Furthermore, this type of method may prove useful when used in conjunction with the behavioural change point analyses (BCPA) method to be able to explain how or why such behavioural changes occurred in the individual’s trajectory. New advances in machine learning tools with the application of unsupervised features such as Hidden Markov Models (HMM) and Generative Adversarial Networks (GAN) could potentially be applied to use the relative-motion method on simultaneous individuals to understand how certain individuals' movement decisions are affected by the simultaneous movements of the group. Such applications may be informative during social interactions in understanding how movements at the periphery of the group informs movements in the center, or in predator-prey interactions in which either a solitary predator or a group of predators search for, and hunt groups of prey individuals. Detailing the movement responses of certain individuals relevant to others may shed light on the dynamic interactions among individuals when exposed to changes in group composition or when undertaking group activities such as cooperative hunting and collective foraging movements.

5.6. Conclusions

In summary, I present data on direct interactions between lions and spotted hyenas and I have provided empirical evidence for the presence and occurrence of important interactions among lions and spotted hyenas where they overlap spatially and temporally. Interactions among lions and hyenas has important implications for their movement ecology and affects how individuals choose to use and move across the landscape. Thus, it becomes prudent to include measures of interactions that detect temporal and spatial differences between the two species, to enhance our understanding of carnivore ecology. Although studies using simultaneous tracking on two species to allow for an analysis on the direct effects of the two species on one another are limited, this type of analysis has enabled us to understand the dynamic interaction that occurs between individuals and the potential effects on their ecology. To our knowledge, previous measures of dynamic interaction do not illustrate following/leadership behaviour, or whether individuals exhibit approach/retreat behaviours. Here, I have used a reliable inferential framework for analyzing the movement interactions of paired individuals, to understand the dynamics of asymmetrical movement interactions. In conclusion of the findings in this thesis, I found that fine scale temporal partitioning of activity periods among lions and spotted hyenas, and reactive local avoidance employed by hyenas, acts as the main mechanisms to allow for the co-existence of the two species in areas where they co-occur. Specifically, spotted hyenas minimize the potential for interference competition by behaviourally adjusting their movements to effectively avoid encountering lions. These findings may prove beneficial when considering the management and conservation initiatives of apex predators, in understanding that the effects of such interactions between competing species are likely to be amplified in smaller reserves and during dry periods, and in ensuring that apex predators are able to mitigate such effects.

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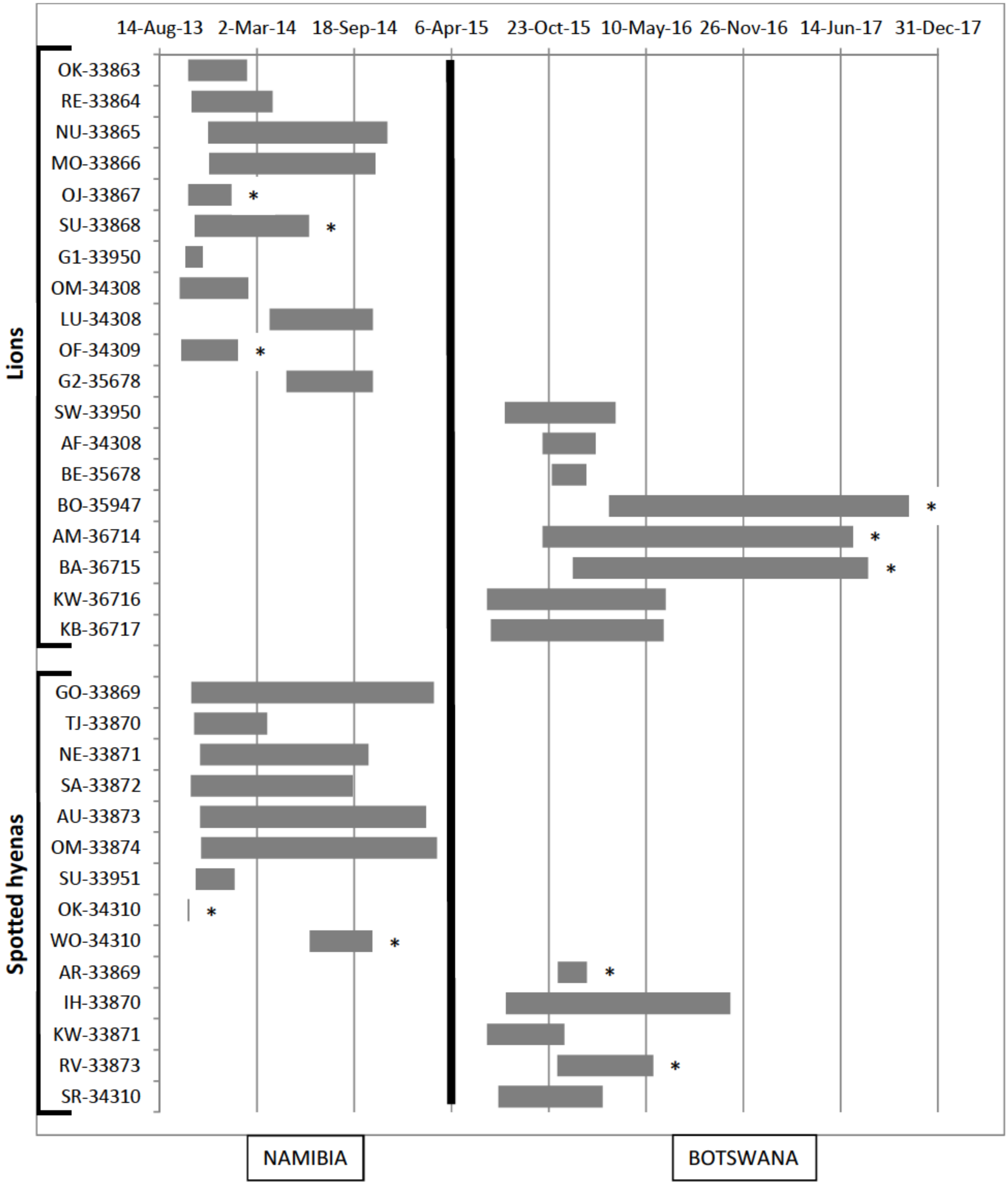
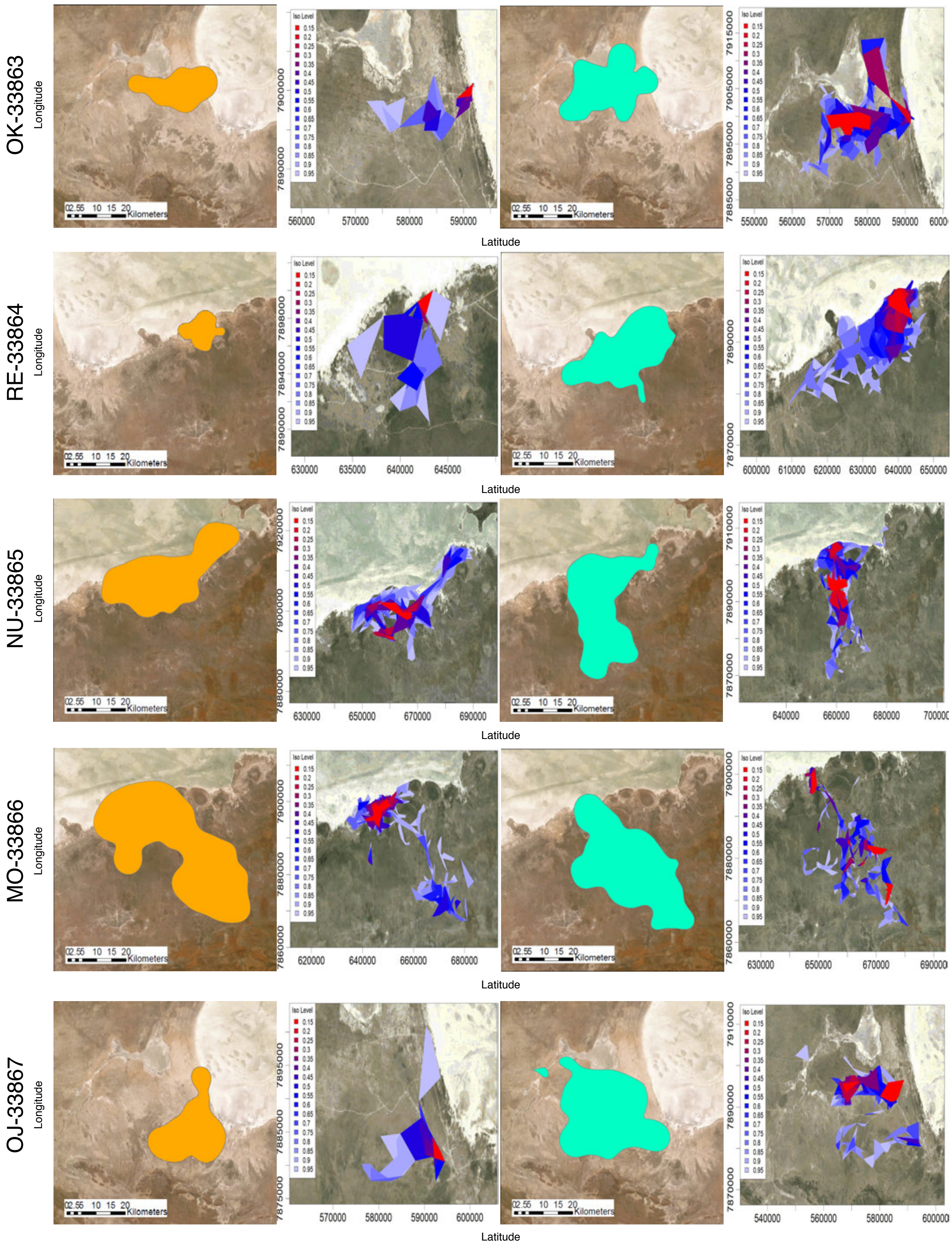
Supplementary materials to Barker et al., *Concurrent spatiotemporal ecology of African lions and Spotted hyenas and the potential for inter- and intraspecific interactions in semi-arid and wetland ecosystems*. Supplemental to Chapter 2.



Appendix 2.1. Temporal schedule of collar overlap for lions and spotted hyenas. Individuals of the Etosha National Park, Namibia (left) are separated from individuals of the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (right) at the bold line indicated on 6 April 2015. Males are denoted with an asterisk.

(a)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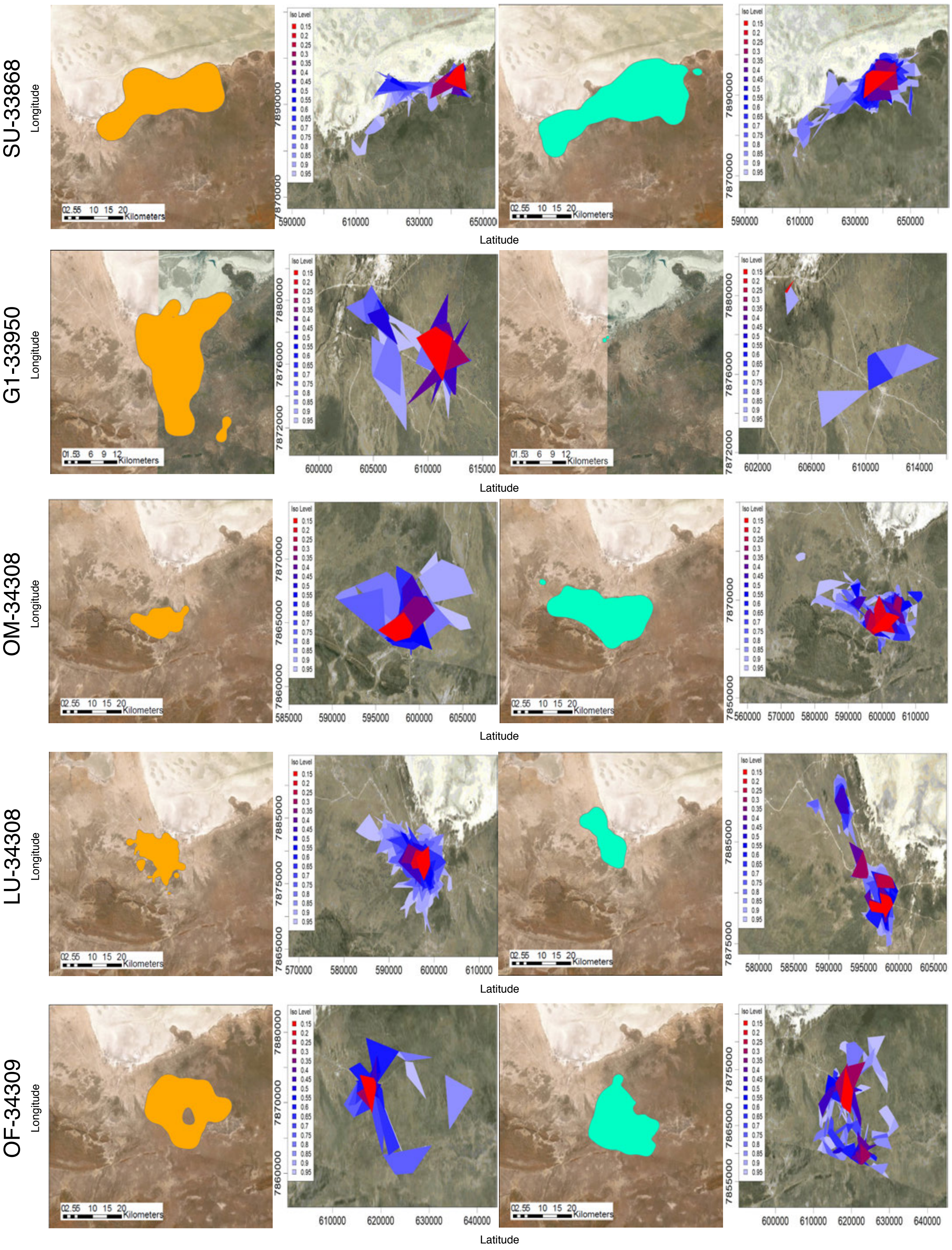
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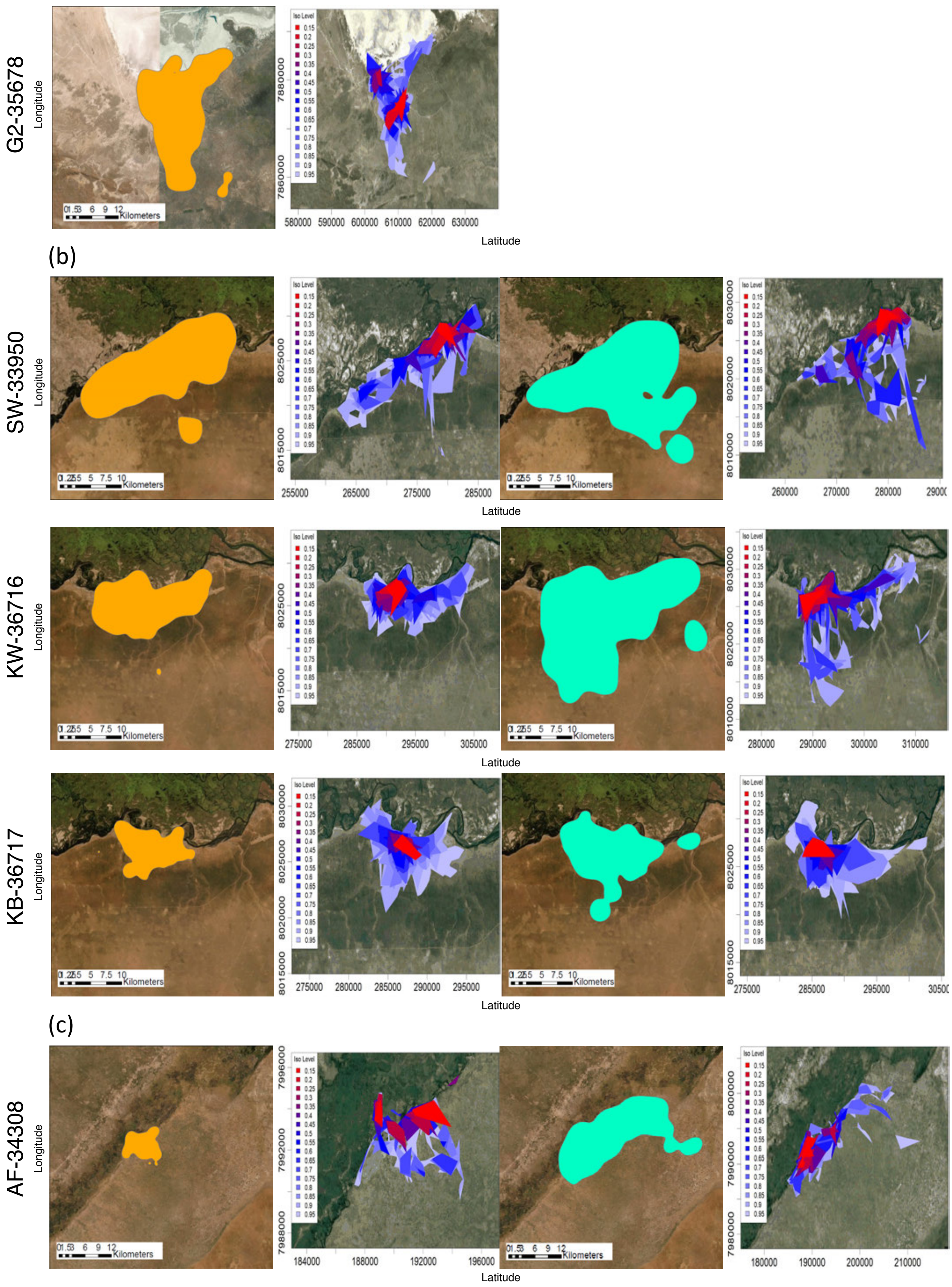
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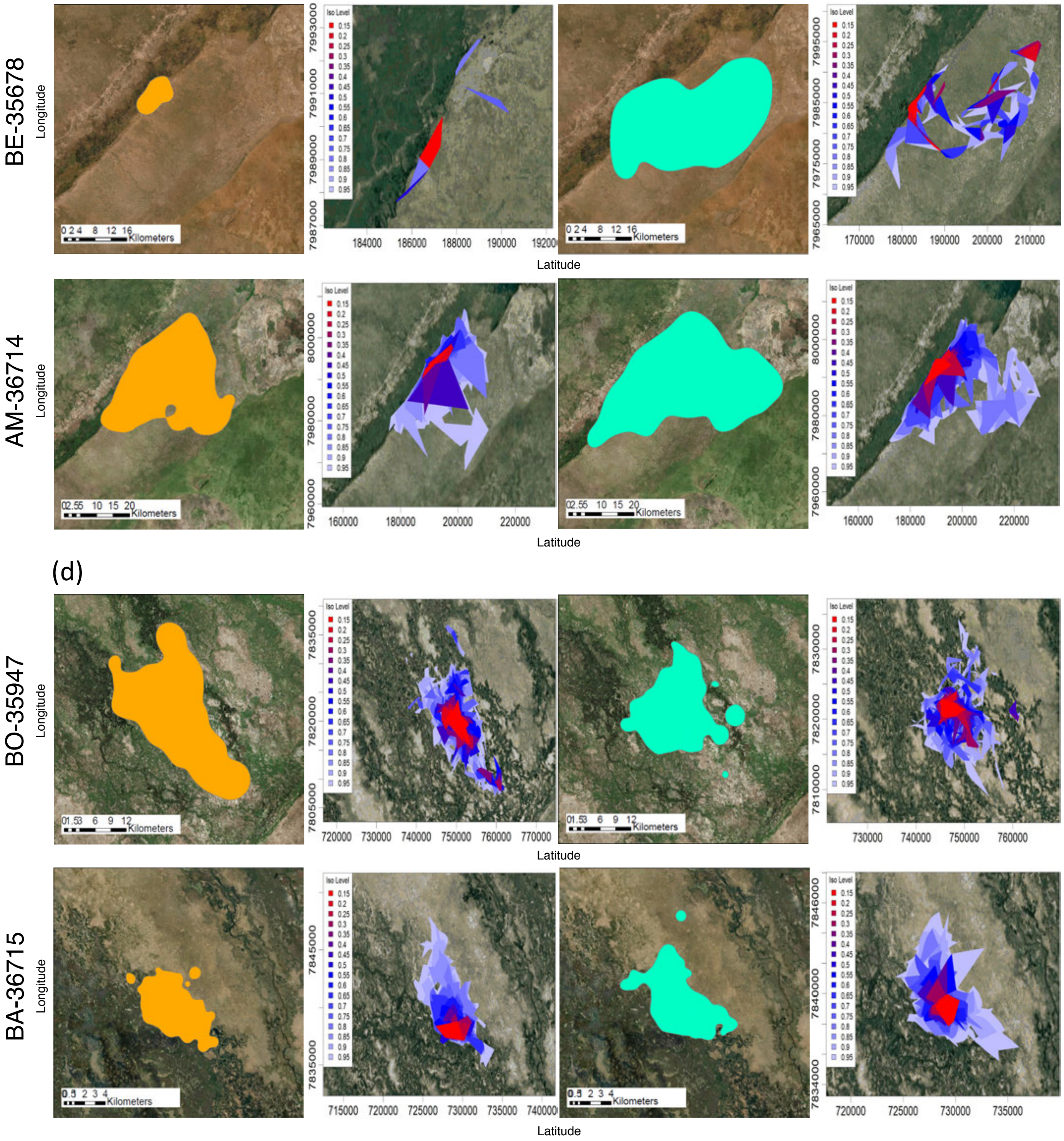
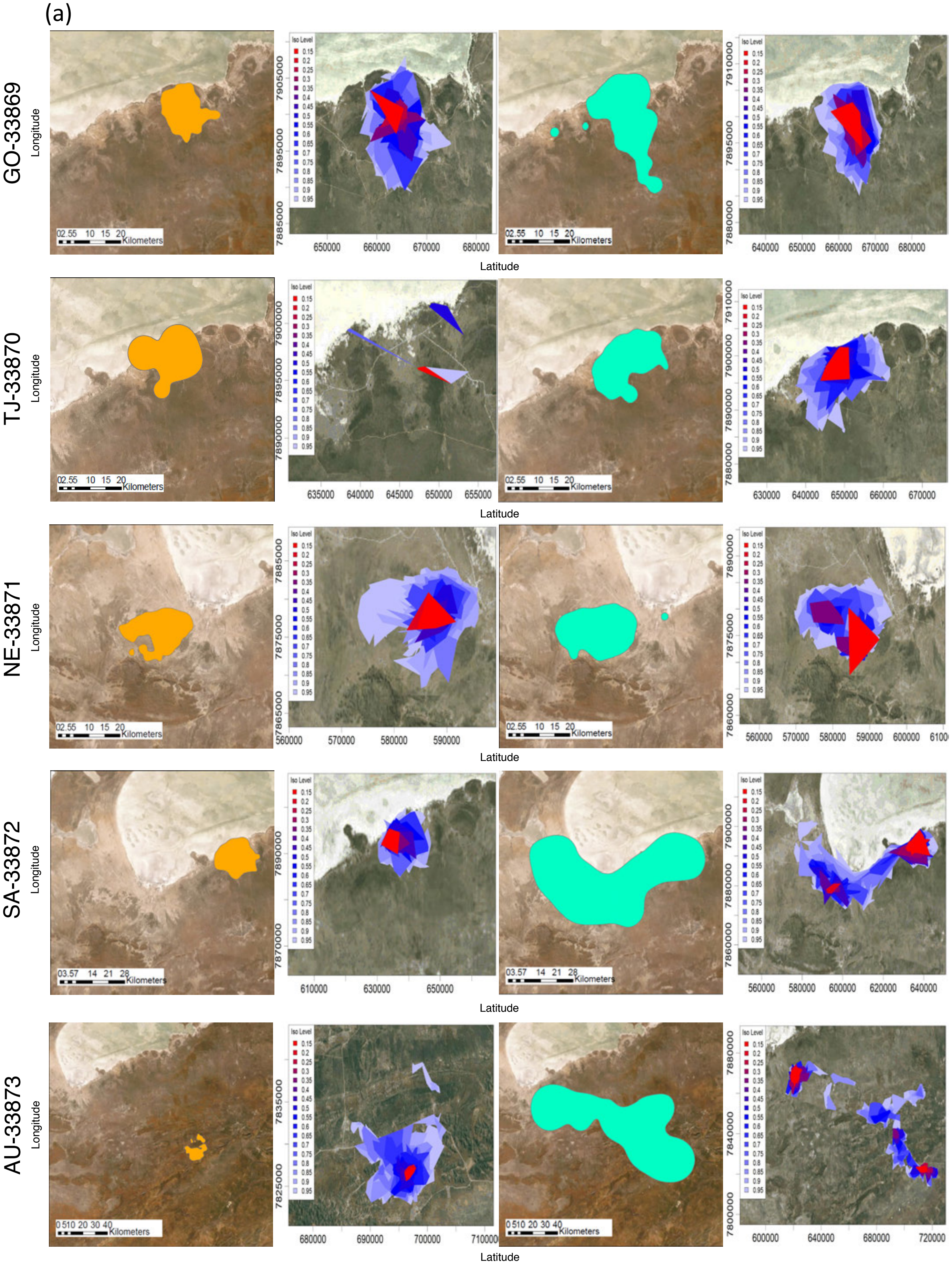


Appendix S2.2.1. Nocturnal space use of lion individuals from the (a) Etosha National Park, Namibia; (b) Chobe National Park; (c) Linyanti Conservancy; and (d) Okavango Delta, Botswana. Utilization distributions were constructed with the KDE (far left and second from right) and LoCoH a-method (second from left and far right). Panels represent the 95% isopleth of the individual's home range for the dry season (left two panels) and wet season (right two panels). Unique identifiers are depicted vertically on the left of each row of maps. Maps indicate the individual's home range on a satellite image of the (a) Etosha National Park with the salt pan visible; (b) Chobe National Park with the Chobe river from west to east; (c) Linyanti Conservancy with the Linyanti river from southwest to northeast; and (d) NG32 concession in the Okavango Delta on the southwestern tip of Chief's Island. Map source: Google Imagery, TerraMetrics.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0.4
0.45
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0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
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03.57 14 21 28 Kilometers
0 510 20 30 40 Kilometers
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7905000
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660000
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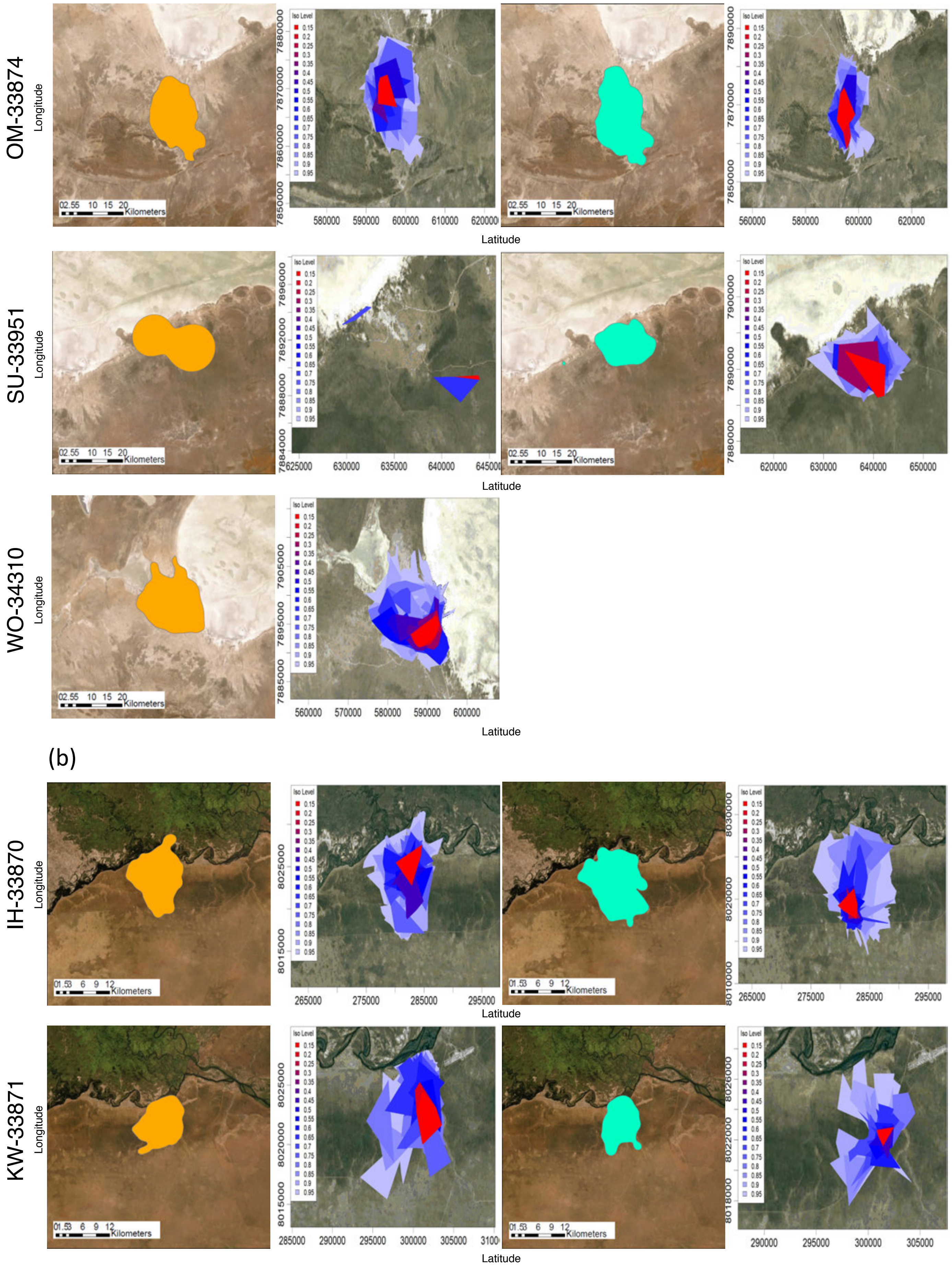
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620000
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Latitude
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Longitude
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Latitude
(b)
IH-33870
Longitude
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01.53 6 9 12 Kilometers
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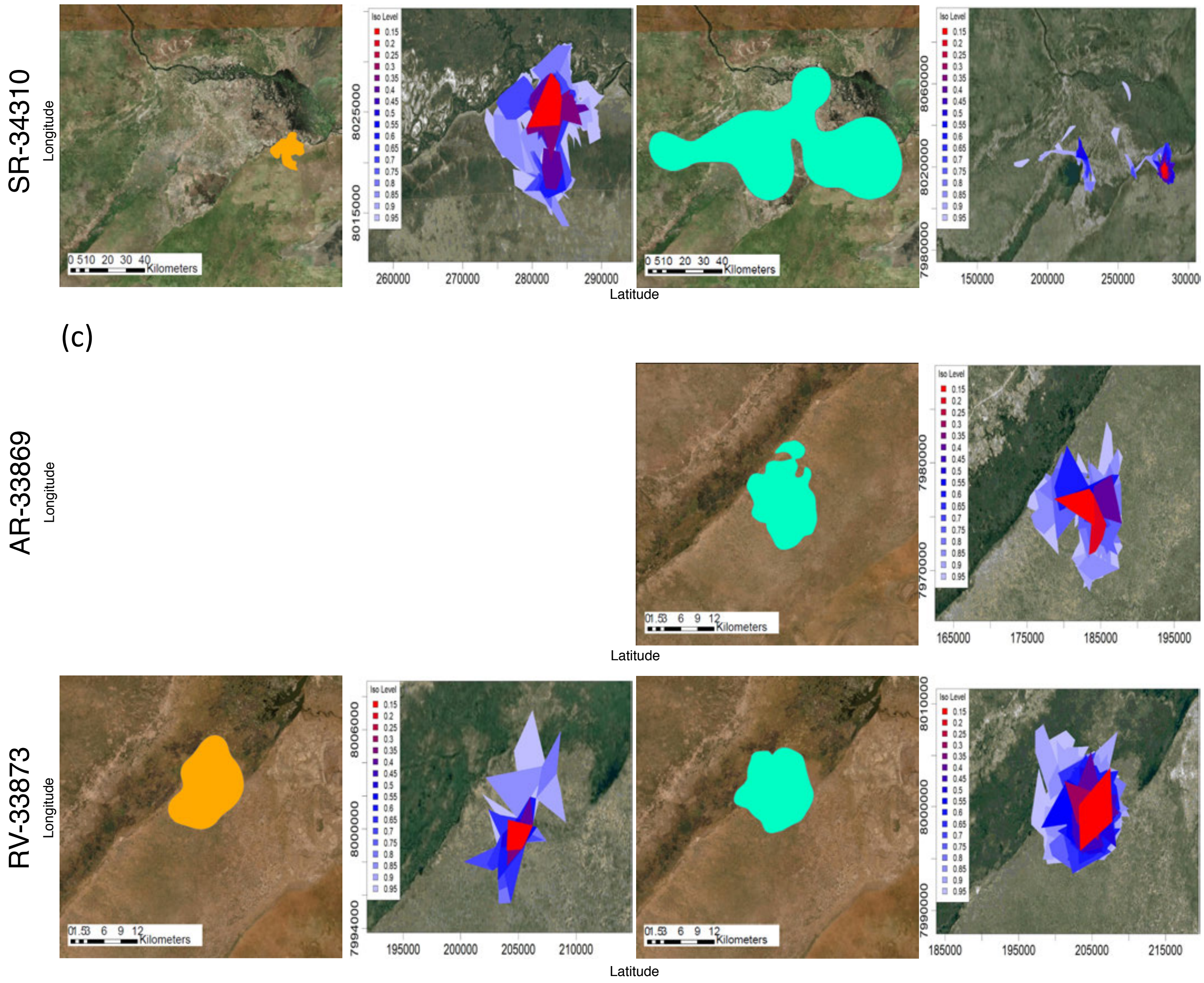
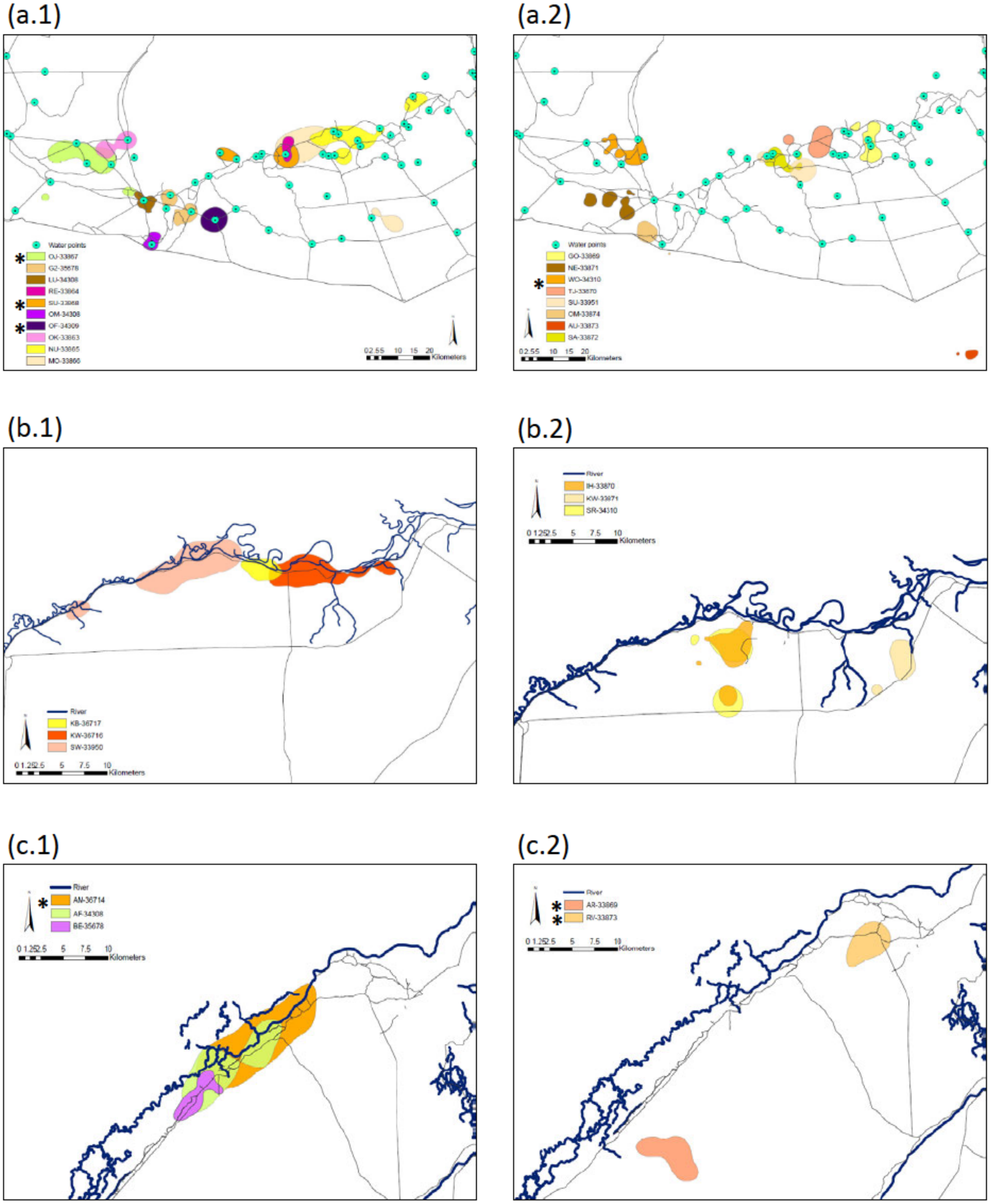
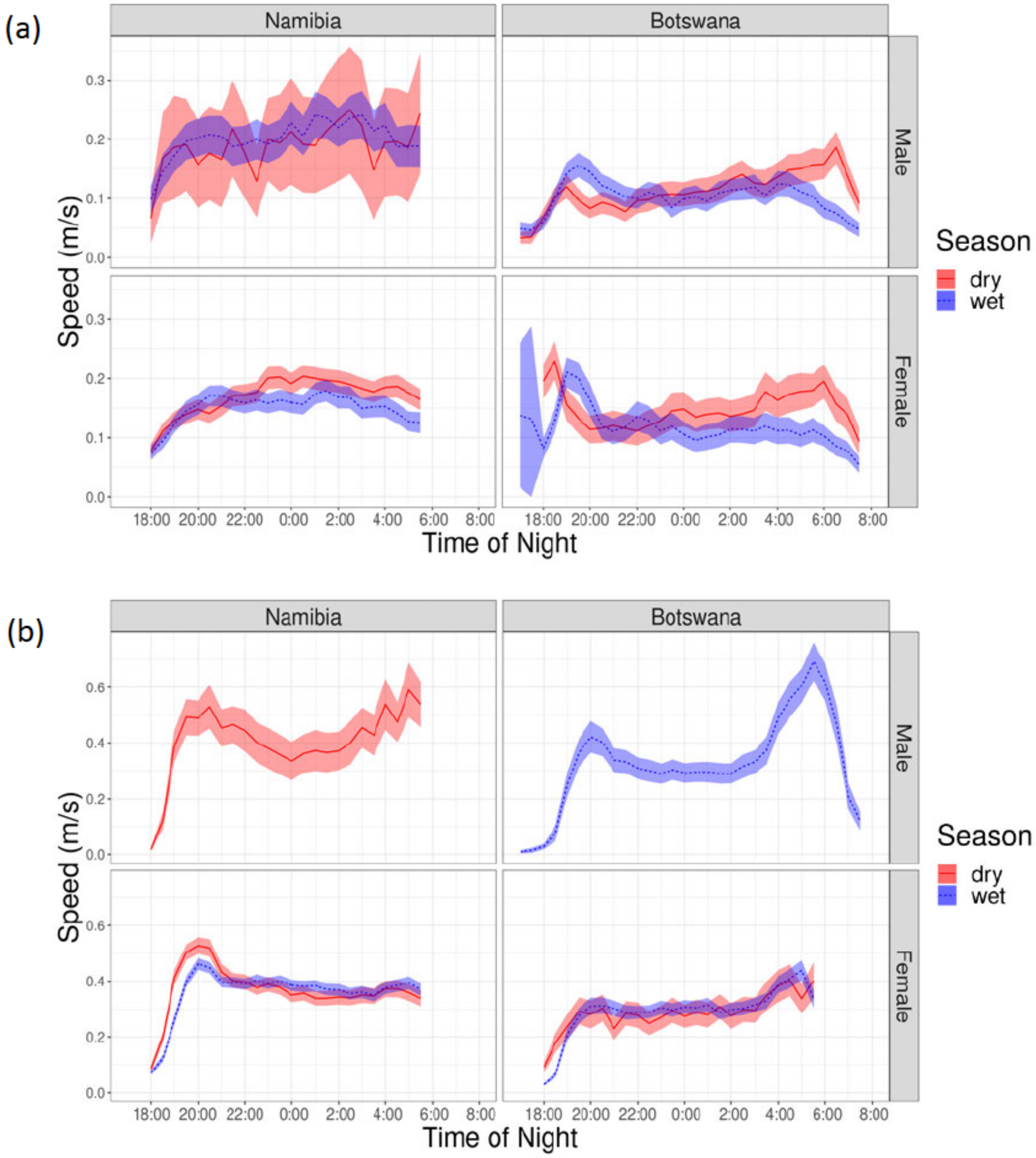


Appendix S2.2.2. Nocturnal space use of spotted hyena individuals from the (a) Etosha National Park, Namibia; (b) Chobe National Park; and (c) Linyanti Conservancy, Botswana. Utilization distributions were constructed with the KDE (far left and second from right) and LoCoH a-method (second from left and far right). Panels represent the 95% isopleth of the individual's home range for the dry season (left two panels) and wet season (right two panels). Unique identifiers are depicted vertically on the left of each row of maps. Maps indicate the individual's home range on a satellite image of the (a) Etosha National Park with the salt pan visible; (b) Chobe National Park with the Chobe river from west to east; and (c) Linyanti Conservancy with the Linyanti river from southwest to northeast. Map source: Google Imagery, TerraMetrics.

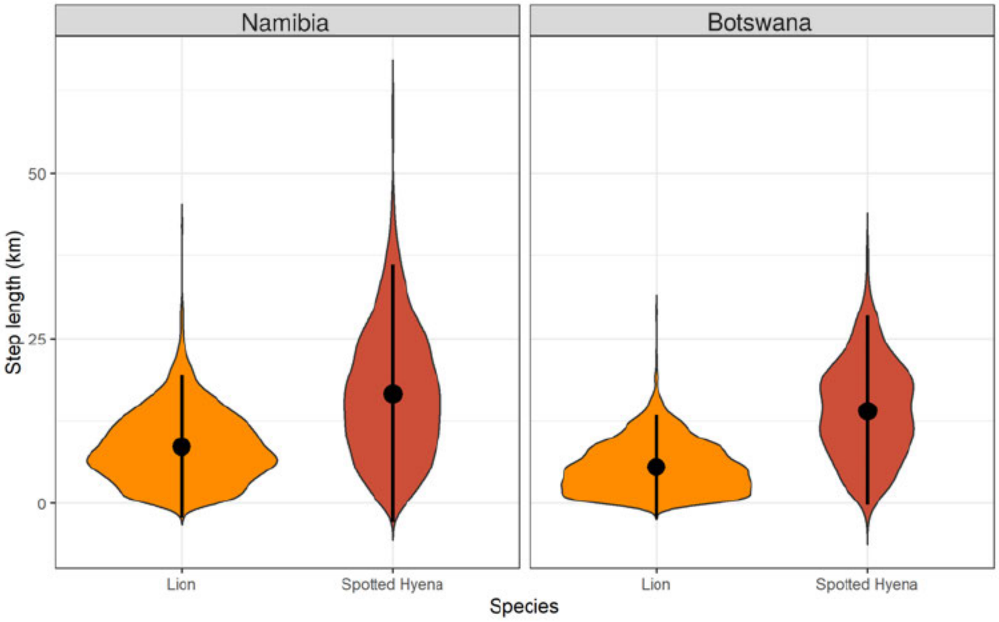


Appendix S2.2.3. Core use areas of individual lions (1) and spotted hyenas (2) in the (a) Etosha National Park, Namibia; (b) Chobe National Park, and (c) Linyanti Conservancy, Botswana. Roads are indicated by grey lines in all figures. Males are denoted with an asterisk.



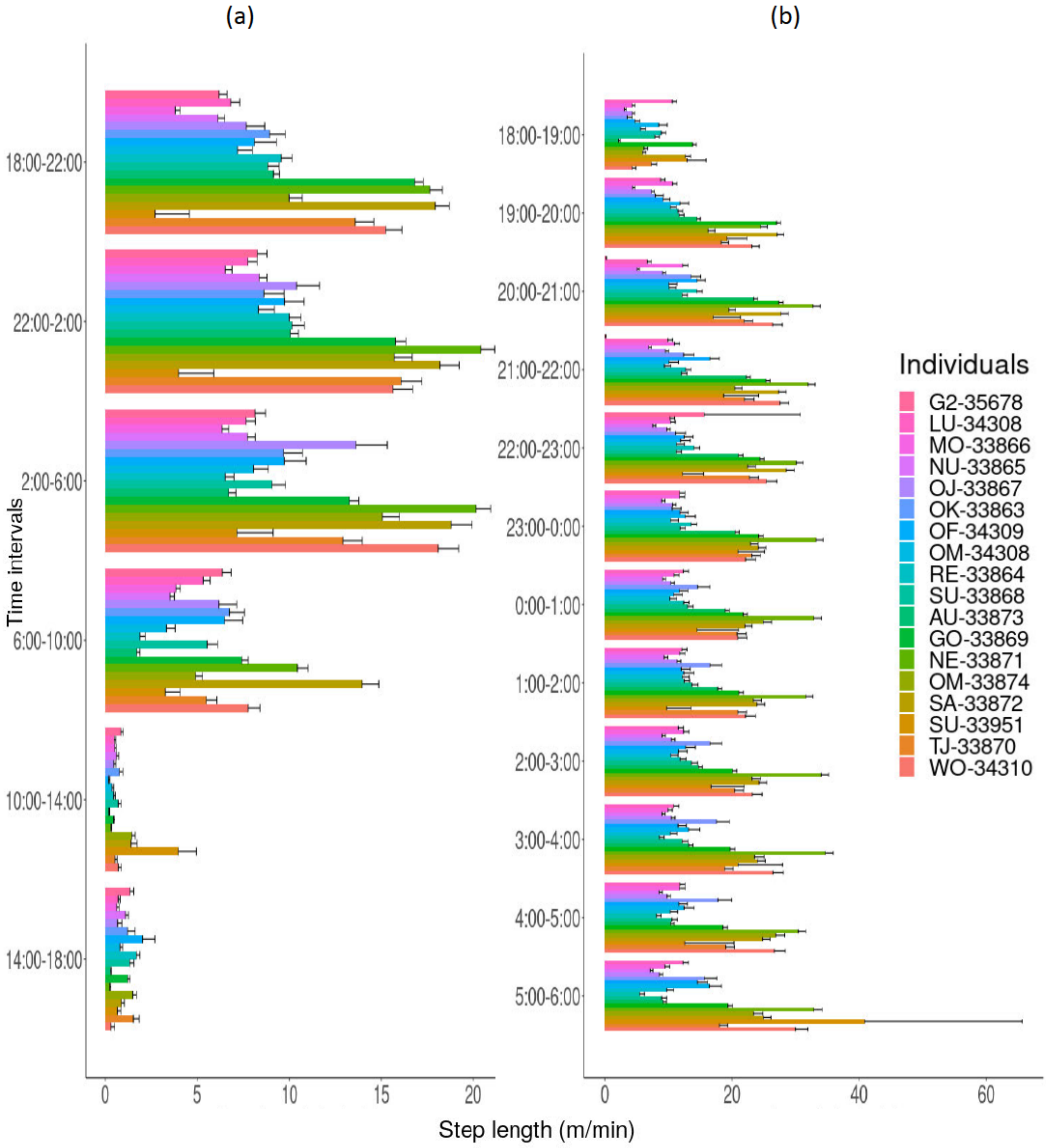
Appendix S2.3.1. Seasonal average speed (m/s) of (a) lions and (b) spotted hyenas from the Etosha National Park, Namibia (left panels) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta[†], Botswana (right panels) during nocturnal periods. Both figures, males upper panels and females lower panels. Dry season = red lines, and wet season = blue lines. Solid lines represent the mean, and shaded bars are 95% CI.

[†] *No spotted hyenas were collared from the Okavango Delta, Botswana.*

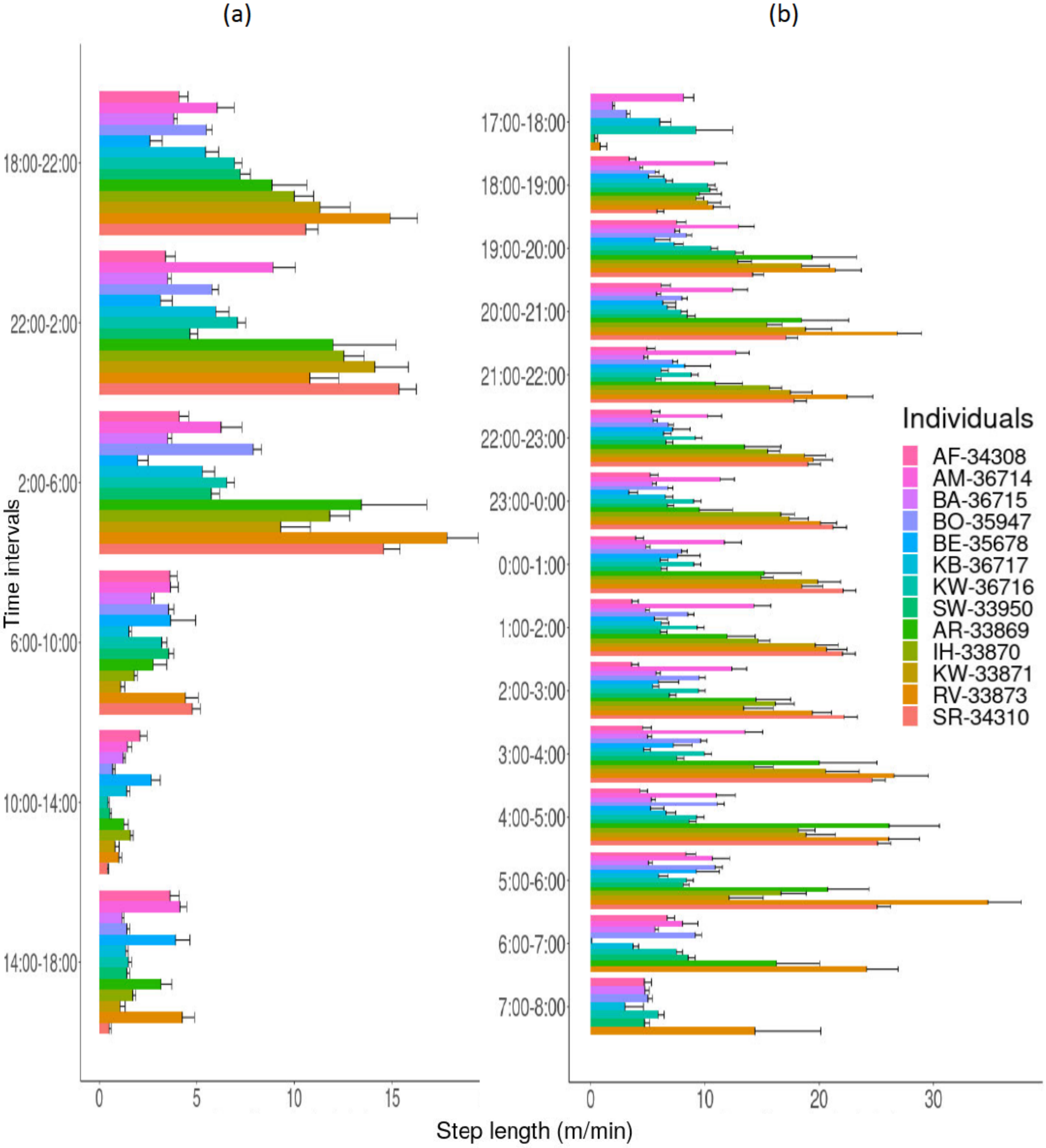


Appendix S2.3.2. Step lengths of lions and spotted hyenas from the Etosha National Park, Namibia (left panel) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta†, Botswana (right panel). Violins depict the probability distribution, with black dots the mean and black lines the 95% confidence intervals.

†*No spotted hyenas were collared from the Okavango Delta, Botswana.*

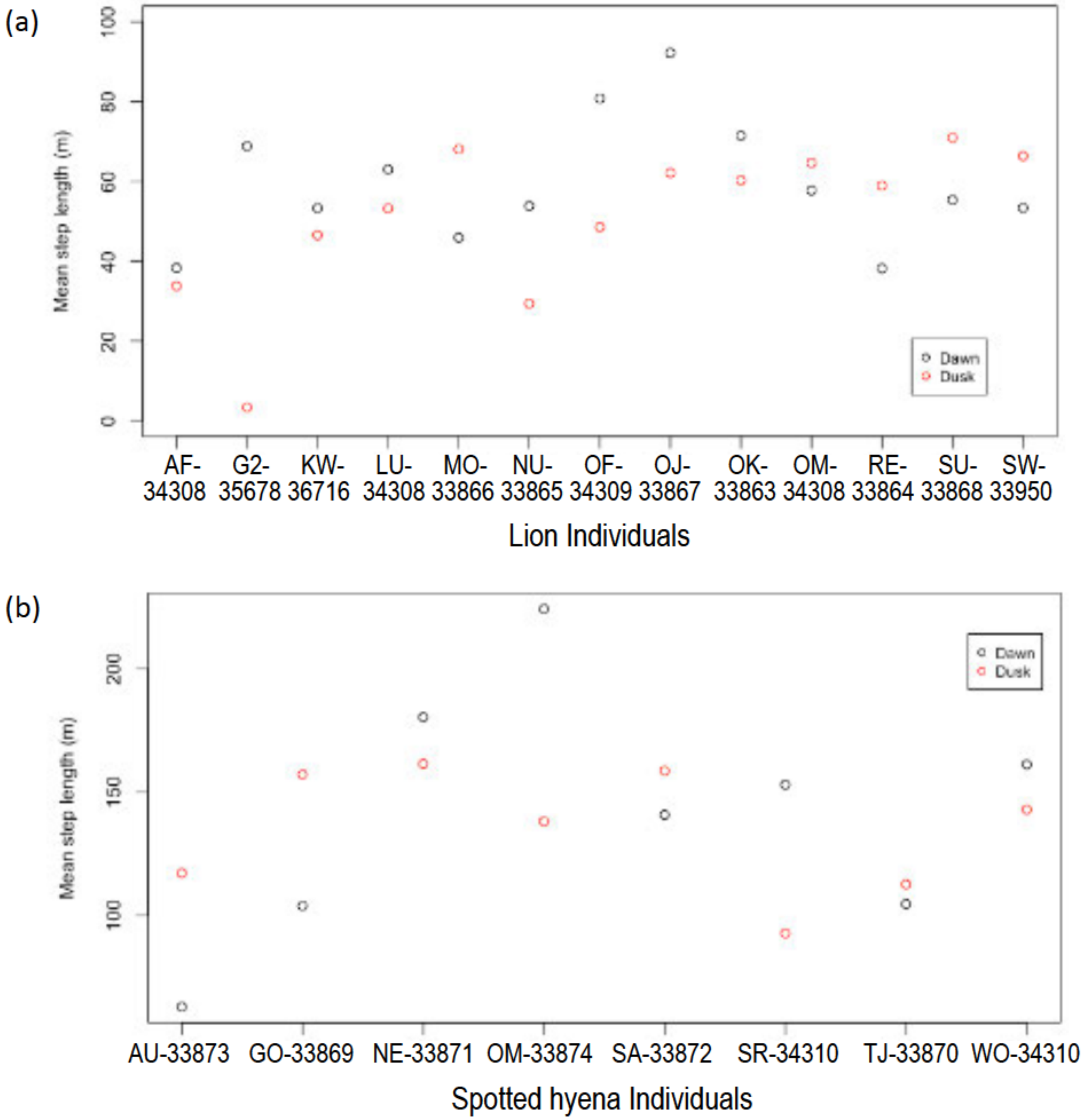


Appendix S2.3.3. Mean step length (m/min) of lions and spotted hyena individuals from the Etosha National Park, Namibia. (a) 24-hour cycle binned into six 4-hour periods. (b) Nocturnal cycle of 18h00-6h00 binned into hourly periods. Bars represent the mean and error bars the SE, only upper error bars are shown. Lion individuals (n = 11) represented by pink/purple/blue colours. Spotted hyena individuals (n = 8) represented by green/yellow/orange colours.

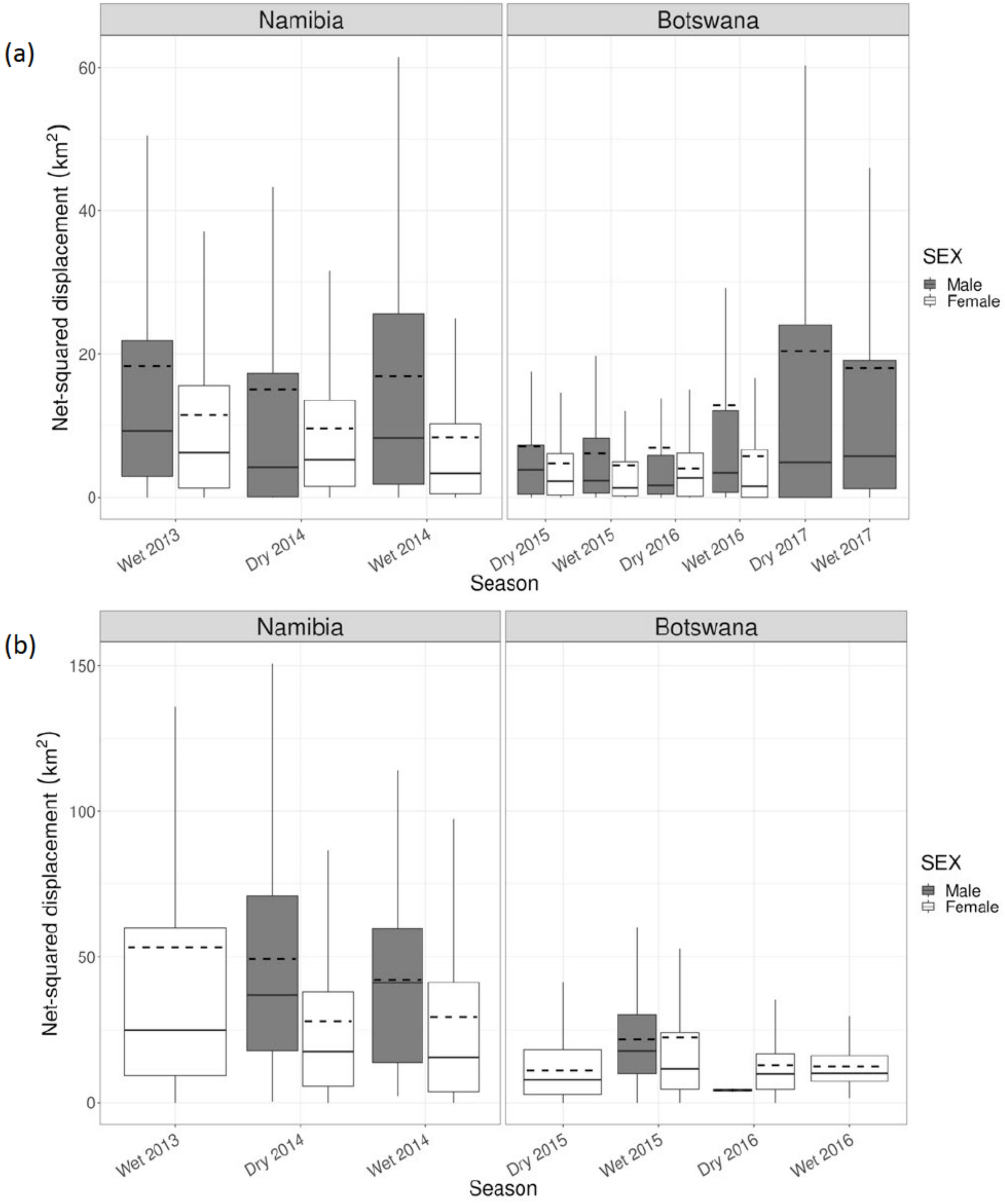


Appendix S2.3.4. Mean step length (m/min) of lions and spotted hyena individuals from the Chobe National Park, Linyanti Conservancy, and Okavango Delta†, Botswana. (a) 24-hour cycle binned into six 4-hour periods. (b) Nocturnal cycle of 17h00-8h00 binned into hourly periods. Bars represent the mean and error bars the SE, only upper error bars are shown. Lion individuals (n = 8) represented by pink/purple/blue/blue-green colours. Spotted hyena individuals (n = 5) represented by green/yellow/orange colours.

†*No spotted hyenas were collared from the Okavango Delta, Botswana.*

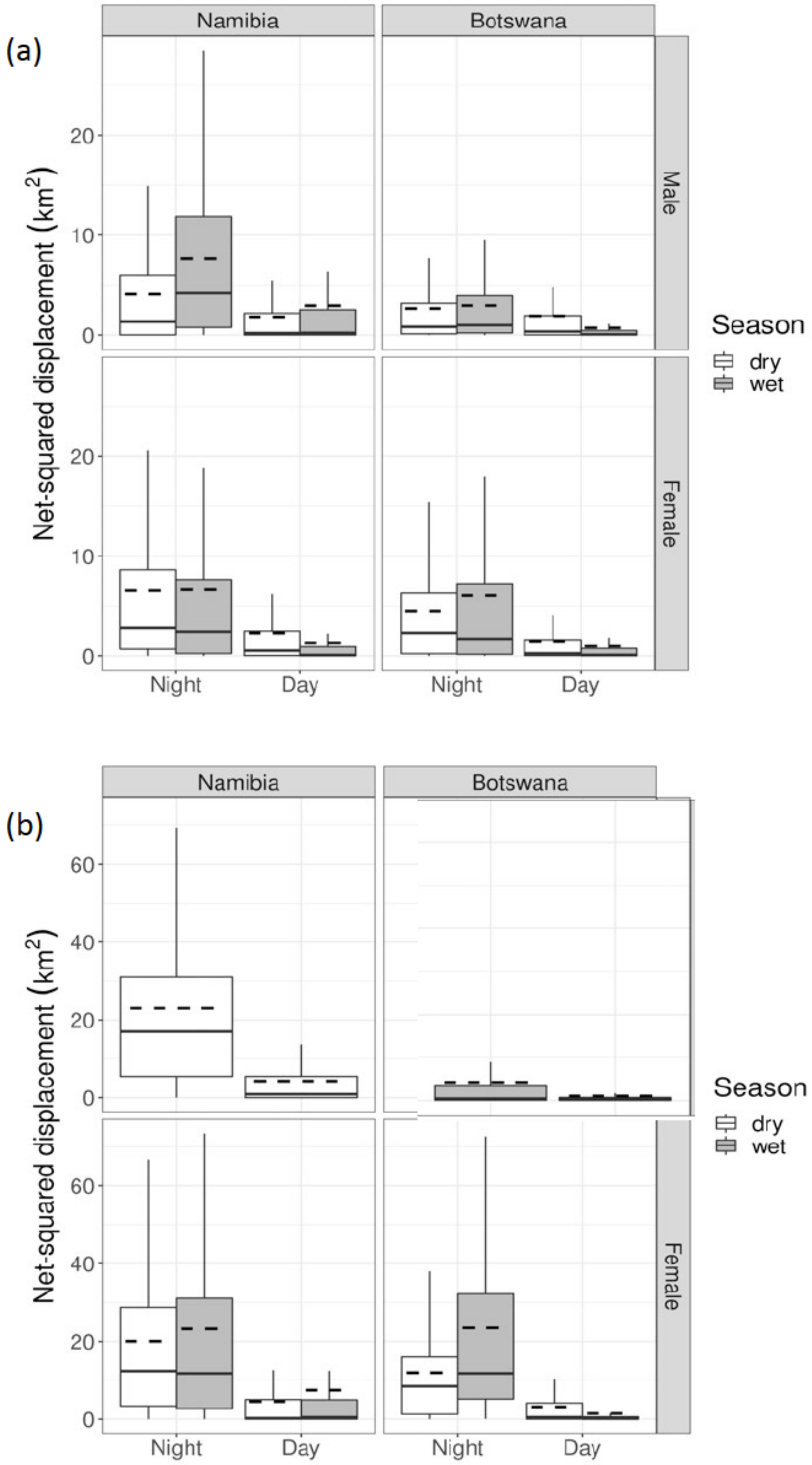


Appendix S2.3.5. Mean step length at dusk (red circles) and dawn (black circles) for lions (a) and spotted hyenas (b) from the Etosha National Park, Namibia and the Chobe National Park and Linyanti Conservancy, Botswana.



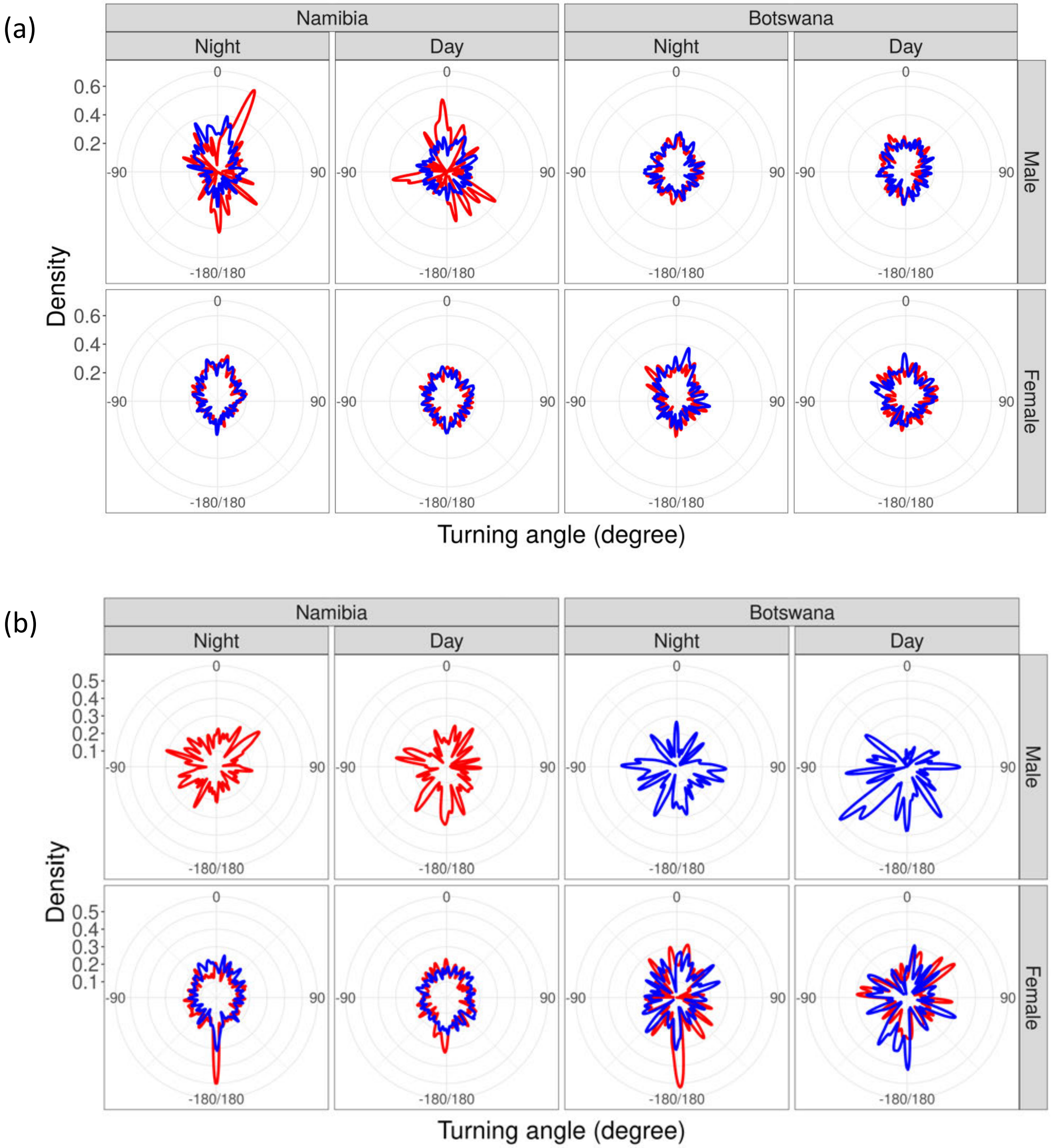
Appendix S2.3.6. Seasonal mean net-squared displacement (km^2) over 24-hour cycles for (a) lions and (b) spotted hyenas across each season from the Etosha National Park, Namibia (left panels) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta[†], Botswana (right panels). Males dark grey boxes, females white boxes. Boxplots show medians, 25% and 75% quartiles. Dashed lines indicate means. Whiskers indicate the IQR range.

[†] *No spotted hyenas were collared from the Okavango Delta, Botswana.*



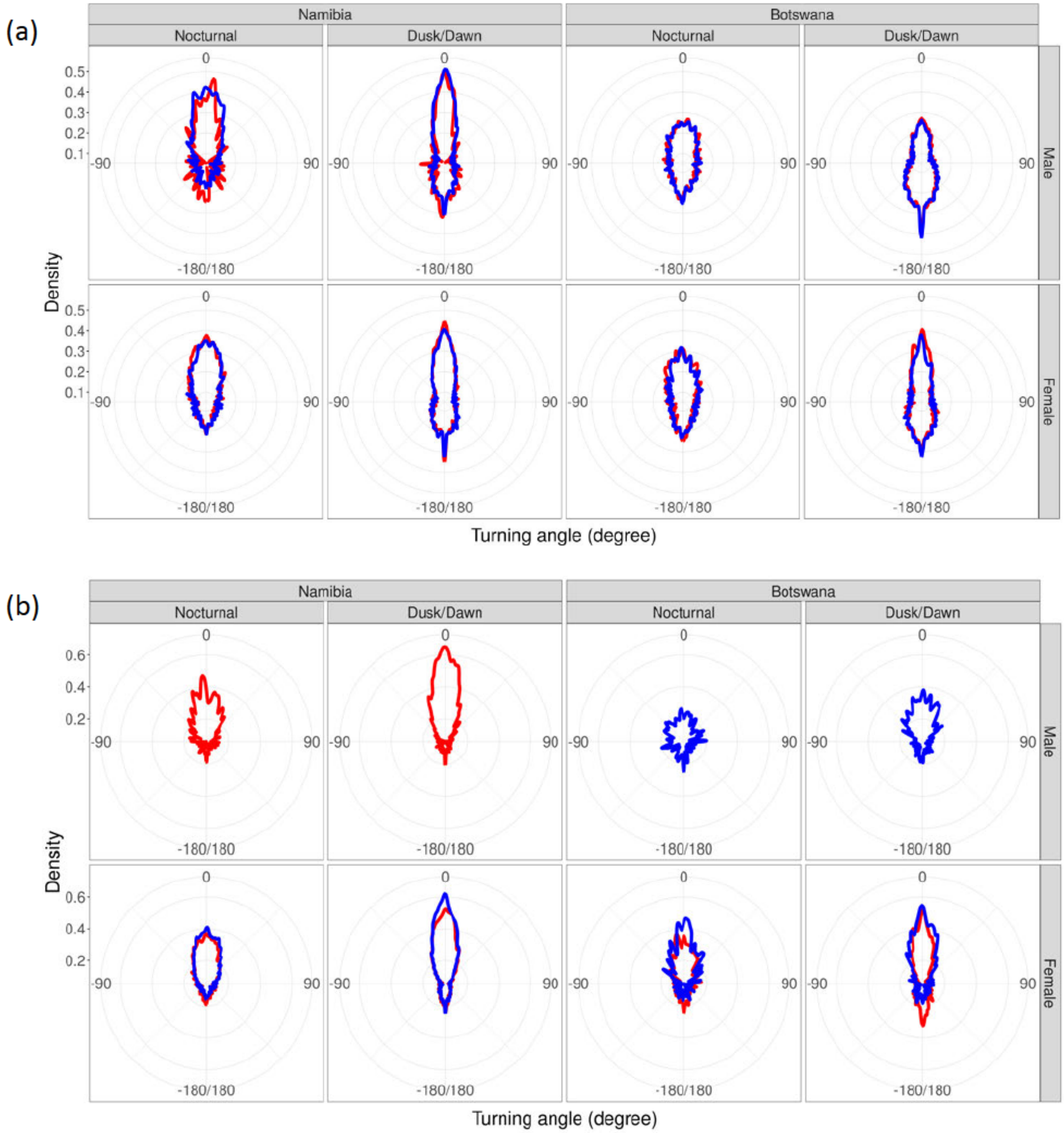
Appendix S2.3.7. Mean net-squared displacement (km^2) of (a) lions and (b) spotted hyenas between nocturnal (sunset – sunrise) and diurnal (sunrise – sunset) periods from the Etosha National Park, Namibia (left panels) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta[†], Botswana (right panels). Both figures, males top panels and females bottom panels. Boxplots show medians, 25% and 75% quartiles. Dashed lines indicate means. Whiskers indicate the IQR range.

[†] *No spotted hyenas were collared from the Okavango Delta, Botswana.*



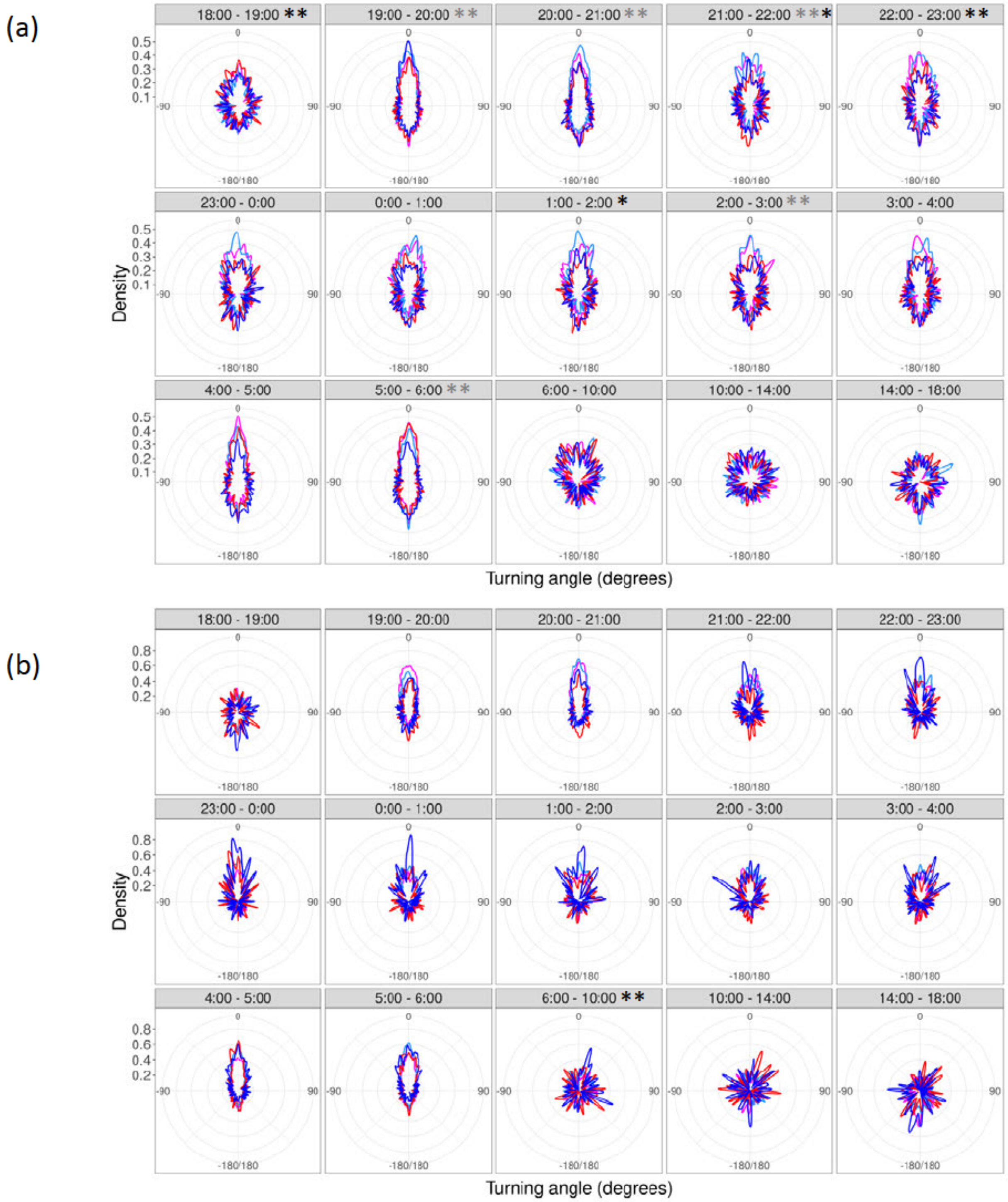
Appendix S2.3.8. Frequency density of seasonal turning angles for (a) lions and (b) spotted hyenas from the Etosha National Park, Namibia (left panels) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta†, Botswana (right panels) during nocturnal (sunset – sunrise) and diurnal (sunrise – sunset) cycles. Both figures, males in upper panels and females in lower panels. Dry season = red lines, wet season = blue lines.

†*No spotted hyenas were collared from the Okavango Delta, Botswana.*

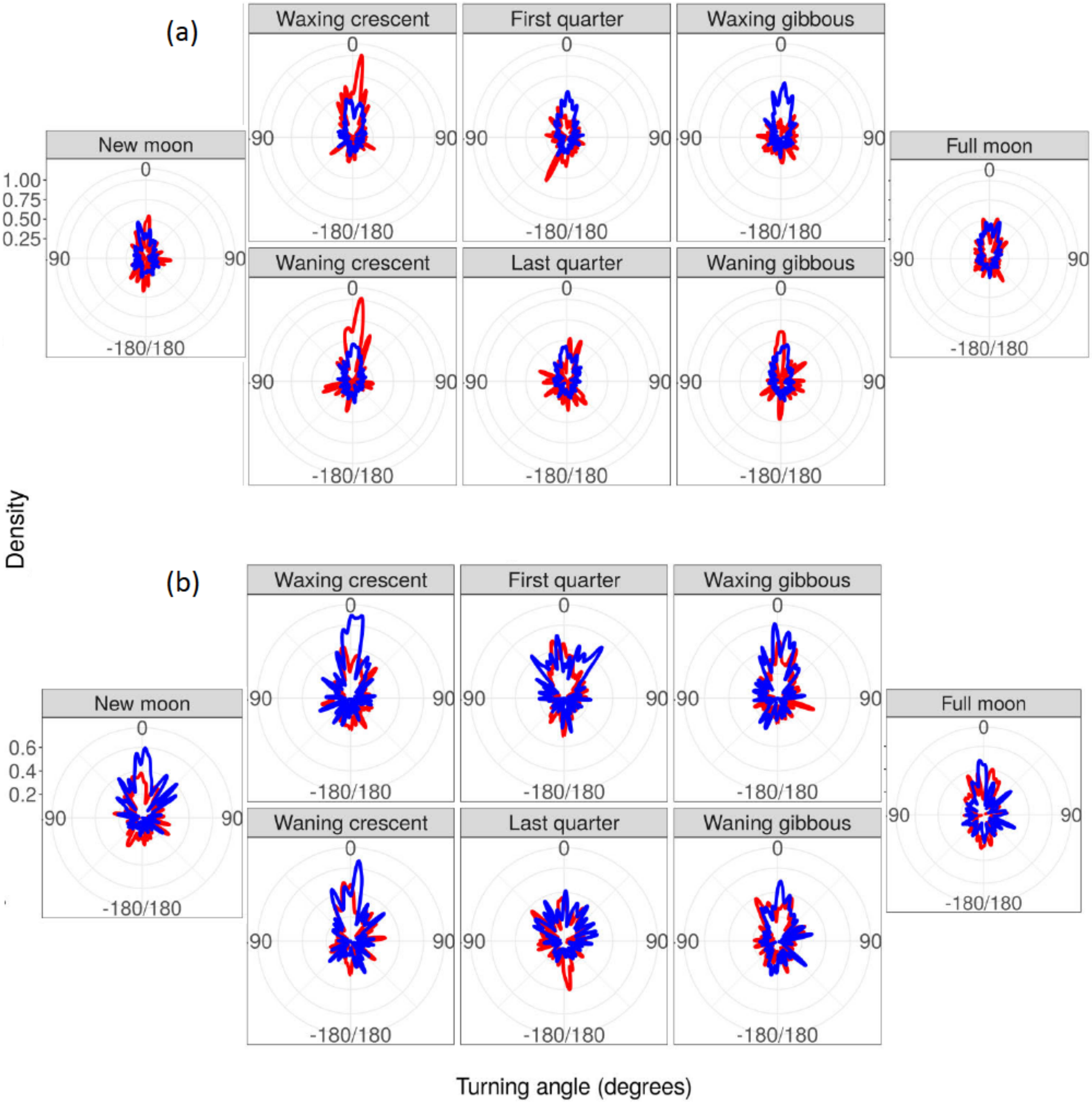


Appendix S2.3.9. Frequency density of seasonal turning angles for (a) lions and (b) spotted hyenas during nocturnal (18h00-6h00 and 17h00-8h00) and dusk/dawn (19h00-21h00 and 4h00-6h00) periods. Etosha National Park, Namibia, left panels and Chobe National Park, Linyanti Conservancy, and Okavango Delta†, Botswana, right panels. Both figures, males upper panels and females lower panels. Dry season = red lines, wet season = blue lines.

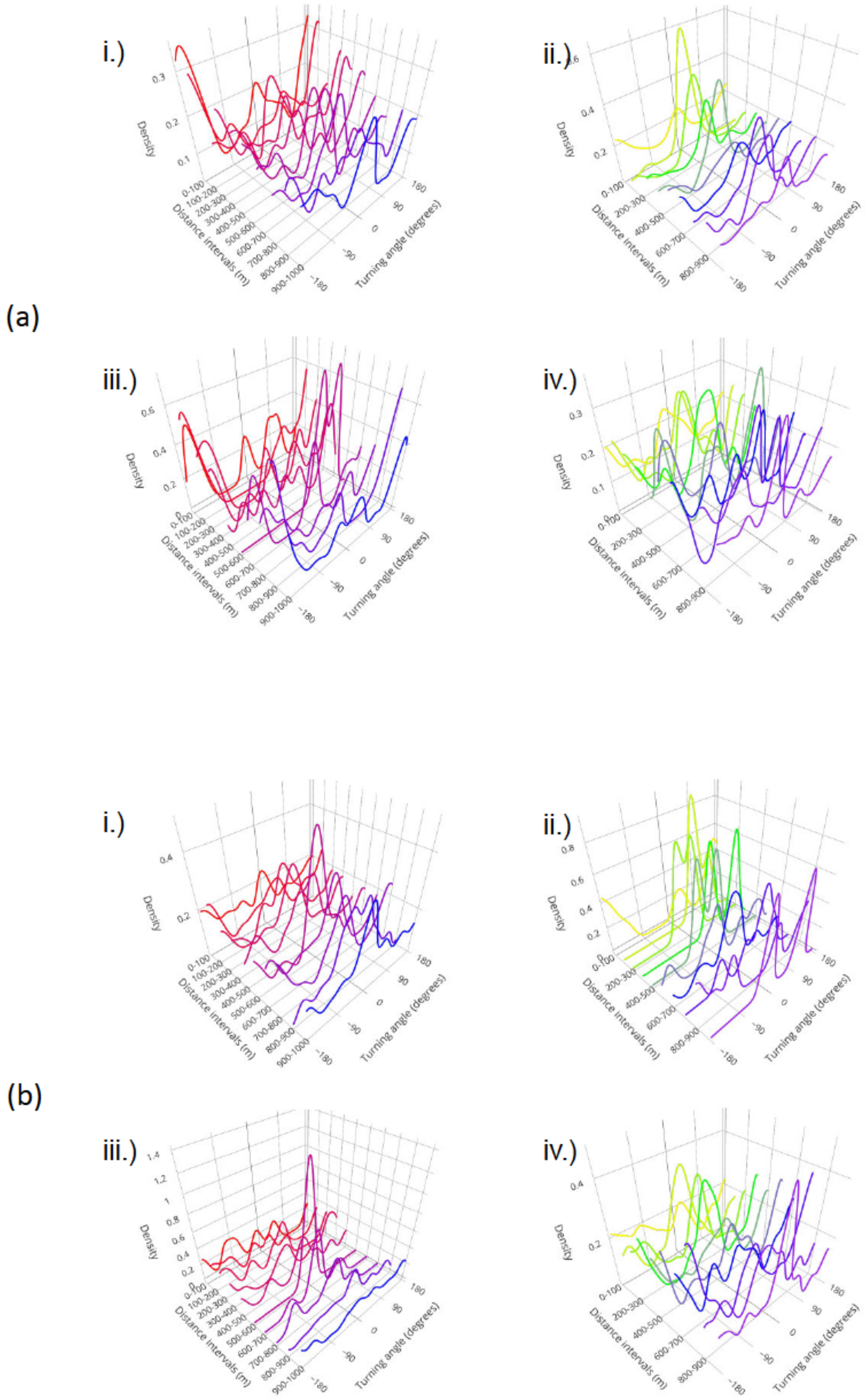
†*No spotted hyenas were collared from the Okavango Delta, Botswana.*



Appendix S2.3.10. Frequency density of seasonal turning angles for (a) lions and (b) spotted hyenas during each hour of the nocturnal period (18h00-6h00) and during 4-hour blocks of the diurnal period (6h00-18h00). Species are from the Etosha National Park, Namibia (dry season = magenta lines; wet season = cyan lines), the Chobe National Park and Linyanti Conservancy, Botswana, with lions from the Okavango Delta, Botswana (dry season = red lines; wet season = blue lines). A double asterisk indicates a significant difference in the Watson's Two-Sample Test of Homogeneity at $p < 0.05$, and a single asterisk approaches significance at $0.5 < p < 0.10$. Placement of the asterisk(s) at the panel's time label denotes the relatively more tortuous species for that time interval, with grey asterisk(s) for Namibia animals and black asterisk(s) for Botswana animals.

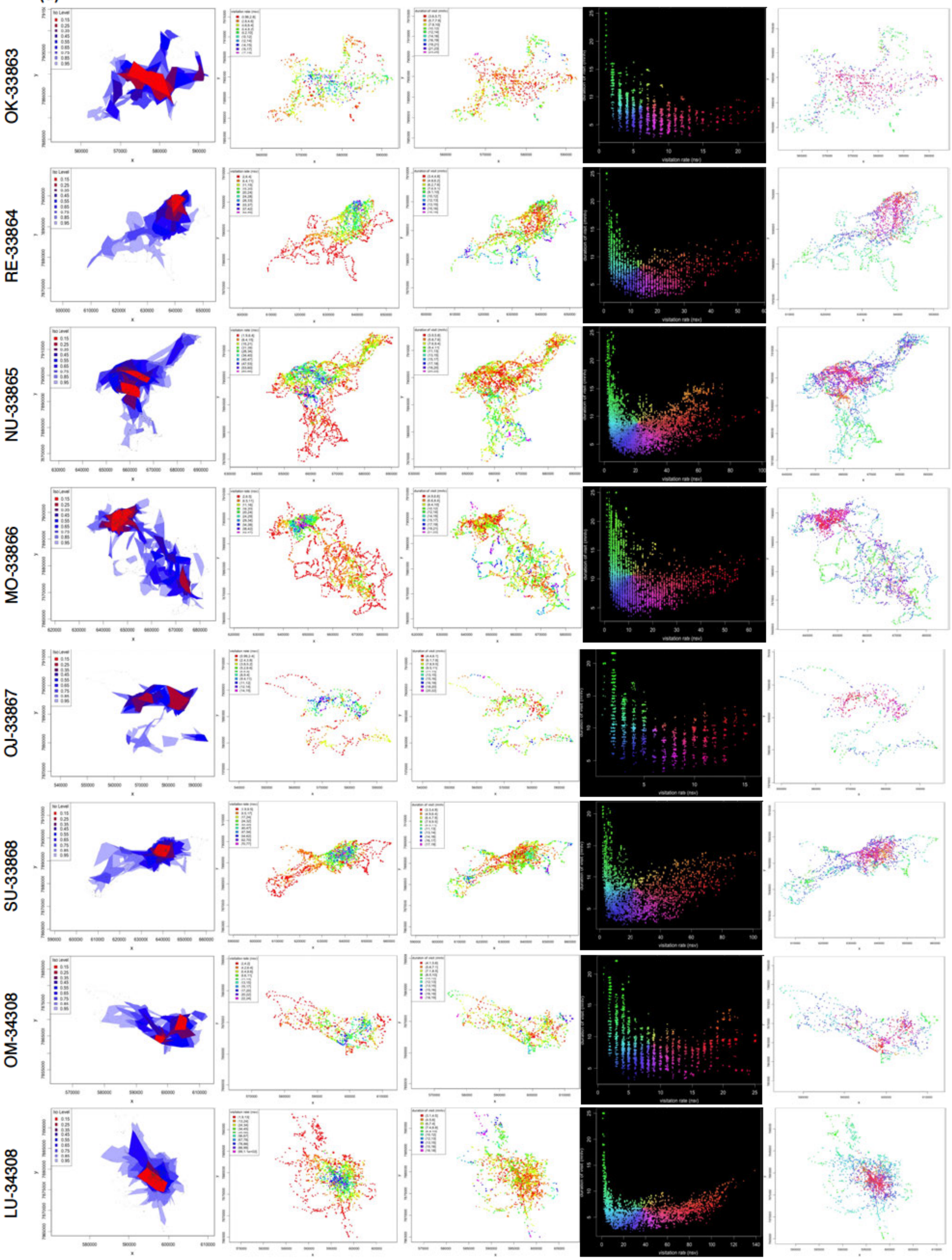


Appendix S2.3.11. Frequency density of seasonal turning angles for (a) Etosha male lions and (b) Chobe/Linyanti female spotted hyenas during the nocturnal period according to various moon phases. Darkest lunar phase (far left panel) increasing to brightest lunar phase (far right panel).



Appendix S2.3.12. Tortuosity of (a) lions and (b) spotted hyenas from the Etosha National Park, Namibia (i & ii) and the Chobe National Park and Linyanti Conservancy, Botswana (iii & iv). Path tortuosity is depicted at different distance intervals from competitors (i & iii), and conspecifics (ii & iv).

(a)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LU-34308
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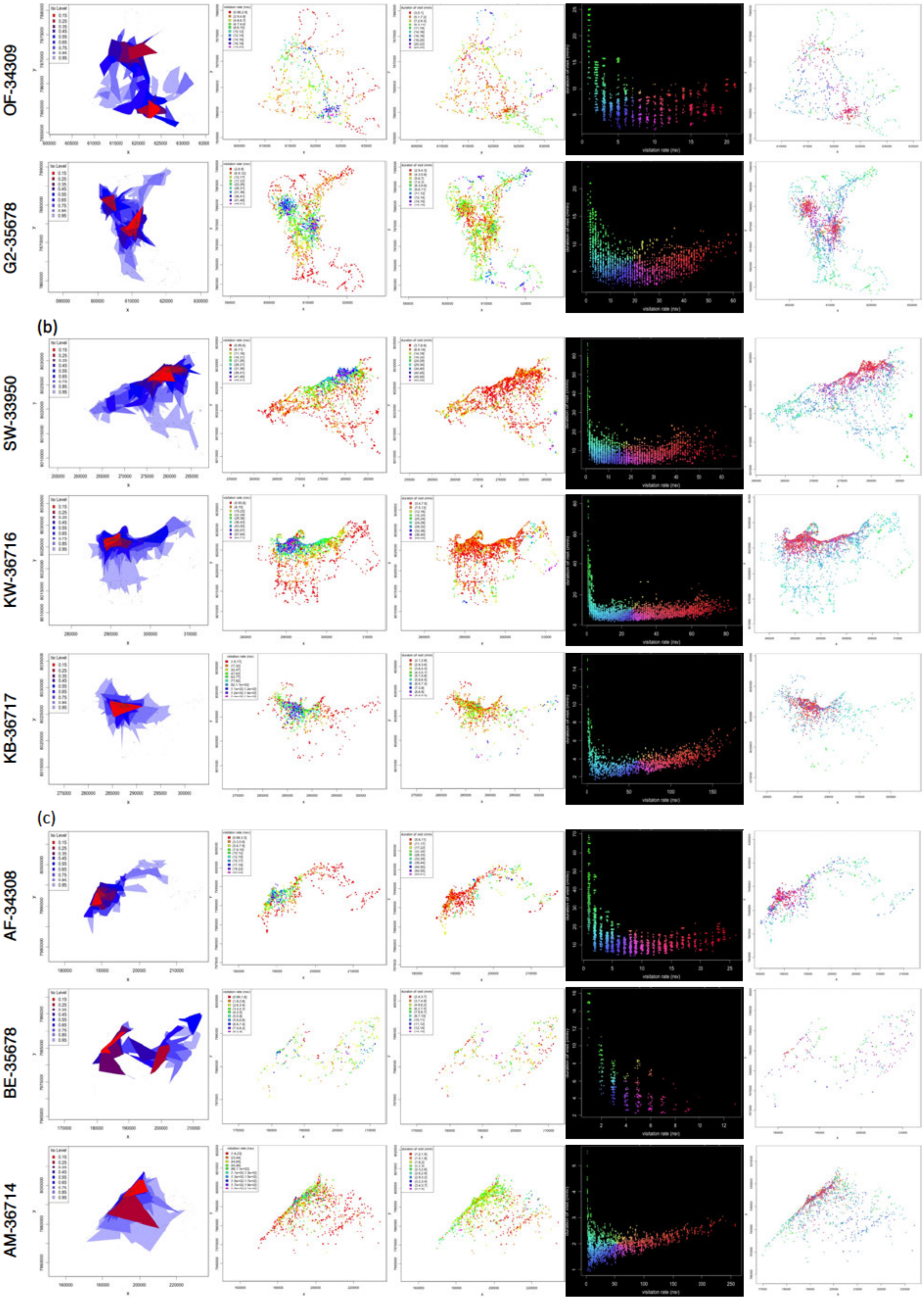
duration of visit (min)
x
y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(b)
SW-33950
KW-36716
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(c)
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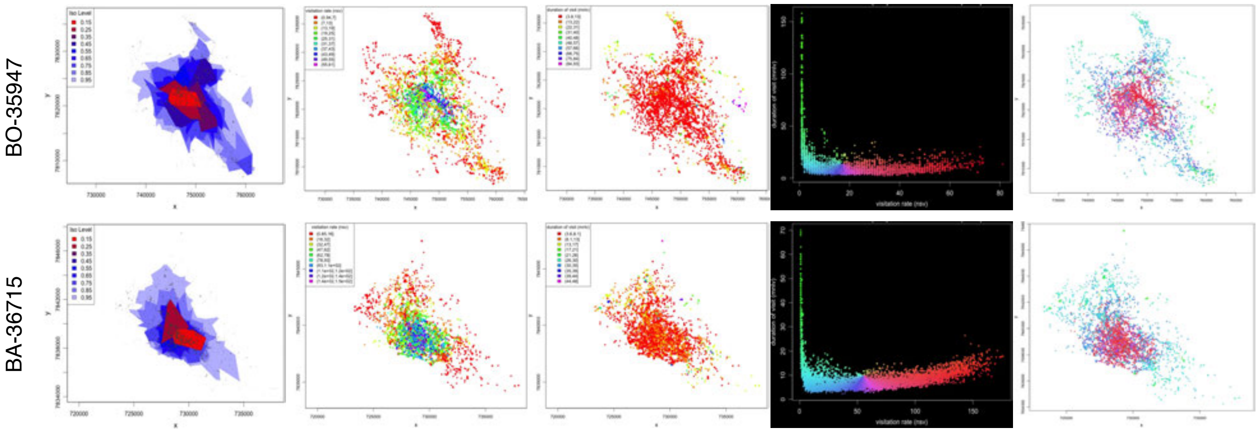
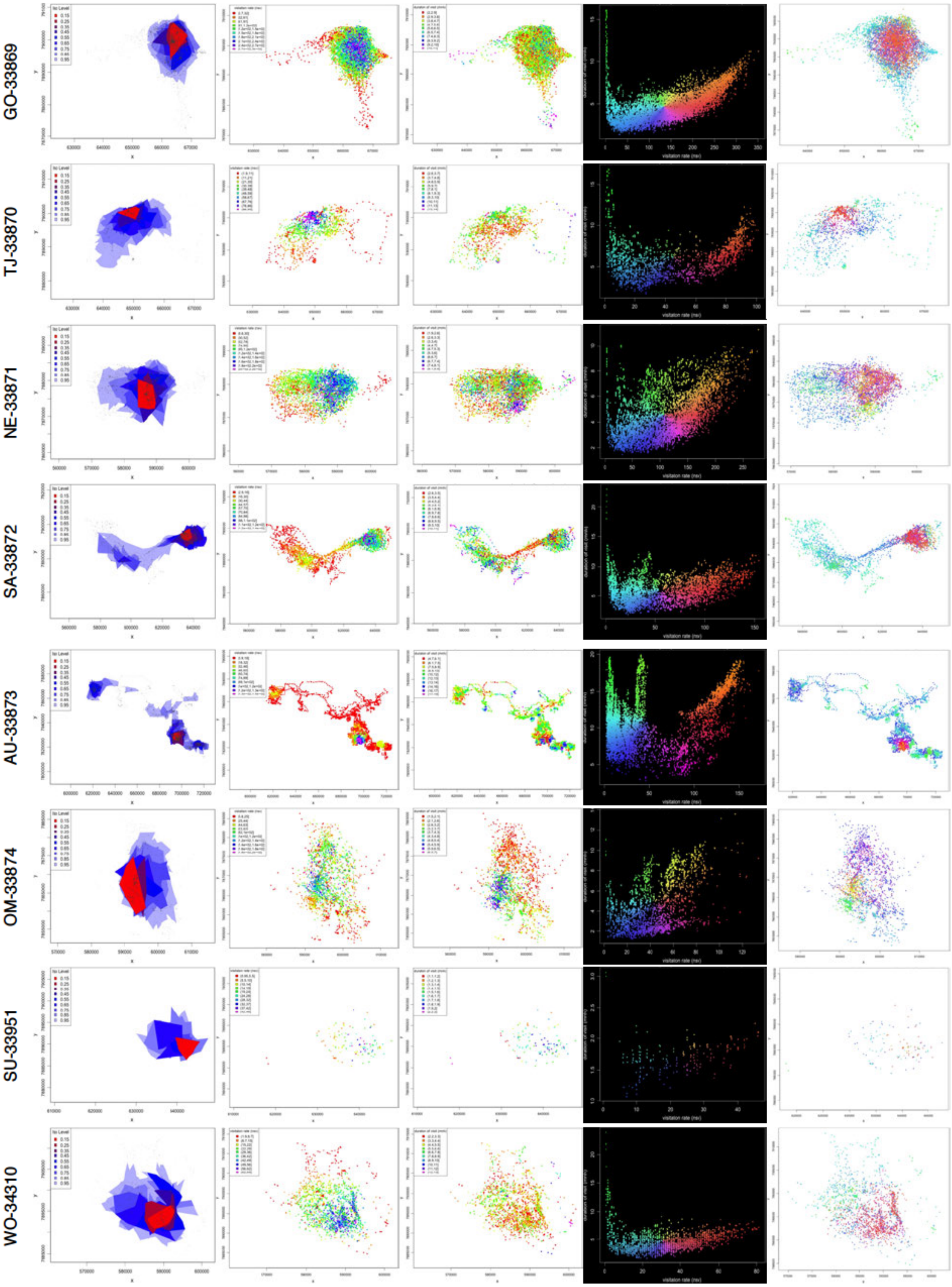
Iso Level
visitation rate (nsv)
duration of visit (mins)
x
y

(d)



Appendix S2.4.1. Time-use constructs of lion individuals from the (a) Etosha National Park, Namibia; (b) Chobe National Park; (c) Linyanti Conservancy; and (d) Okavango Delta, Botswana. Unique identifiers are depicted vertically on the left of each row of figures. α-LoCoH hulls of individual's utilization distributions (far left). Hull parent points coloured by visitation rate (nsv, number of separate visits; second from left), and duration of visit (mnlv, mean number of locations in the hull per visit; third from left). RD space scatterplots (second from right) with X-axis = visitation rate (nsv), and Y-axis = duration of visit (mnlv), provide a legend for revisitation/duration (RD) values for the map (far right). Points in the RD space have been jiggled to better see point density, and each point represents a hull. Points on the maps are coloured by their location in the RD space. Separate visits are defined by an inter-visit gap period ≥ 12hours. Hulls were created using the adaptive method. Duplicate points are offset by 1 map unit.

(a)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SU-33951
WO-34310
Iso Level
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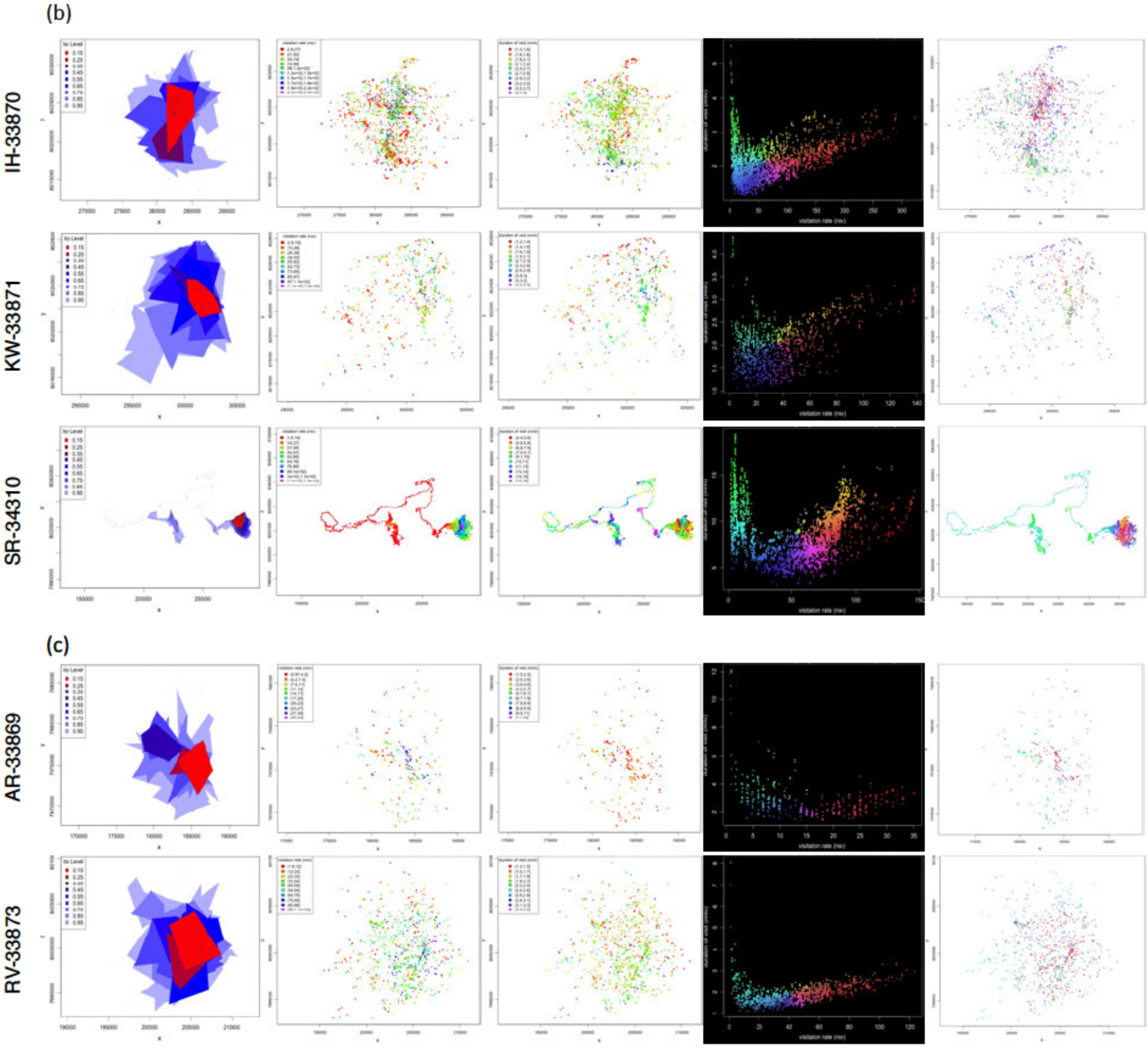
0.25
0.35
0.45
0.55
0.65
0.75
0.85
0.95
x
y
visitation rate (nsv)
duration of visit (mins)



Appendix S2.4.2. Time-use constructs of spotted hyena individuals from the (a) Etosha National Park, Namibia; (b) Chobe National Park; and (c) Linyanti Conservancy, Botswana. Unique identifiers are depicted vertically on the left of each row of figures. α-LoCoH hulls of individual's utilization distributions (far left). Hull parent points coloured by visitation rate (nsv, number of separate visits; second from left), and duration of visit (mnlv, mean number of locations in the hull per visit; third from left). RD space scatterplots (second from right) with X-axis = visitation rate (nsv), and Y-axis = duration of visit (mnlv), provide a legend for revisitation/duration (RD) values for the map (far right). Points in the RD space have been jiggled to better see point density, and each point represents a hull. Points on the maps are coloured by their location in the RD space. Separate visits are defined by an inter-visit gap period ≥ 12hours. Hulls were created using the adaptive method. Duplicate points are offset by 1 map unit.

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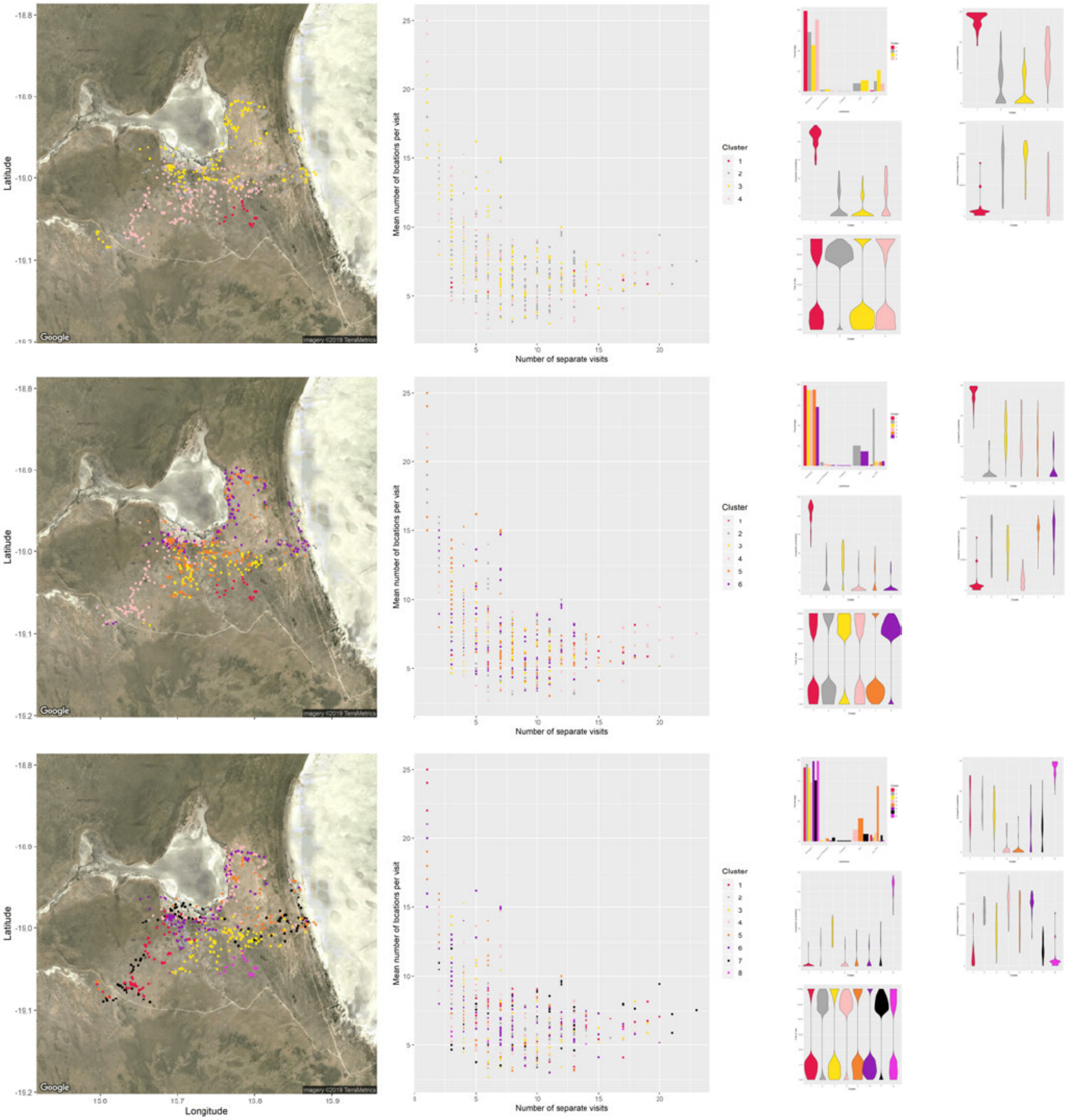
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Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
Number of separate visits
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Cluster
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4
5
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7
8

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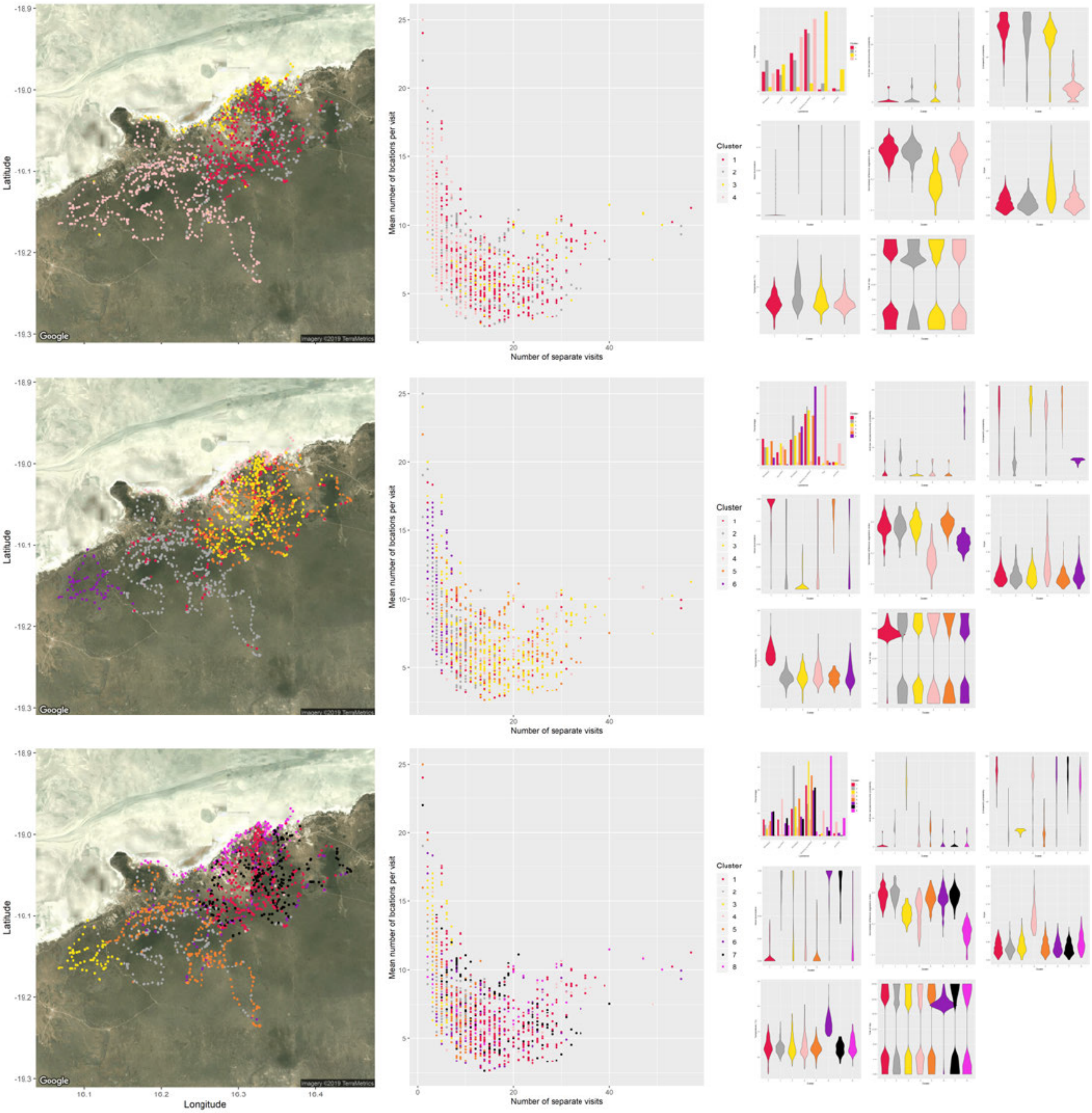
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Google
Imagery ©2019 TerraMetrics
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Longitude
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15
10
5
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Mean number of locations per visit
Number of separate visits
Cluster
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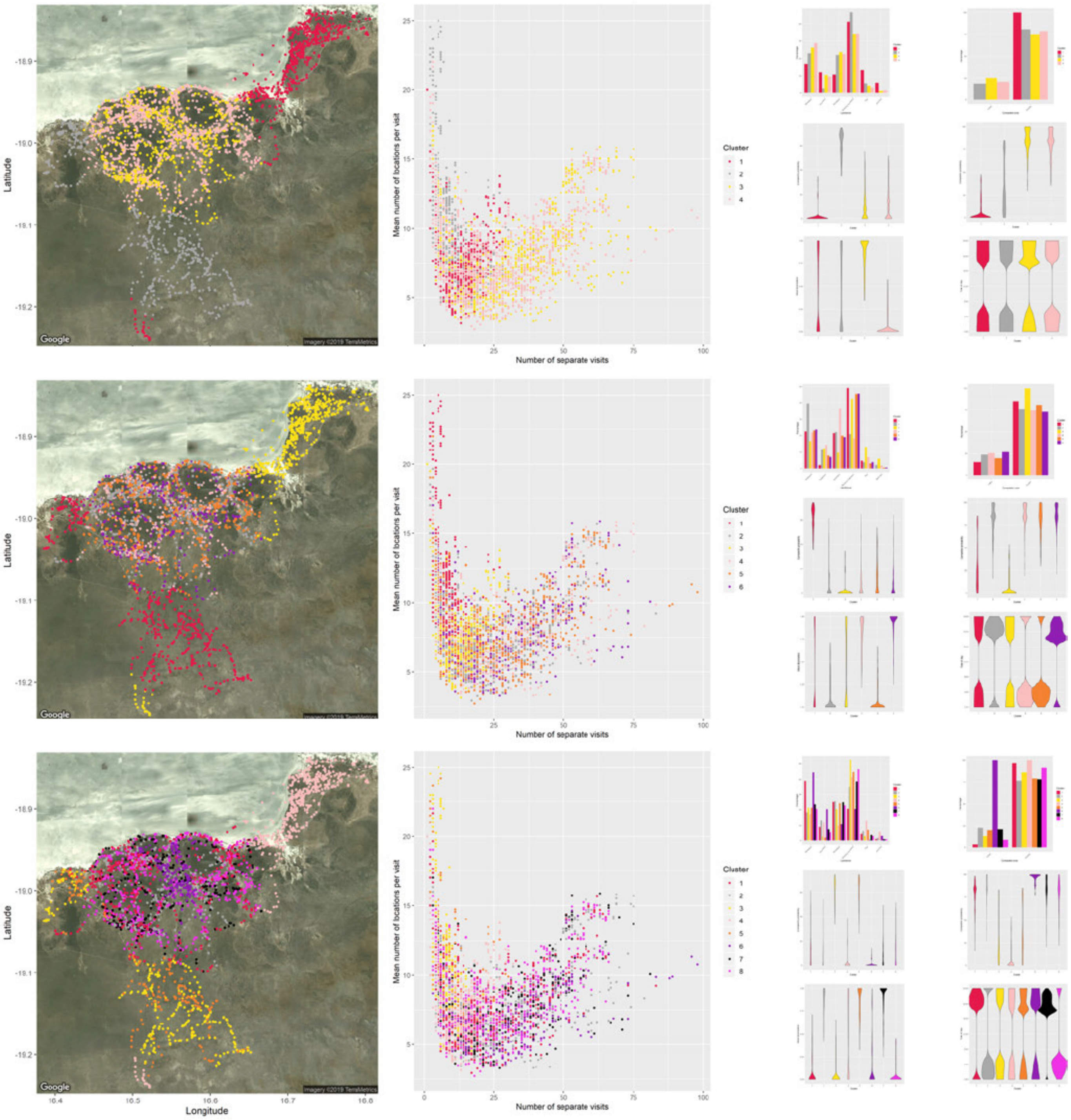

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Longitude
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10.6
10.7
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Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
Number of separate visits
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Cluster
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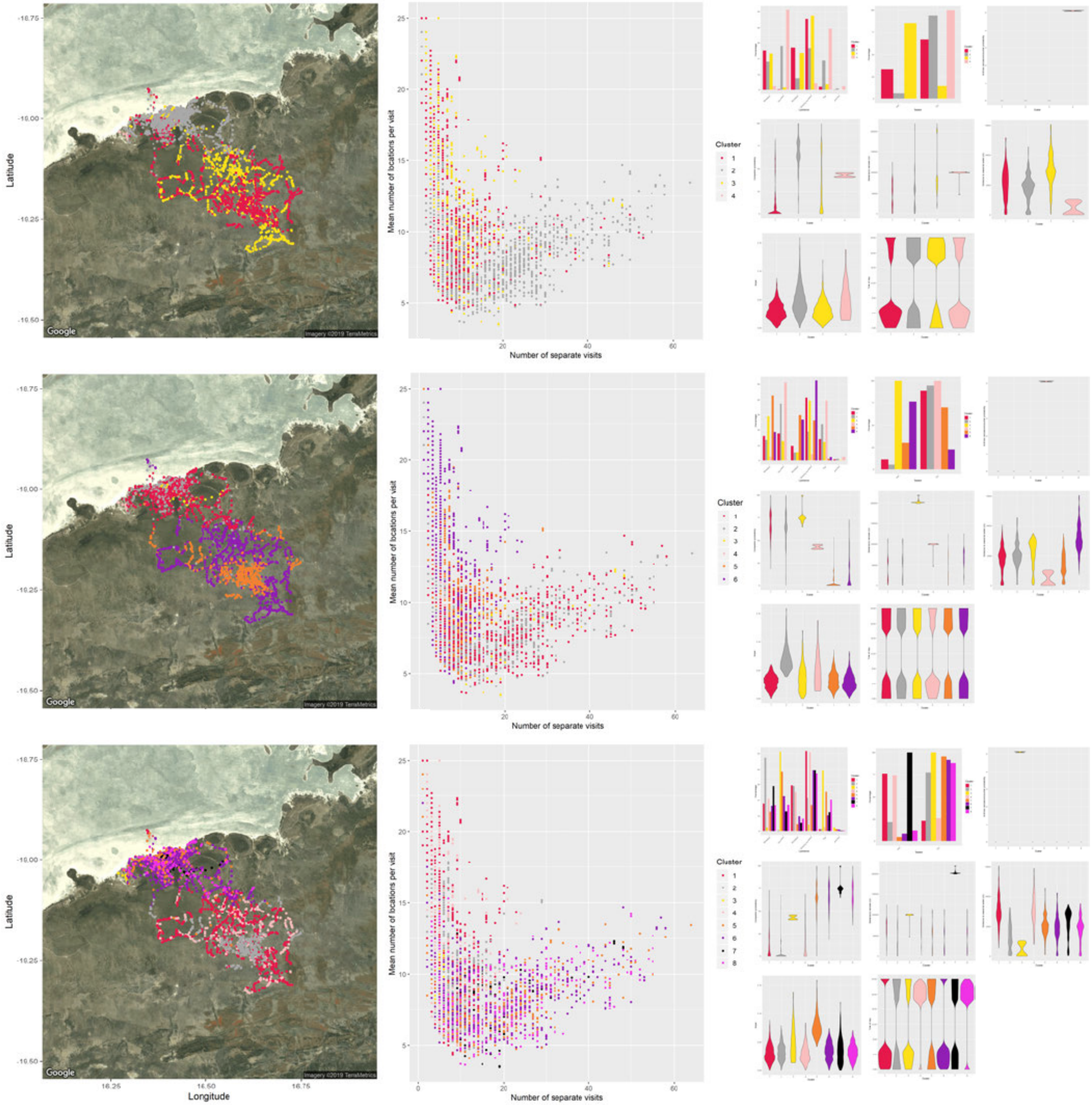
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20
15
10
5
Mean number of locations per visit
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Number of separate visits
Cluster
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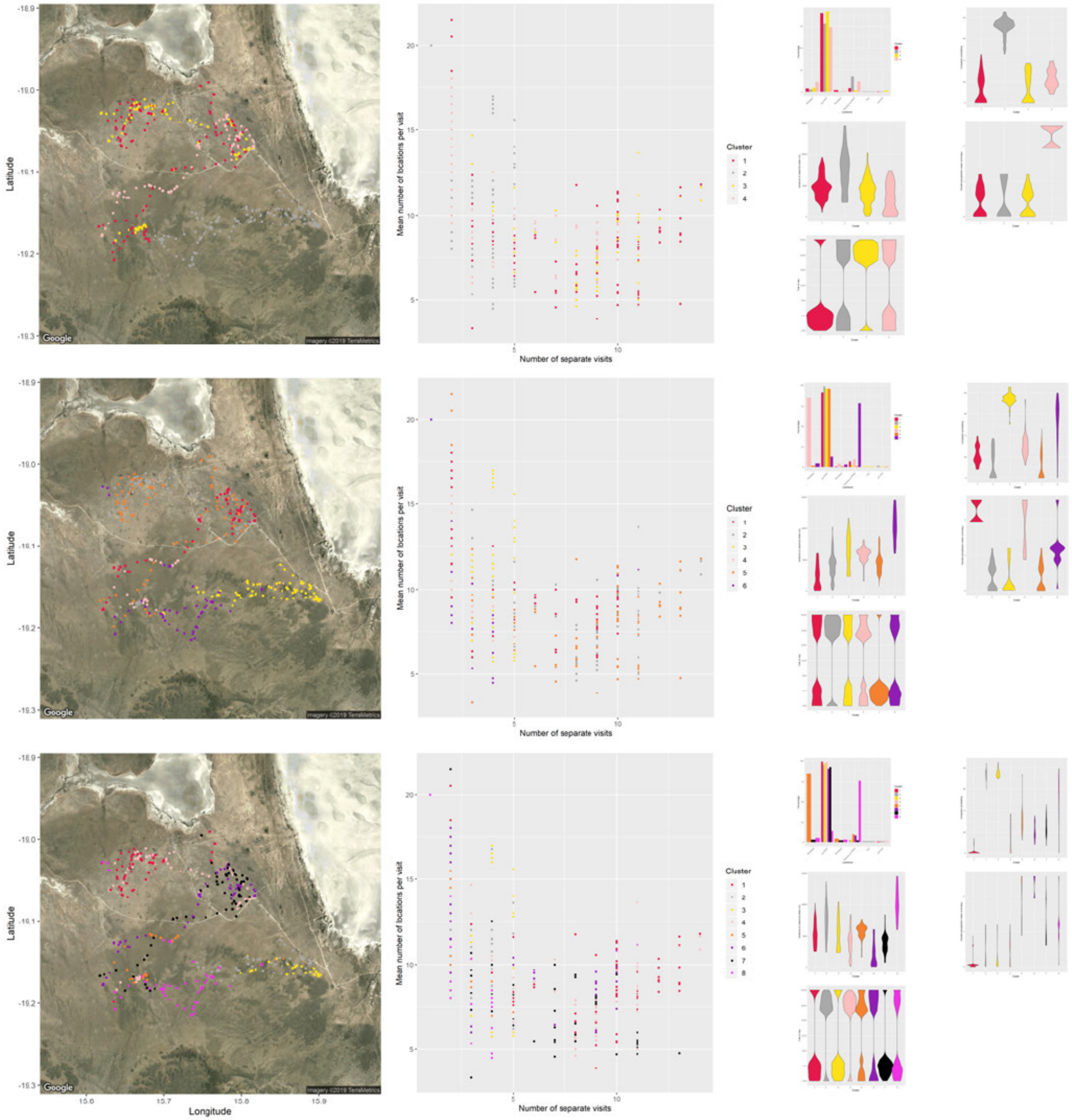
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Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
Number of separate visits
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Cluster
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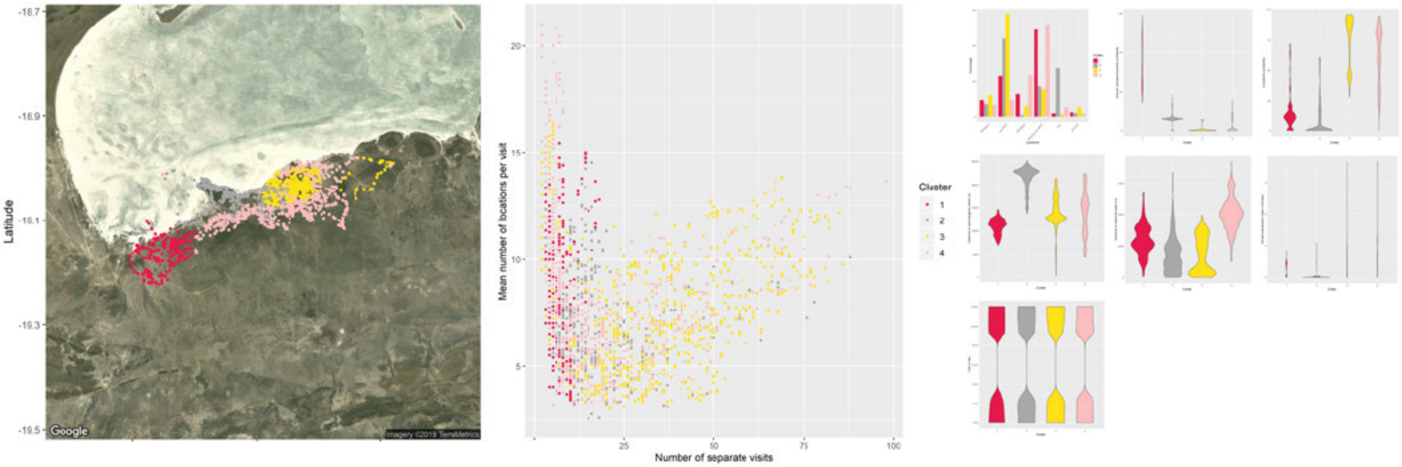
(a.6) SU-33868



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Google
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20
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10
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Mean number of locations per visit
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50
75
100
Number of separate visits
Cluster
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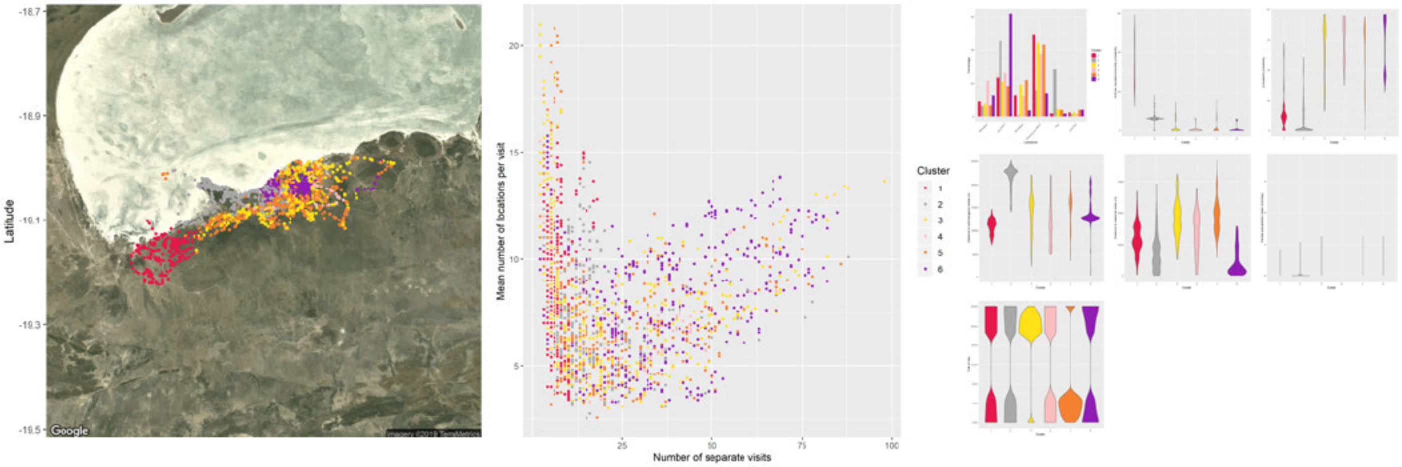
2
3
4



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Google
Imagery ©2019 TerraMetrics
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Mean number of locations per visit
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50
75
100
Number of separate visits
Cluster
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2
3
4
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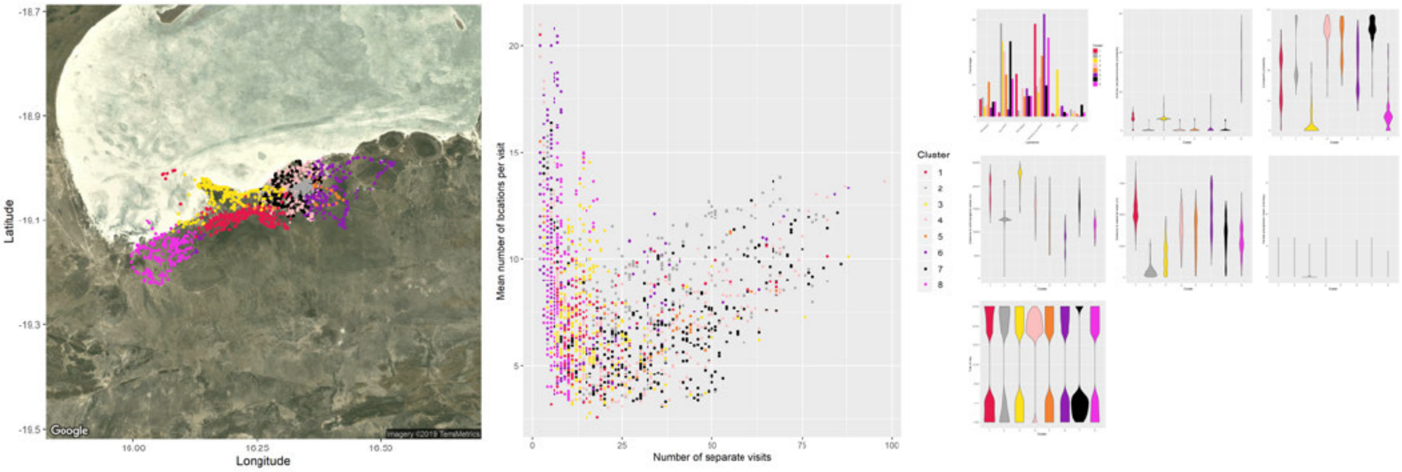
6



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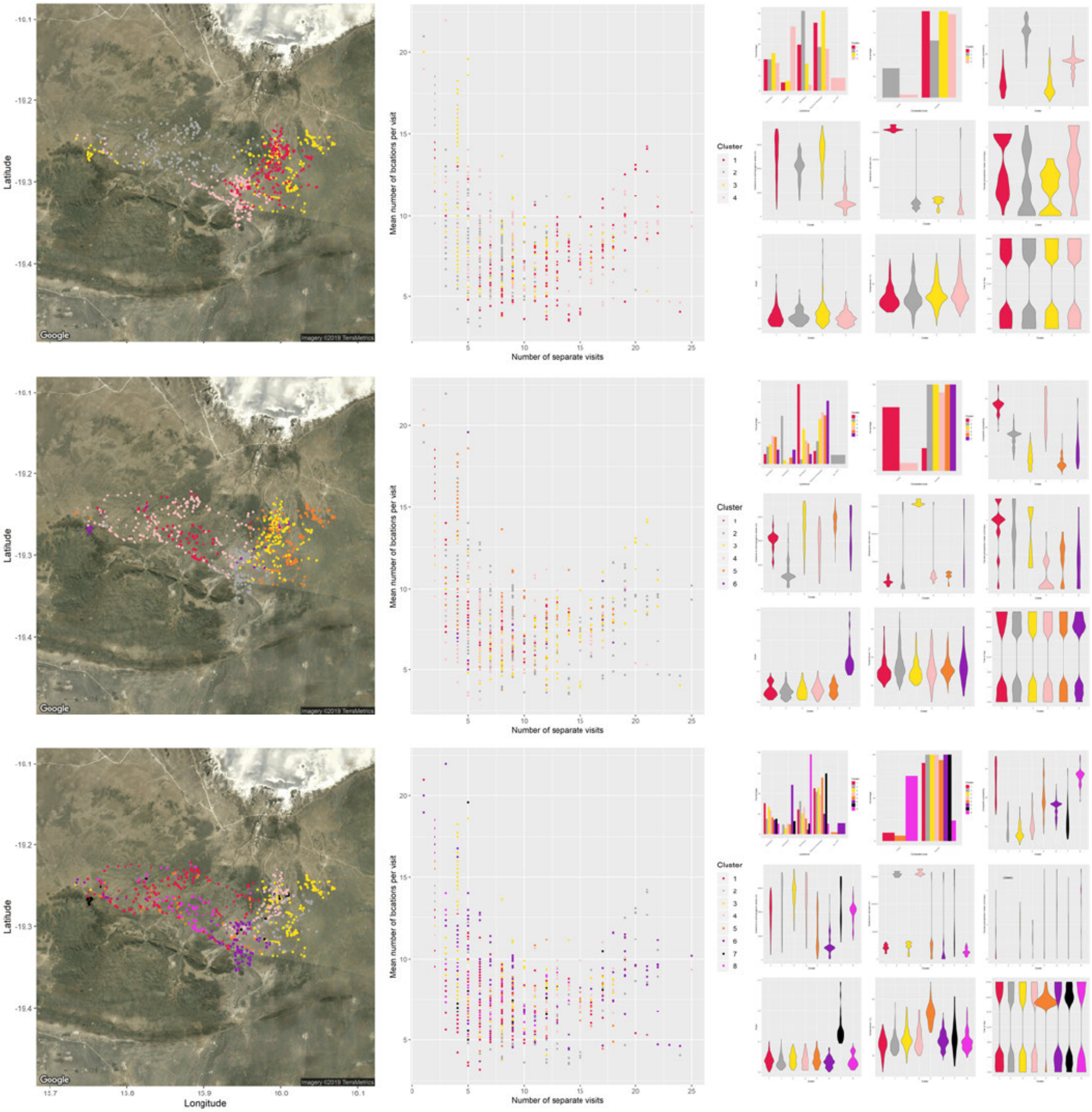
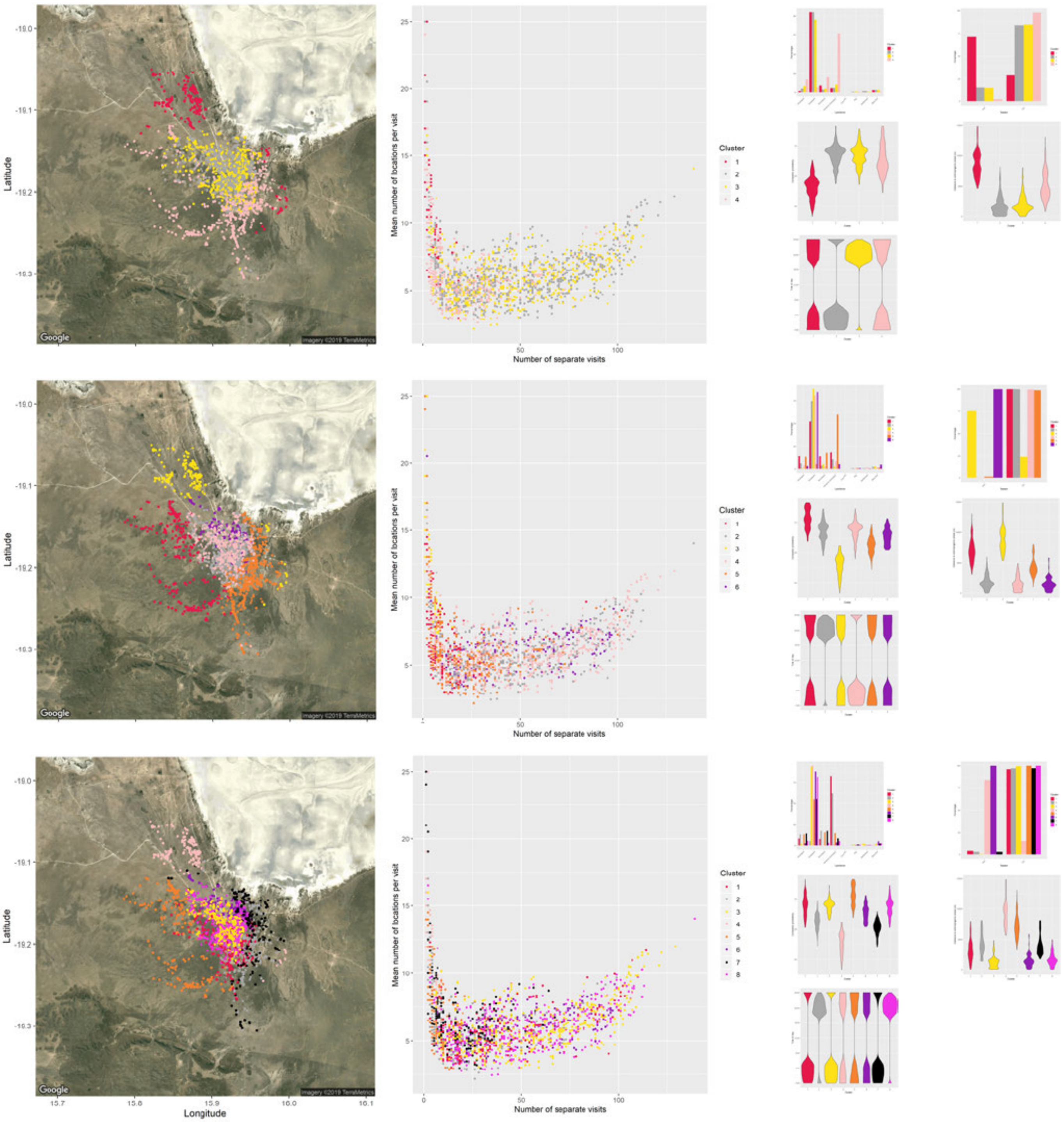
Imagery ©2019 TerraMetrics
16.00
16.25
16.50
Longitude
20
15
10
5
Mean number of locations per visit
0
25
50
75
100
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

(a.7) OM-34308

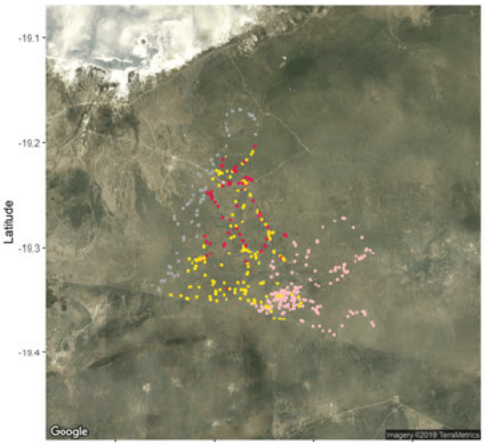


Latitude
-19.1
-19.2
-19.3
-19.4
Google
Imagery ©2019 TerraMetrics
15.7
15.8
15.9
16.0
16.1
Longitude
Mean number of locations per visit
5
10
15
20
Number of separate visits
0
5
10
15
20
25
Cluster
1
2
3
4
5
6
7
8

(a.8) LU-34308


Latitude
-19.0
-19.1
-19.2
-19.3
Longitude
15.7
15.8
15.9
16.0
16.1
Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
5
10
15
20
25
Number of separate visits
50
100
Cluster
1
2
3
4
Cluster
1
2
3
4
5
6
Cluster
1
2
3
4
5
6
7
8

(a.9) OF-34309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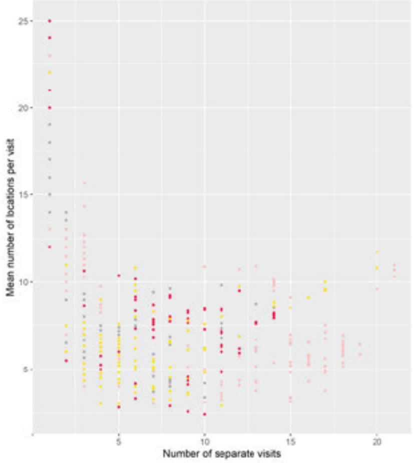
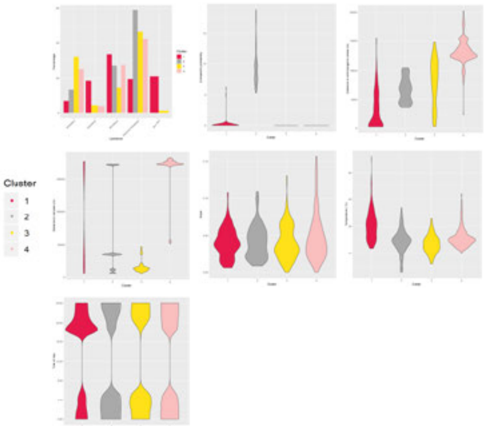
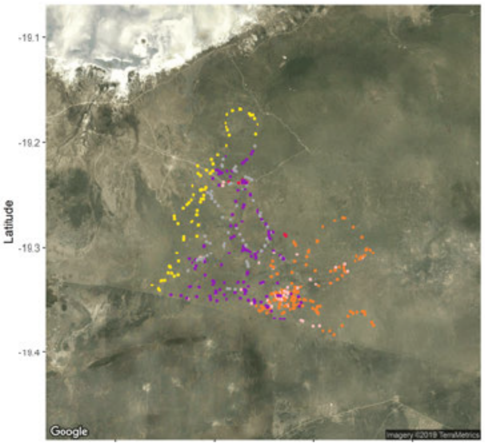
-19.2
-19.3
-19.4
Latitude
Google
Imagery ©2019 TerraMetrics


25
20
15
10
5
Mean number of locations per visit
5
10
15
20
Number of separate visits


Cluster
1
2
3
4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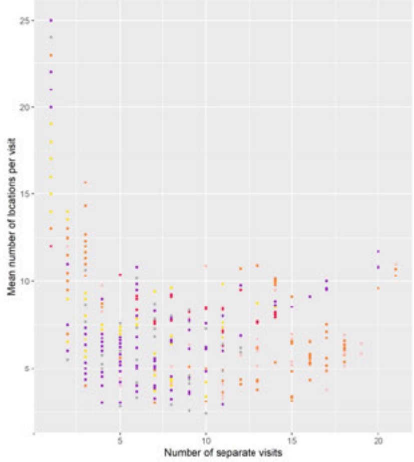
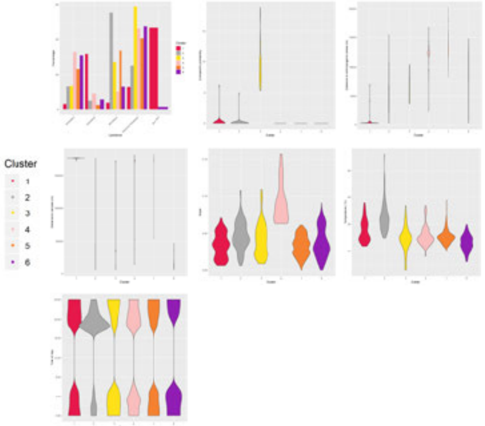
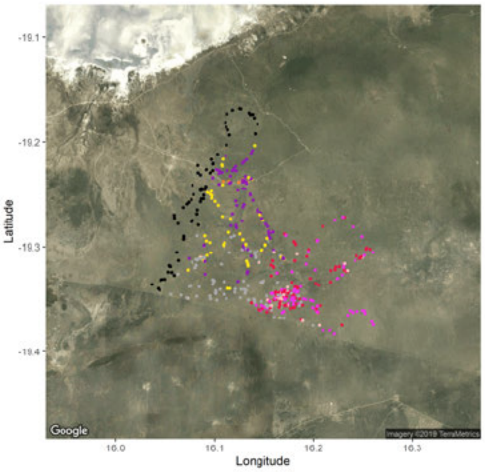
-19.2
-19.3
-19.4
Latitude
Google
Imagery ©2019 TerraMetrics


25
20
15
10
5
Mean number of locations per visit
5
10
15
20
Number of separate visits


Cluster
1
2
3
4
5
6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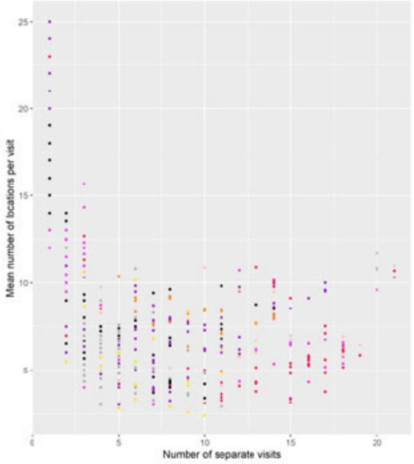
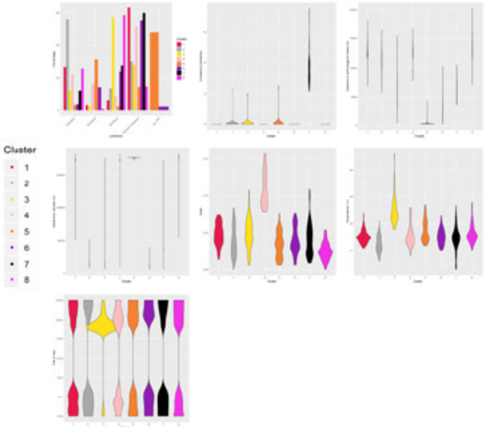
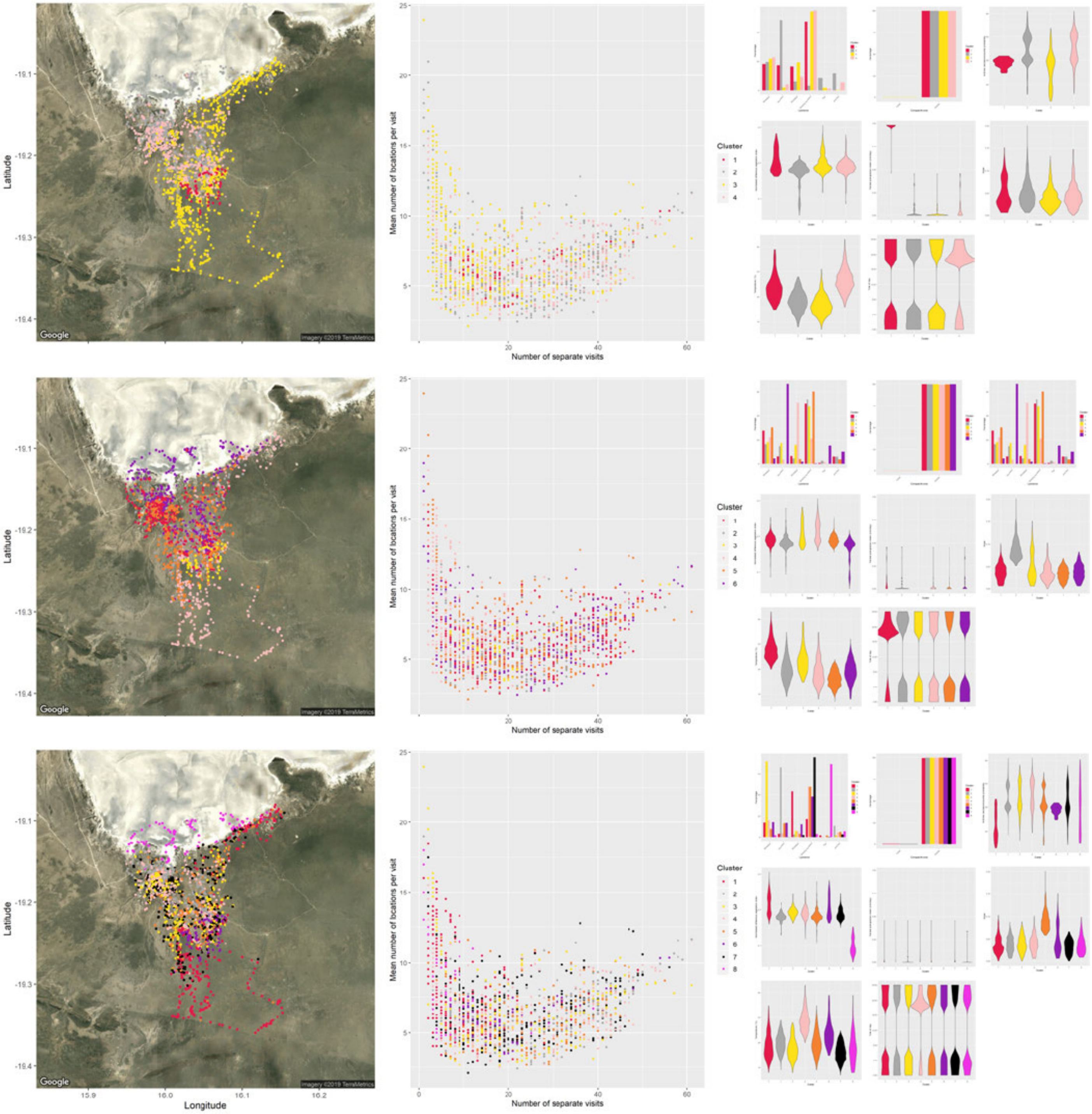
-19.4
Latitude
Google
Imagery ©2019 TerraMetrics
10.0
10.1
10.2
10.3
Longitude

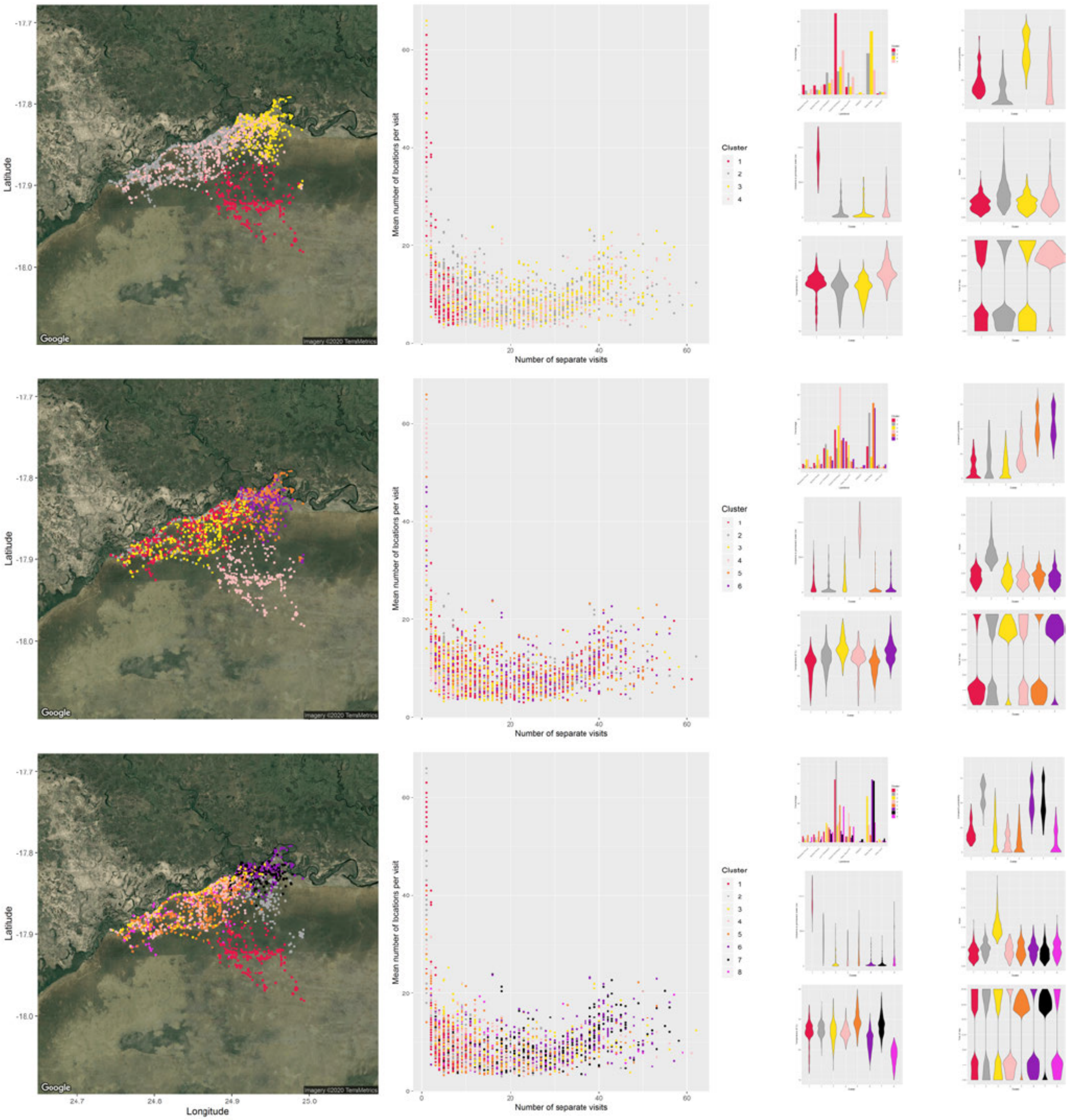

25
20
15
10
5
Mean number of locations per visit
0
5
10
15
20
Number of separate visits


Cluster
1
2
3
4
5
6
7
8

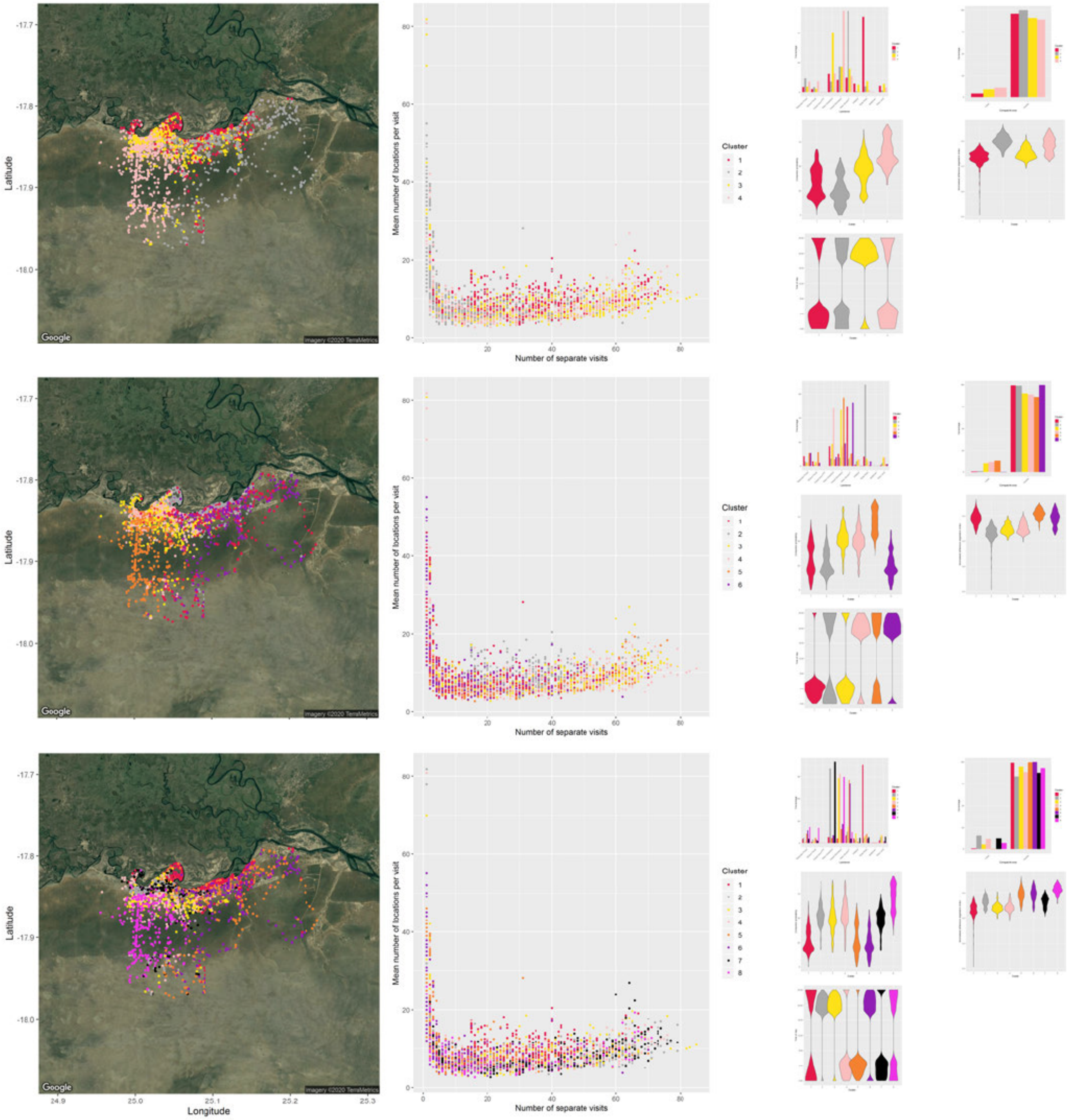
(a.10) G2-35678


Latitude
-19.1
-19.2
-19.3
-19.4
Google
Imagery ©2019 TerraMetrics
15.9
16.0
16.1
16.2
Longitude
Mean number of locations per visit
25
20
15
10
5
0
20
40
60
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

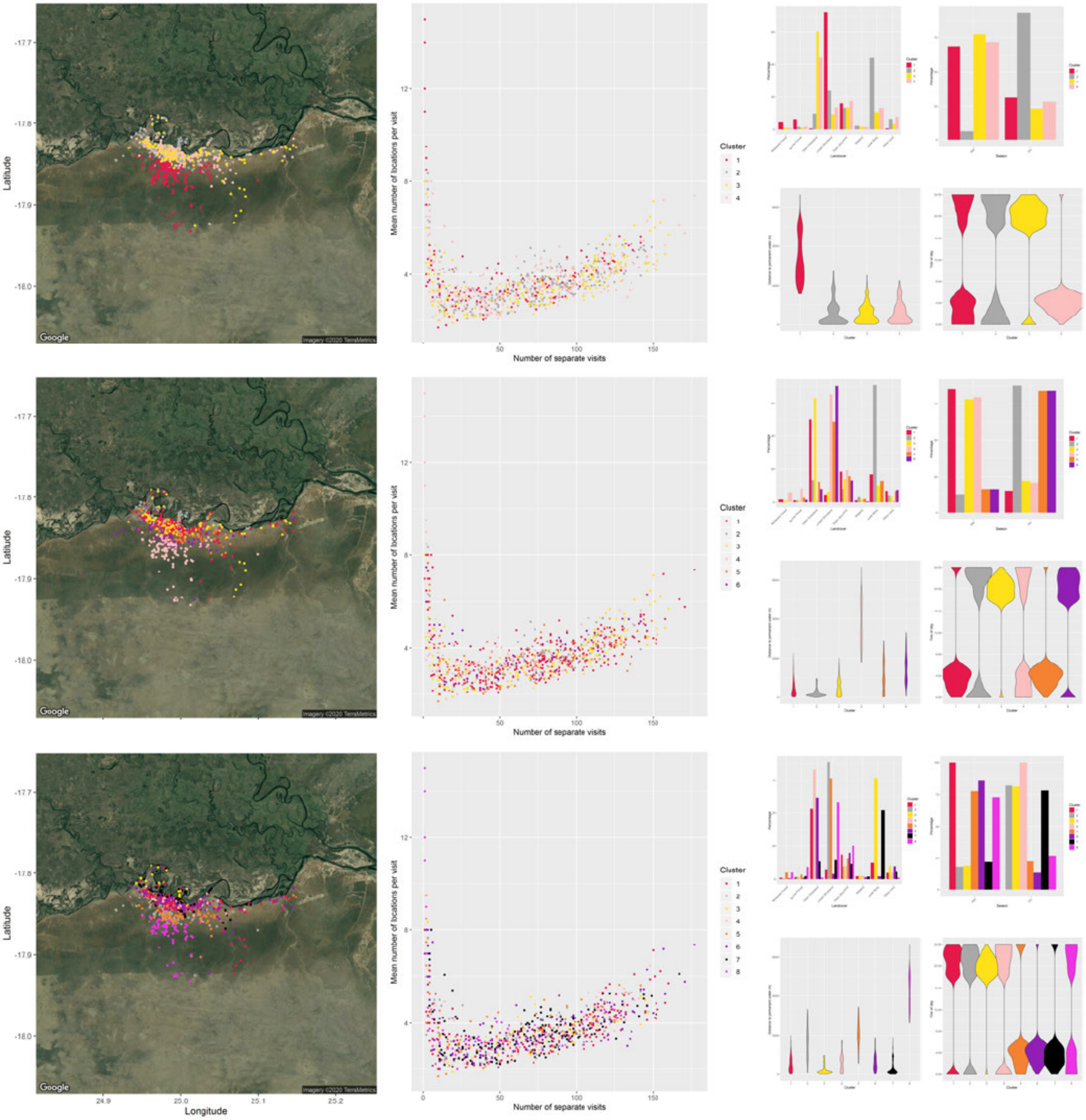
(b.1) SW-33950


Latitude
-17.7
-17.8
-17.9
-18.0
Longitude
24.7
24.8
24.9
25.0
Google
Imagery ©2020 TerraMetrics
Mean number of locations per visit
Number of separate visits
0
20
40
60
Cluster
1
2
3
4
5
6
7
8

(b.2) KW-36716

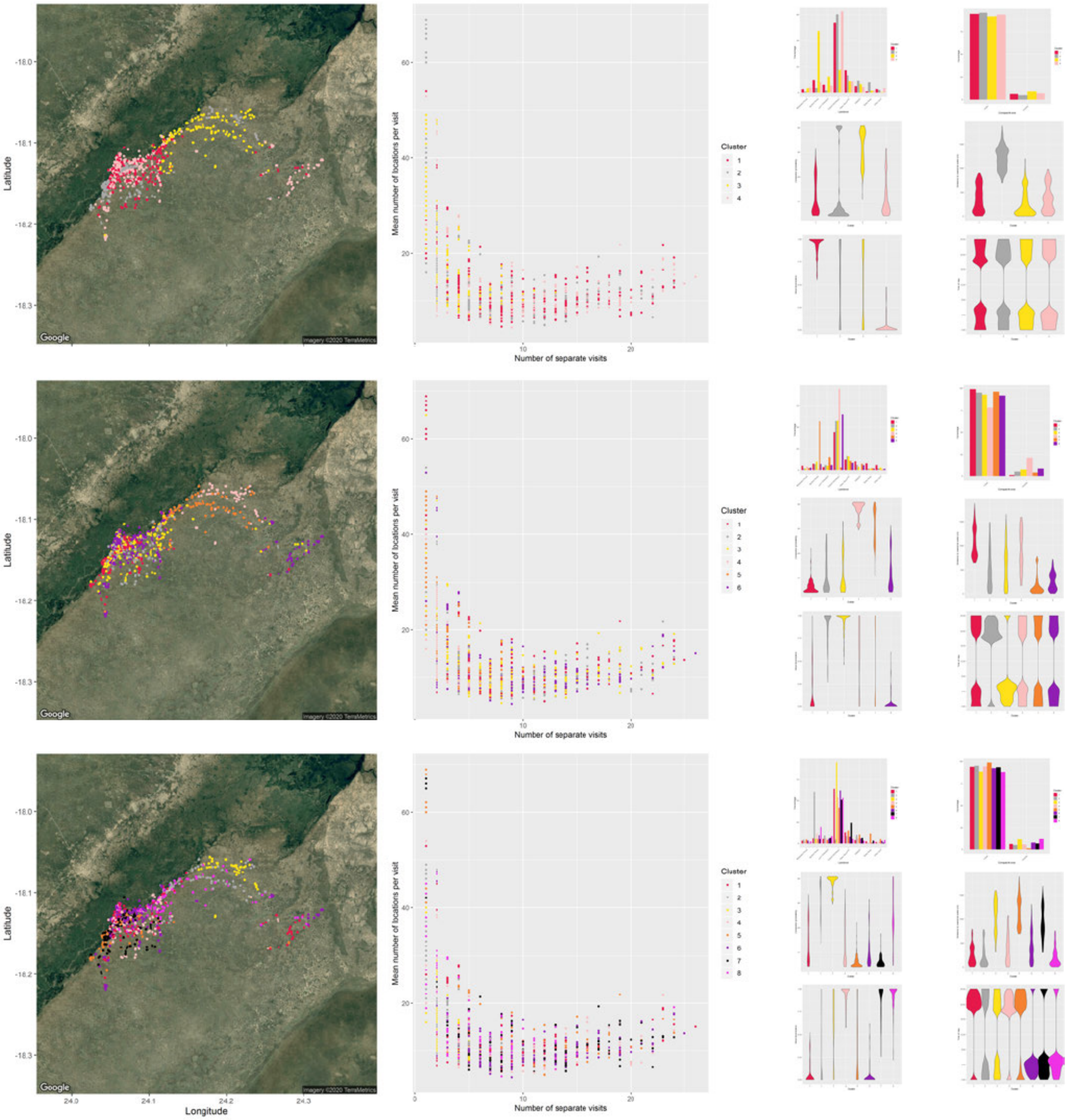

Latitude
-17.7
-17.8
-17.9
-18.0
Google
Imagery ©2020 TerraMetrics
Longitude
24.9
25.0
25.1
25.2
25.3
Mean number of locations per visit
0
20
40
60
80
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

(b.3) KB-36717

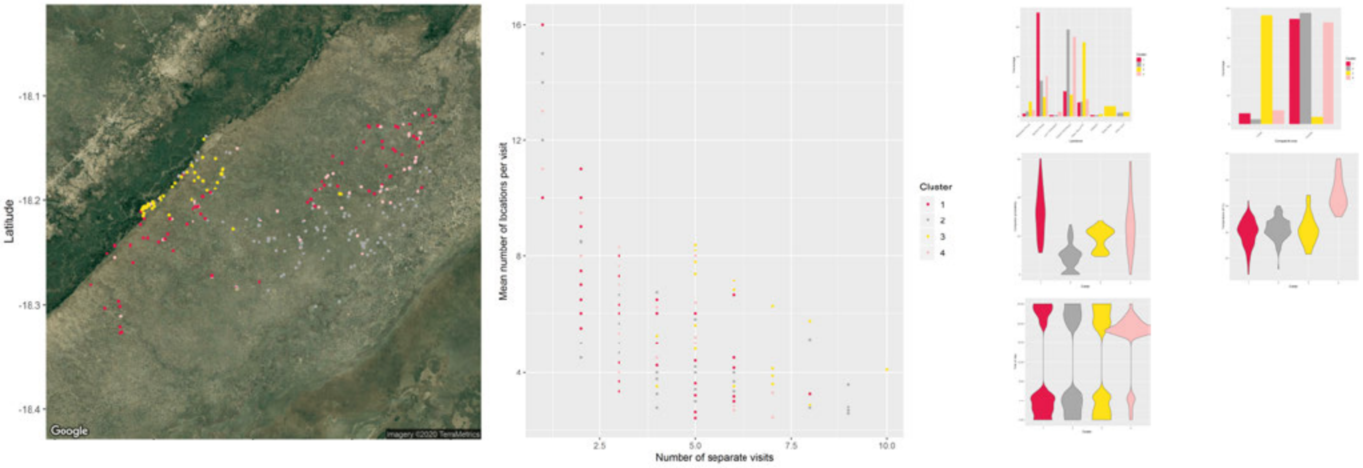


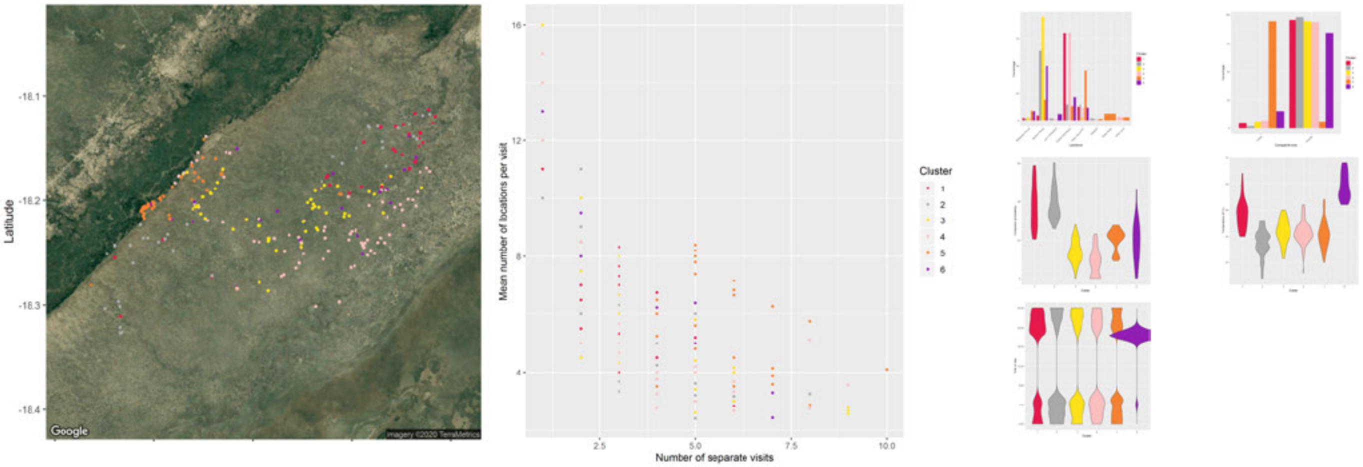
Latitude
-17.7
-17.8
-17.9
-18.0
24.9
25.0
25.1
25.2
Longitude
Google
Imagery ©2020 TerraMetrics
Mean number of locations per visit
4
8
12
0
50
100
150
Number of separate visits
Cluster
1
2
3
4
5
6
7
8
Percentage
Landcover
Season
Distance to permanent water (m)
Time of day
Cluster

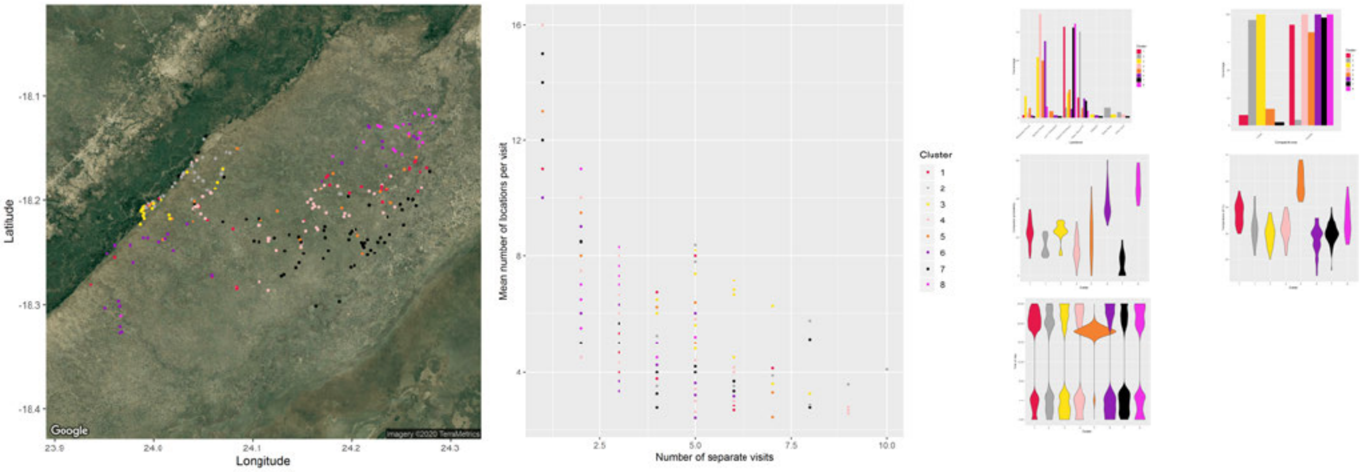
(c.1) AF-34308


-18.0
-18.1
-18.2
-18.3
Latitude
Google
Imagery ©2020 TerraMetrics
24.0
24.1
24.2
24.3
Longitude
Mean number of locations per visit
60
40
20
0
10
20
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

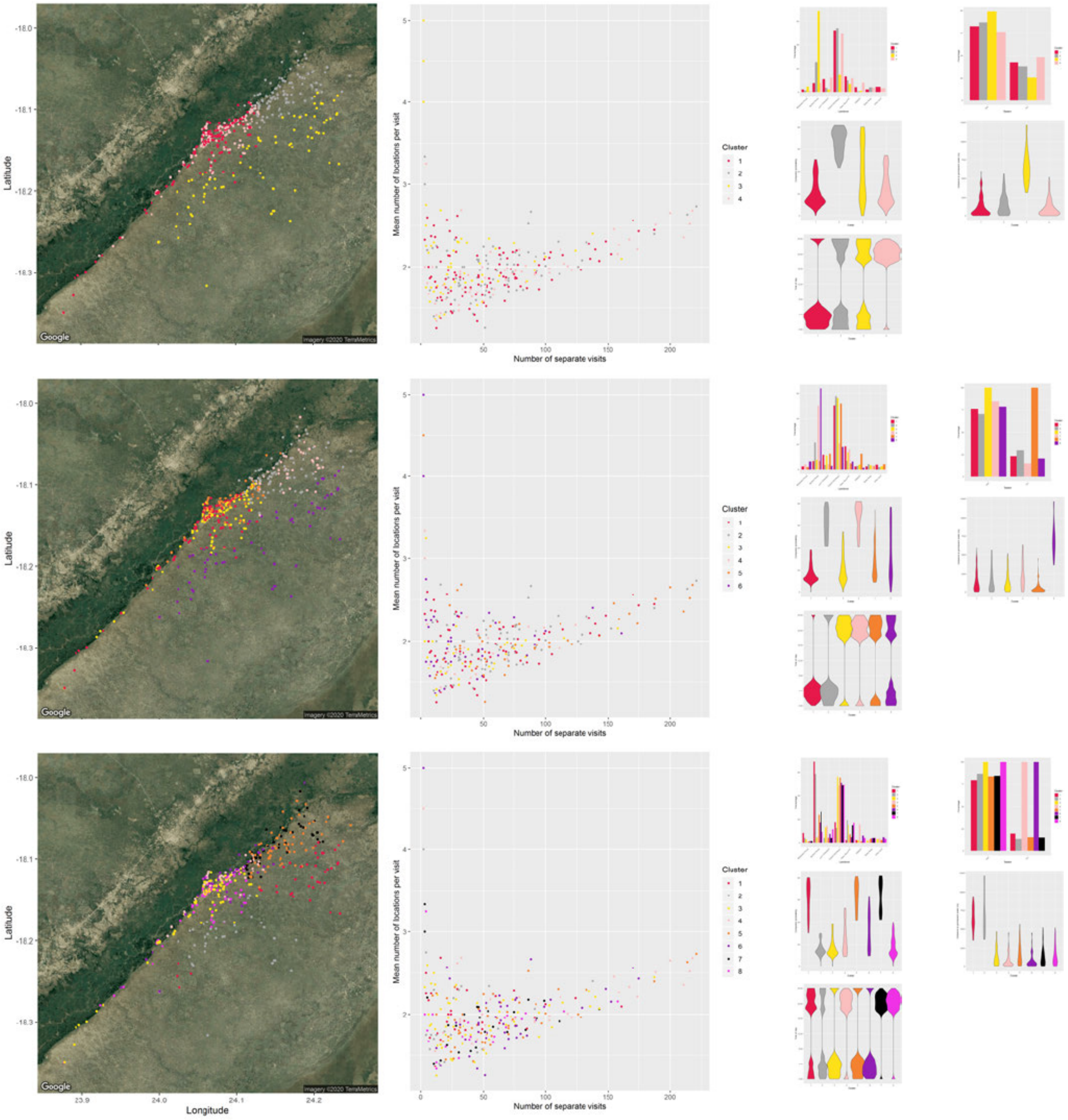
(c.2) BE-35678


Latitude
-18.1
-18.2
-18.3
-18.4
Google
Imagery ©2020 TerraMetrics
Mean number of locations per visit
16
12
8
4
2.5
5.0
7.5
10.0
Number of separate visits
Cluster
1
2
3
4

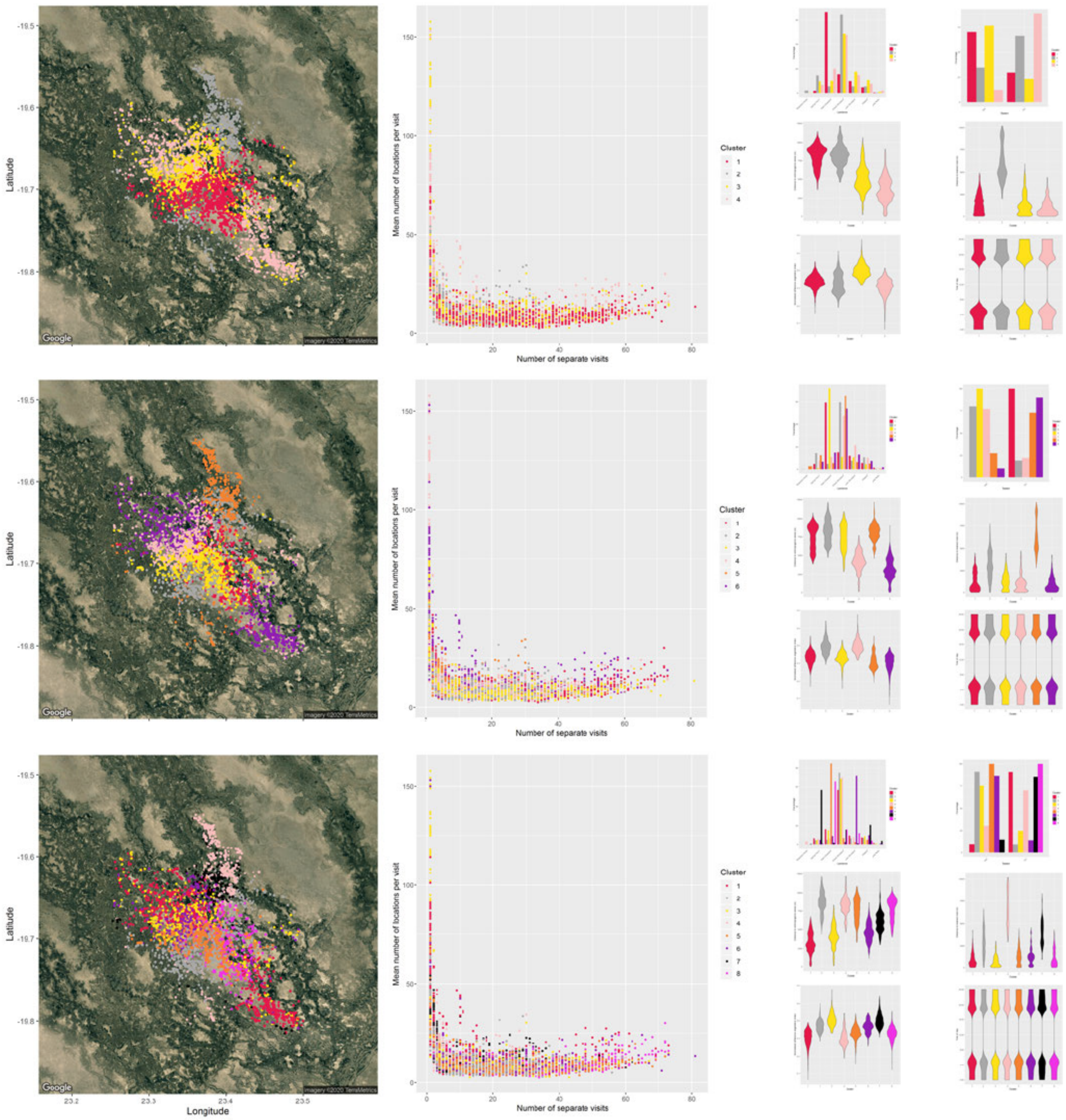

Latitude
-18.1
-18.2
-18.3
-18.4
Google
Imagery ©2020 TerraMetrics
Mean number of locations per visit
16
12
8
4
2.5
5.0
7.5
10.0
Number of separate visits
Cluster
1
2
3
4
5
6


Latitude
-18.1
-18.2
-18.3
-18.4
Google
Imagery ©2020 TerraMetrics
23.9
24.0
24.1
24.2
24.3
Longitude
Mean number of locations per visit
16
12
8
4
2.5
5.0
7.5
10.0
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

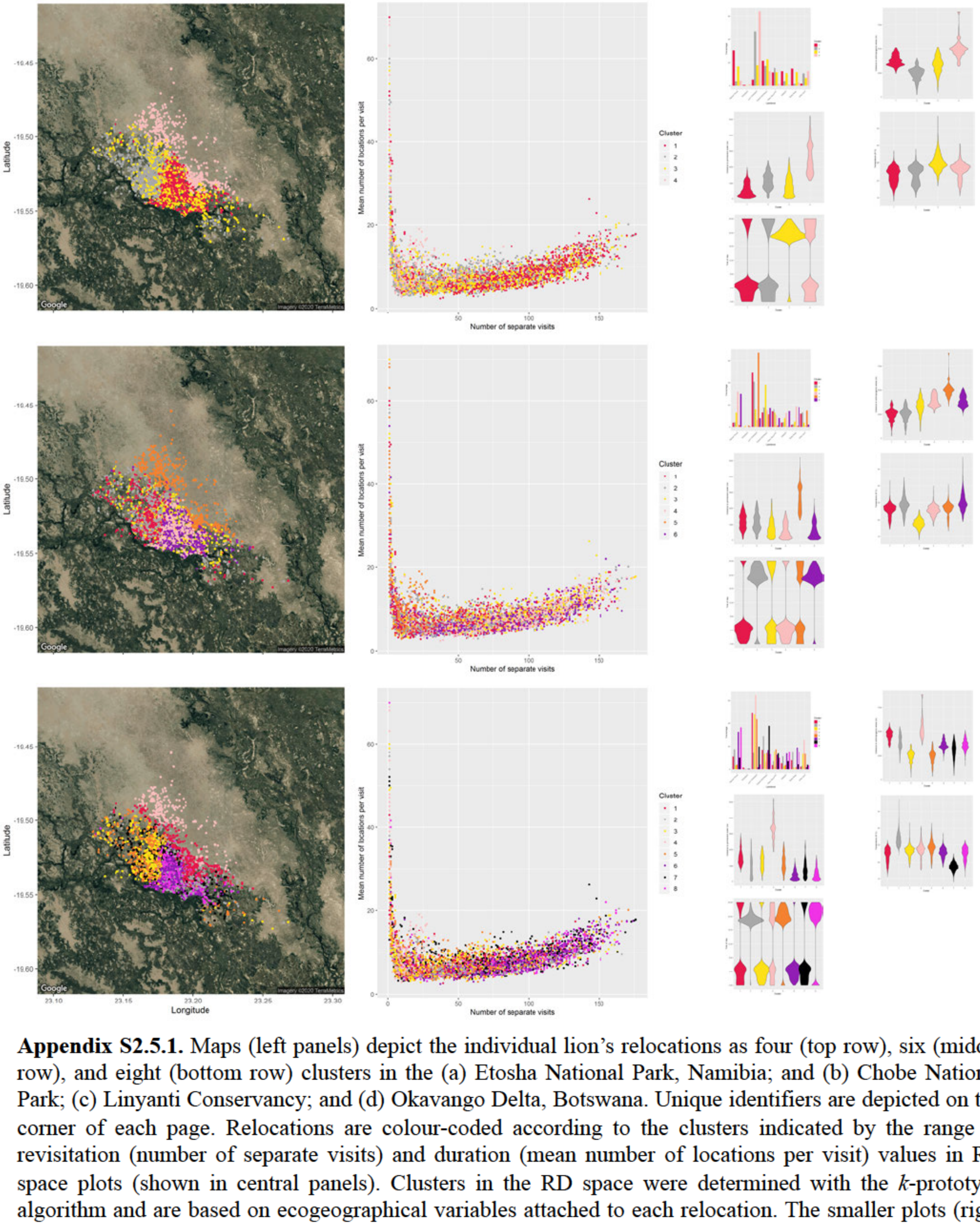
(c.3) AM-36714


Latitude
-18.0
-18.1
-18.2
-18.3
Google
Imagery ©2020 TerraMetrics
Longitude
23.9
24.0
24.1
24.2
Mean number of locations per visit
Number of separate visits
0
50
100
150
200
2
3
4
5
Cluster
1
2
3
4
5
6
7
8

(d.1) BO-35947

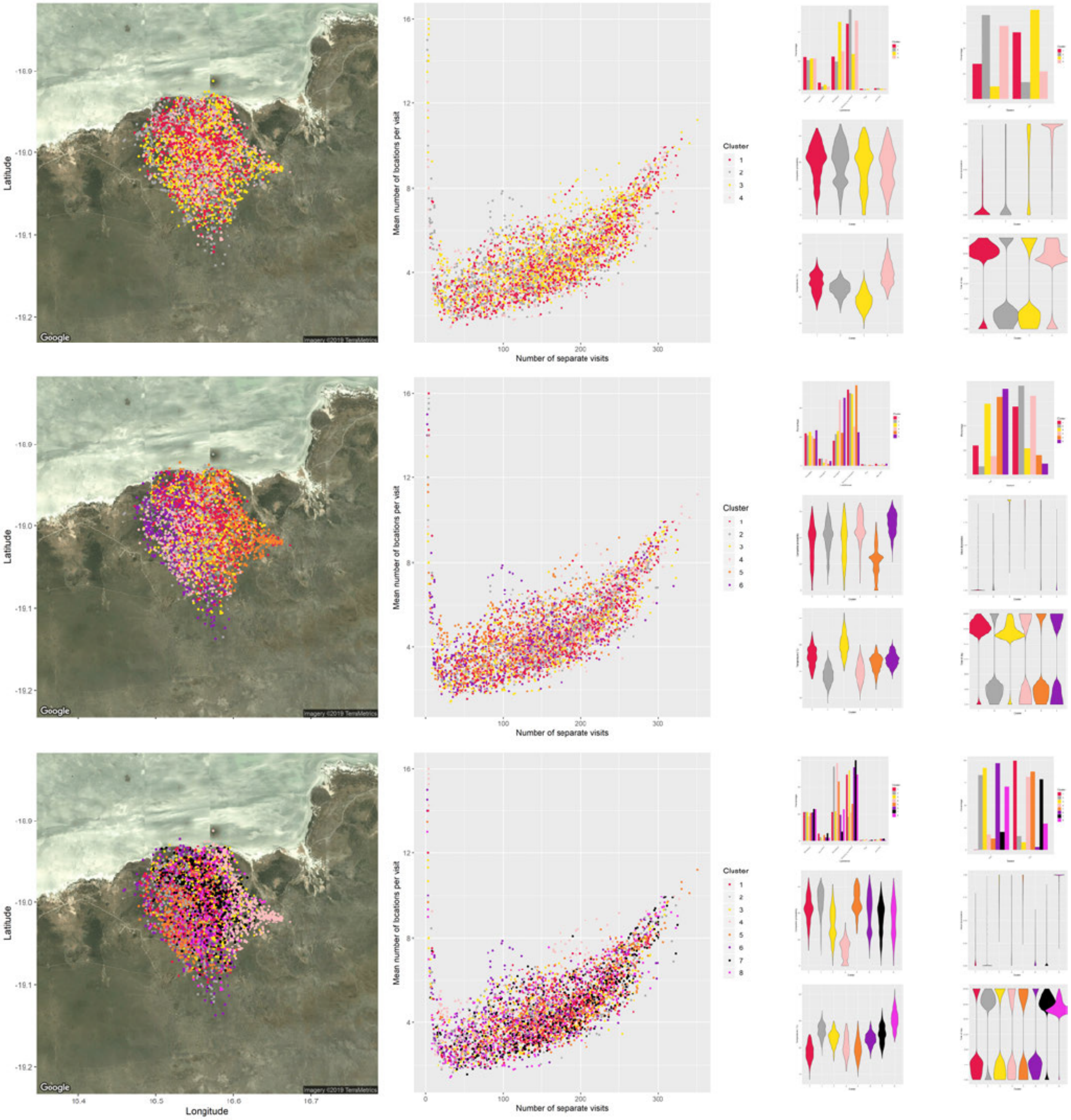

-19.5
-19.6
-19.7
-19.8
Latitude
Google
Imagery ©2020 TerraMetrics
150
100
50
0
Mean number of locations per visit
20
40
60
80
Number of separate visits
Cluster
1
2
3
4
5
6
7
8
23.2
23.3
23.4
23.5
Longitude

(d.2) BA-36715

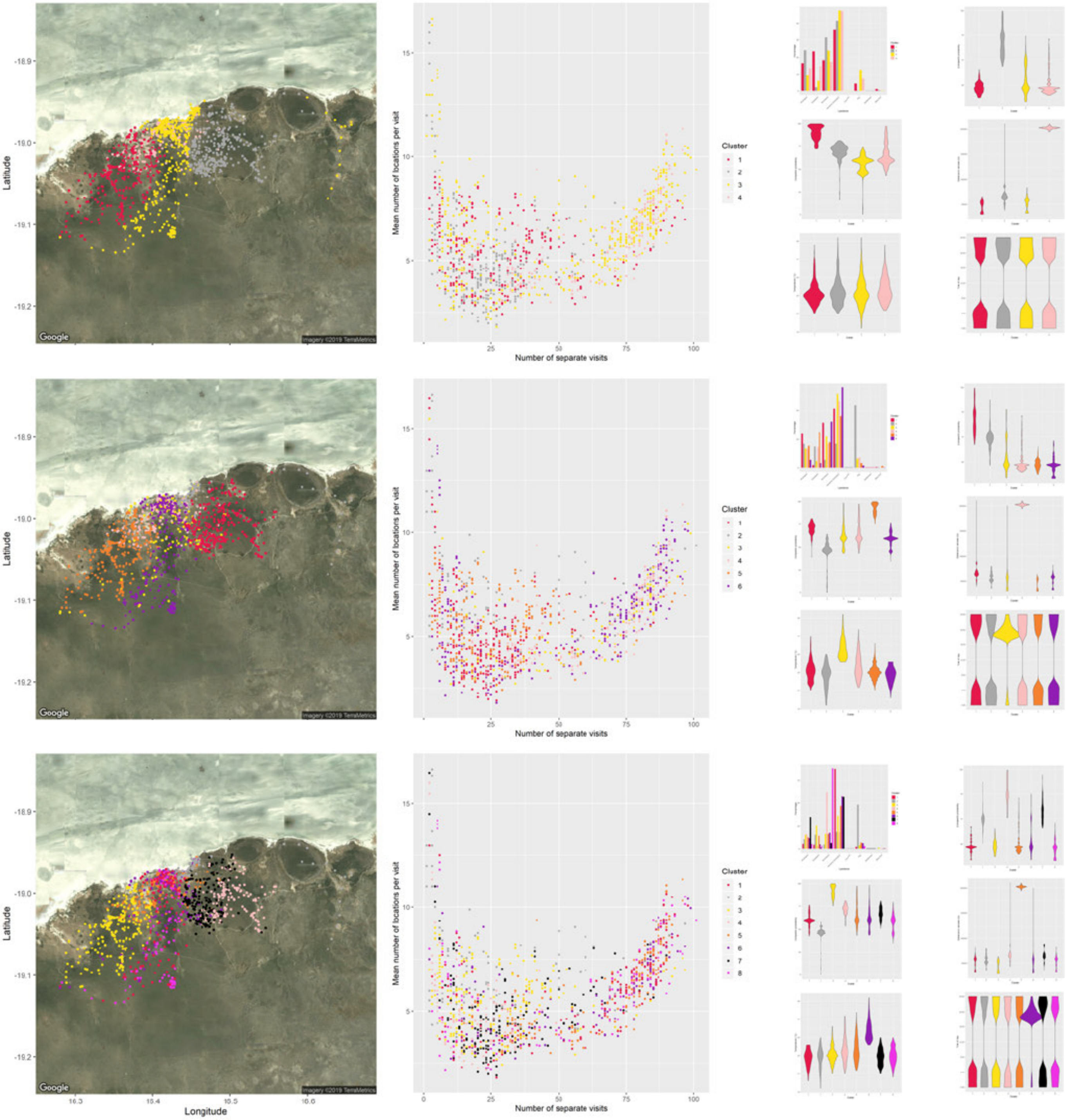


Appendix S2.5.1. Maps (left panels) depict the individual lion's relocations as four (top row), six (middle row), and eight (bottom row) clusters in the (a) Etosha National Park, Namibia; and (b) Chobe National Park; (c) Linyanti Conservancy; and (d) Okavango Delta, Botswana. Unique identifiers are depicted on top corner of each page. Relocations are colour-coded according to the clusters indicated by the range of revisitation (number of separate visits) and duration (mean number of locations per visit) values in RD space plots (shown in central panels). Clusters in the RD space were determined with the *k*-prototype algorithm and are based on ecogeographical variables attached to each relocation. The smaller plots (right panels) present the distribution and percent category of each cluster for each of the ecogeographical variables selected from the FAMD analysis.

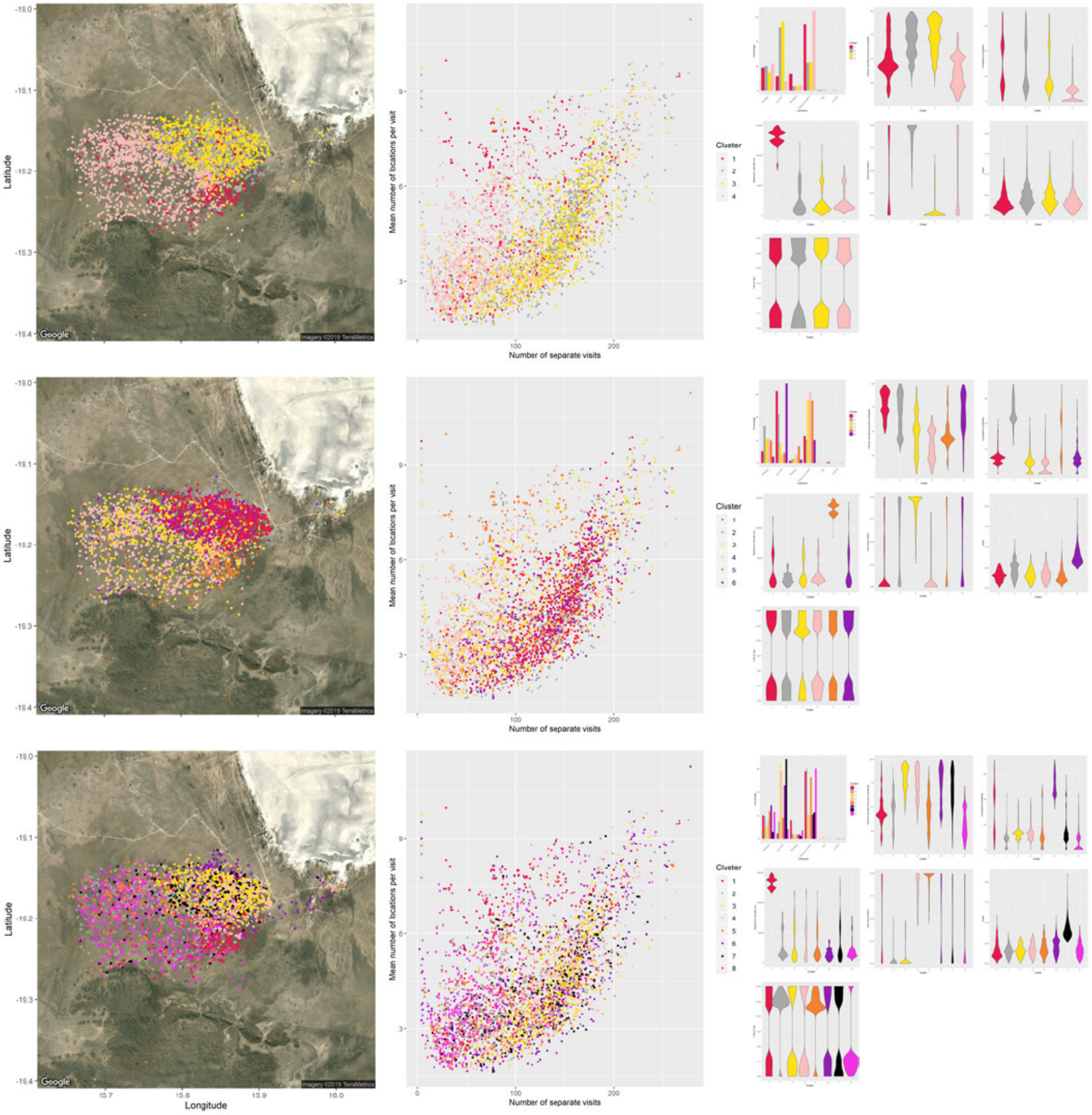
(a.1) GO-33869


Latitude
-18.9
-19.0
-19.1
-19.2
Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
16
12
8
4
Number of separate visits
0
100
200
300
Cluster
1
2
3
4
5
6
7
8
10.4
10.5
10.6
10.7
Longitude

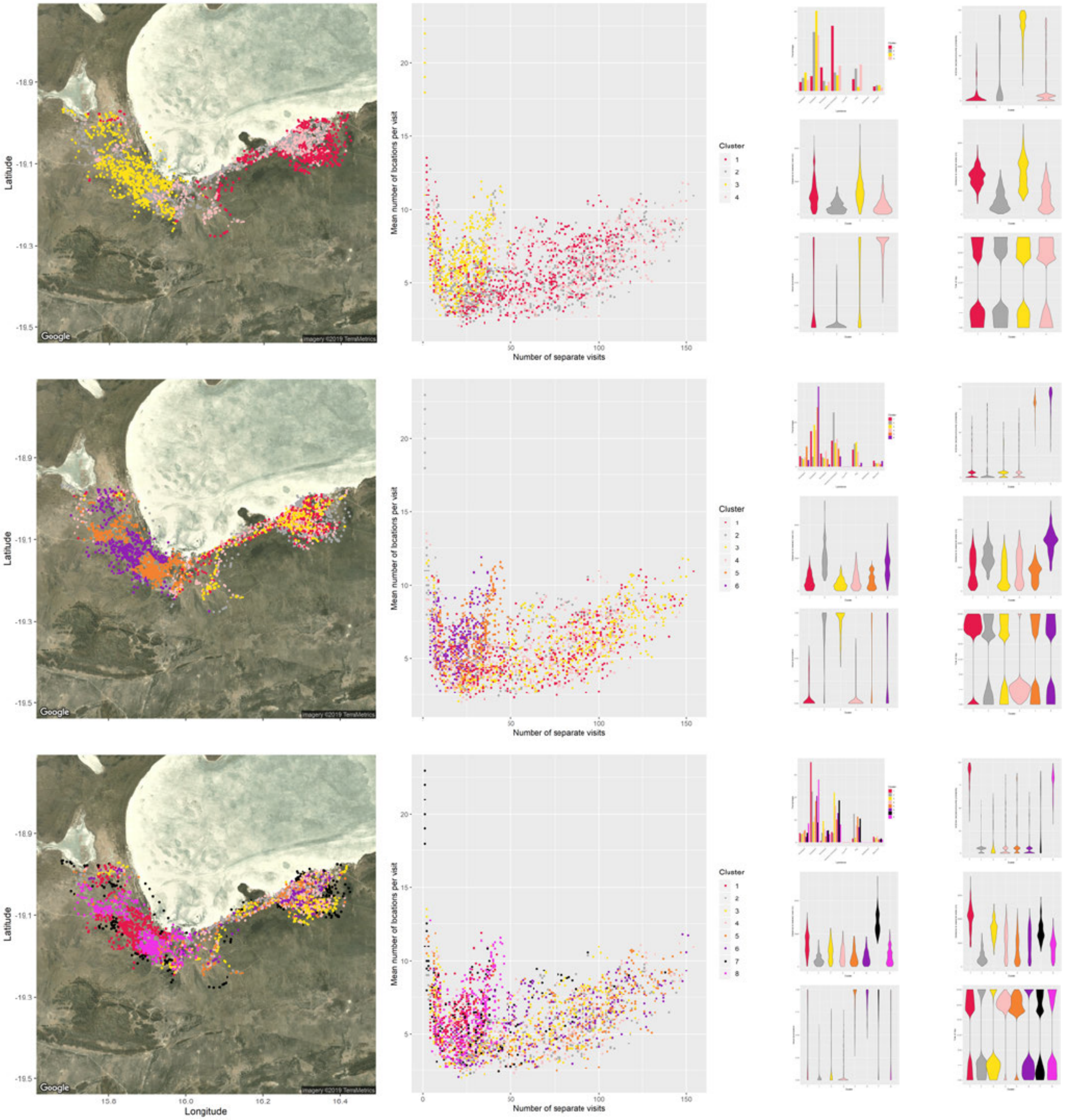
(a.2) TJ-33870


Latitude
-18.9
-19.0
-19.1
-19.2
Longitude
16.3
16.4
16.5
16.6
Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
15
10
5
Number of separate visits
0
25
50
75
100
Cluster
1
2
3
4
5
6
7
8

(a.3) NE-33871

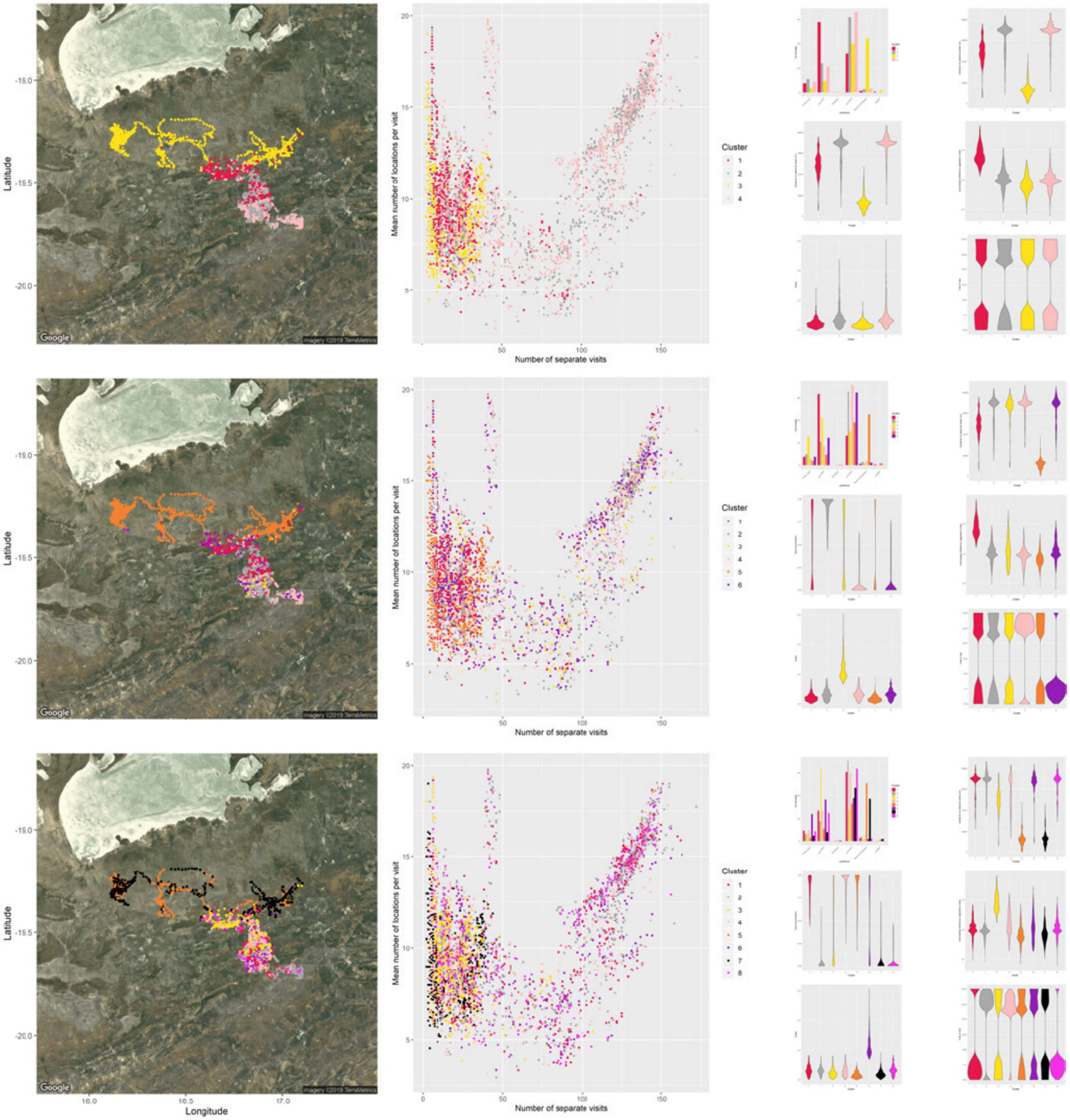

-19.0
-19.1
-19.2
-19.3
-19.4
Latitude
15.7
15.8
15.9
16.0
Longitude
Google
Imagery ©2019 TerraMetrics
Mean number of locations per visit
3
6
9
0
100
200
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

(a.4) SA-33872

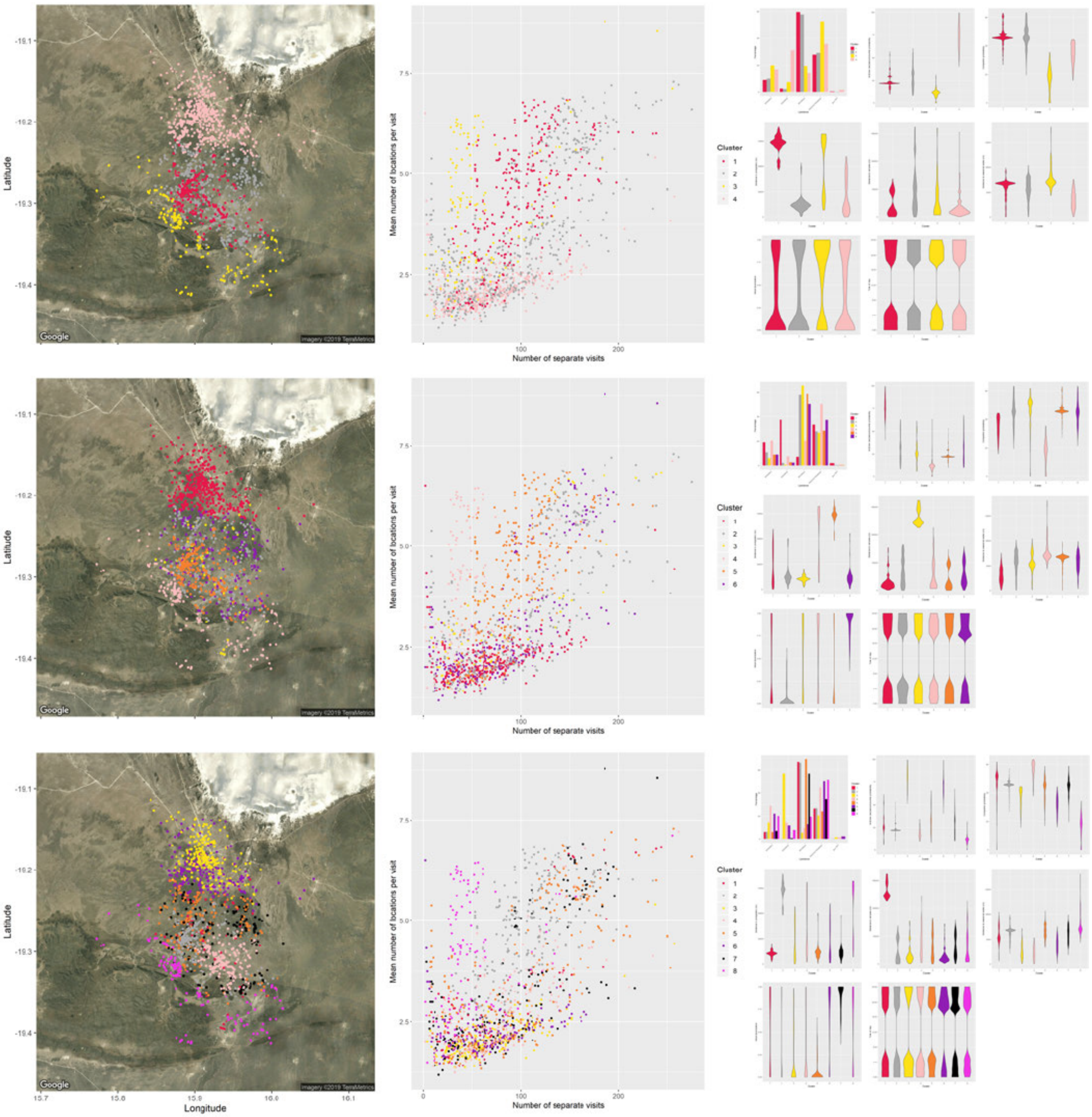


Latitude
-18.9
-19.1
-19.3
-19.5
Google
Imagery ©2019 TerraMetrics
15.8
16.0
16.2
16.4
Longitude
Mean number of locations per visit
20
15
10
5
0
50
100
150
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

(a.5) AU-33873

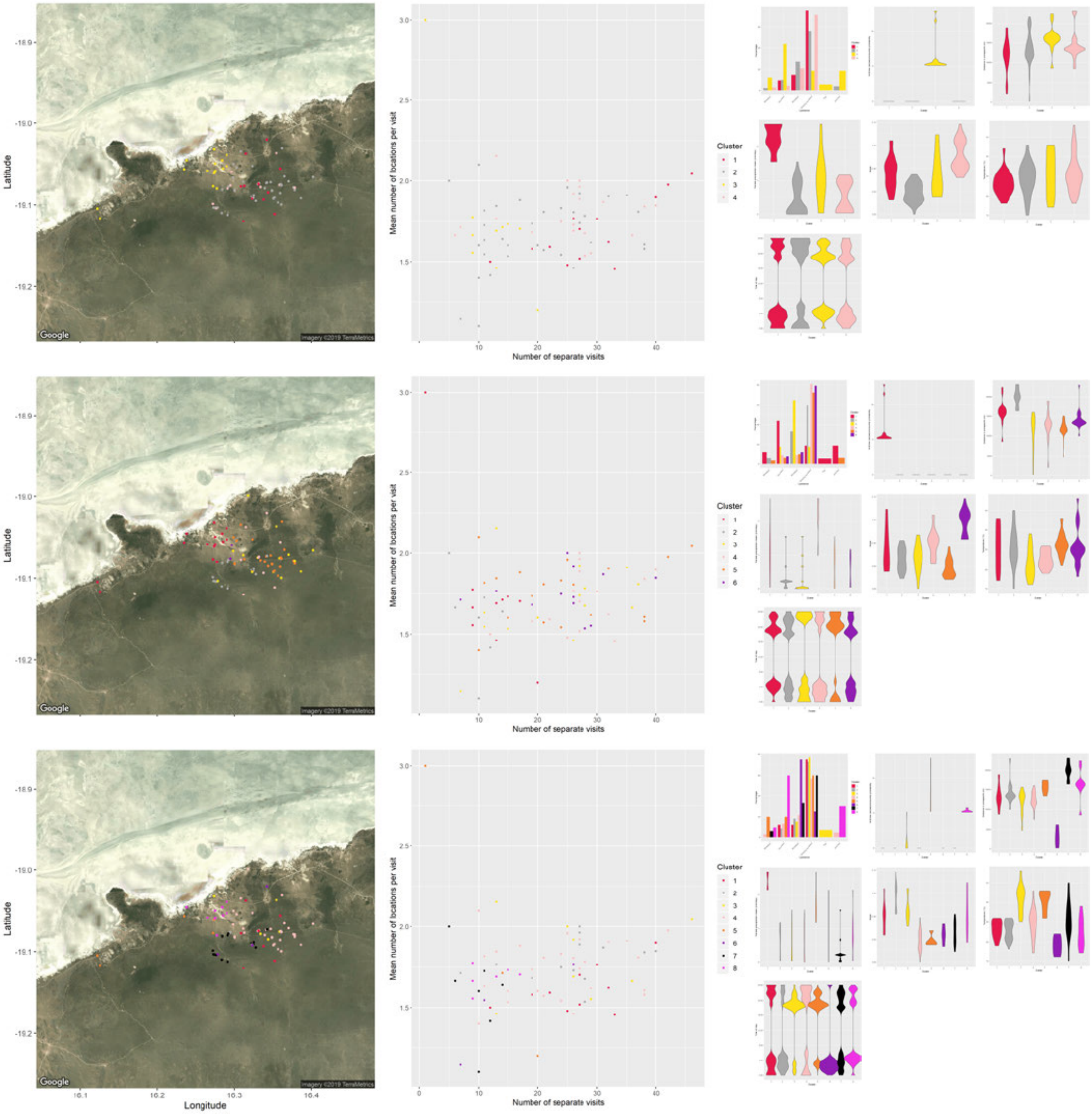

Latitude
-19.0
-19.5
-20.0
Google
Imagery ©2019 TerraMetrics
16.0
16.5
17.0
Longitude
Mean number of locations per visit
5
10
15
20
0
50
100
150
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

(a.6) OM-33874

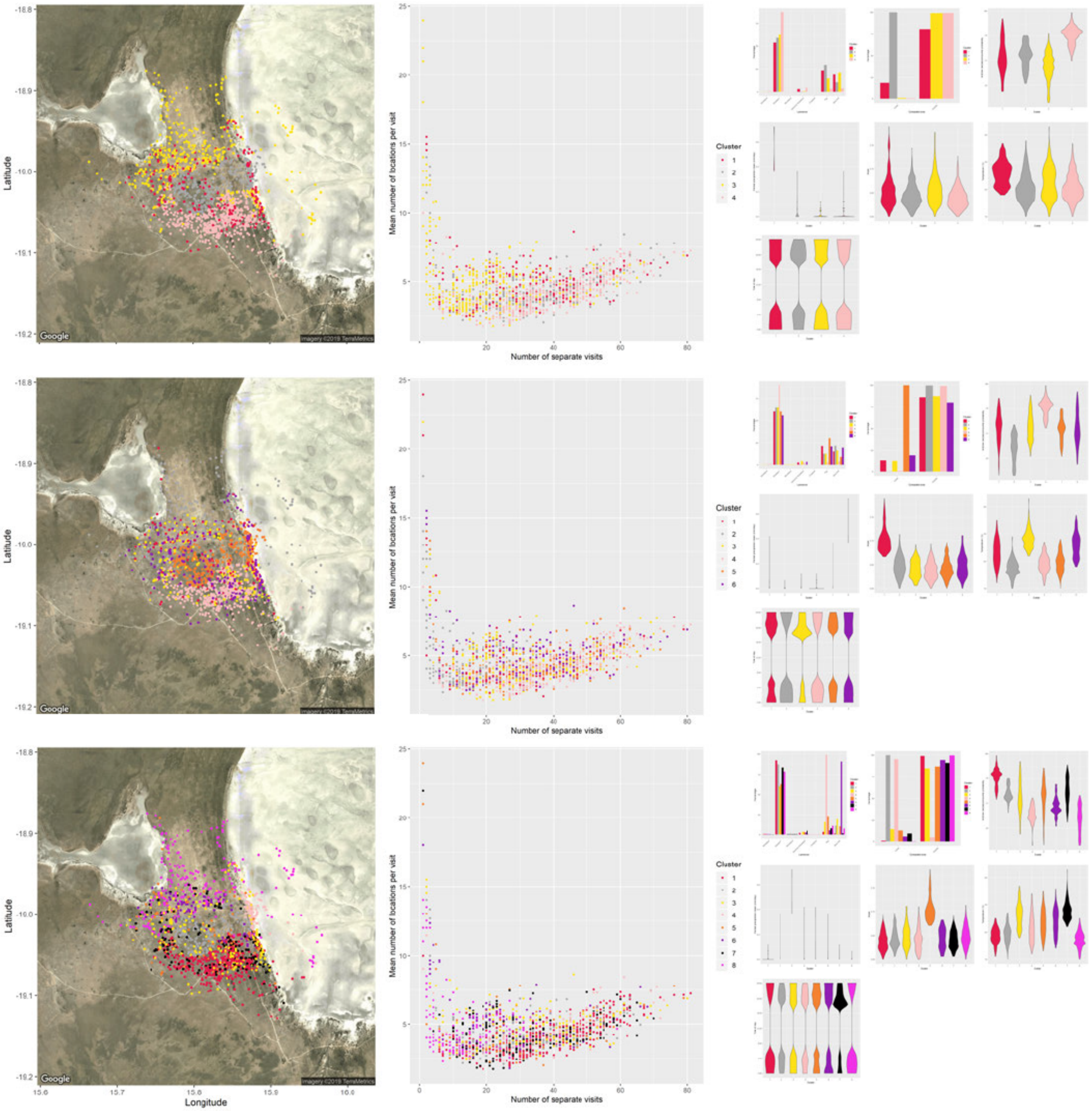


Latitude
-19.1
-19.2
-19.3
-19.4
Google
Imagery ©2019 TerraMetrics
Longitude
15.7
15.8
15.9
16.0
16.1
Mean number of locations per visit
7.5
5.0
2.5
Number of separate visits
0
100
200
Cluster
1
2
3
4
5
6
7
8

(a.7) SU-33951

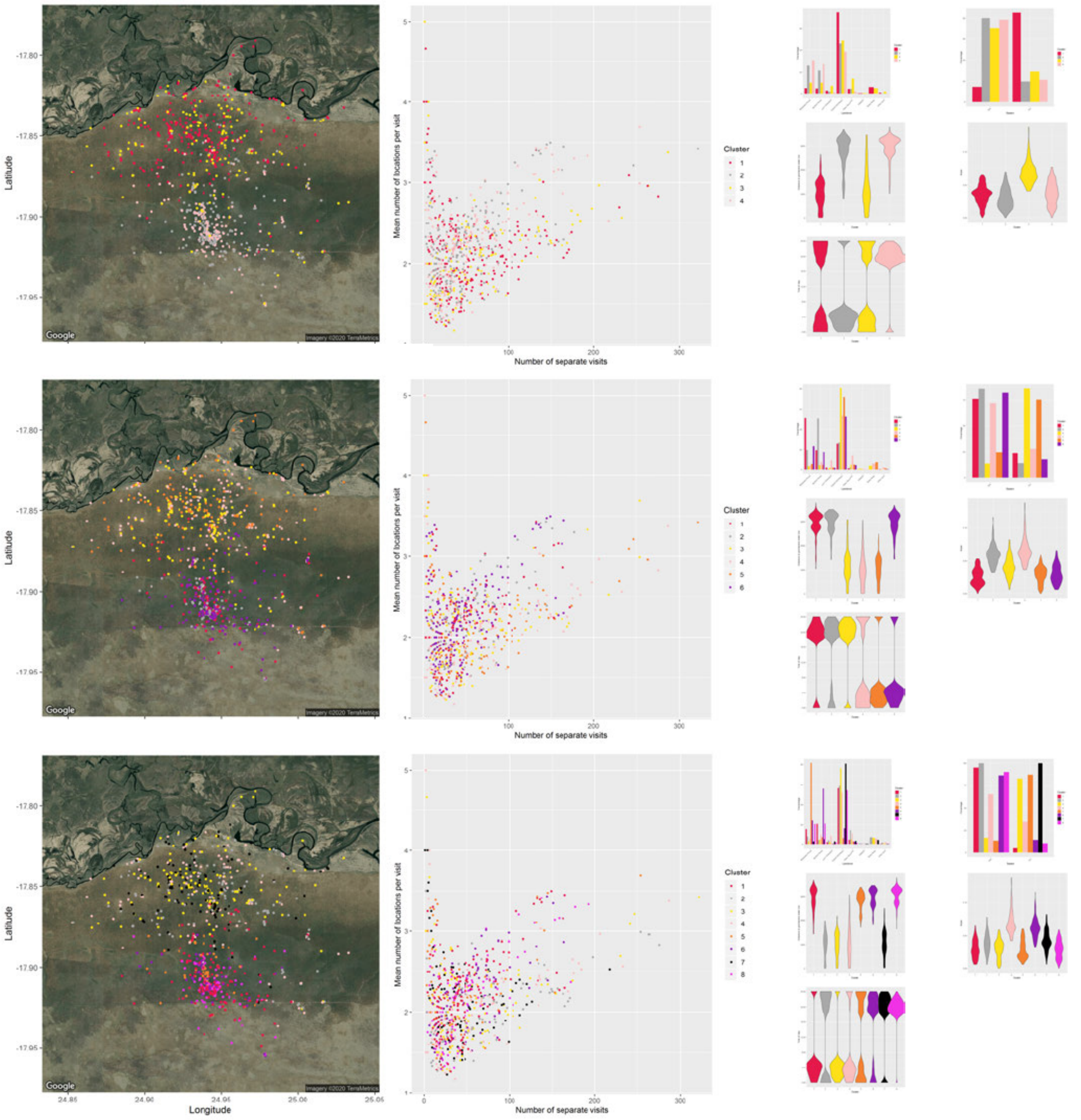

Latitude
-18.9
-19.0
-19.1
-19.2
Google
Imagery ©2019 TerraMetrics
Longitude
10.1
10.2
10.3
10.4
Mean number of locations per visit
3.0
2.5
2.0
1.5
Number of separate visits
0
10
20
30
40
Cluster
1
2
3
4
5
6
7
8

(a.8) WO-34310

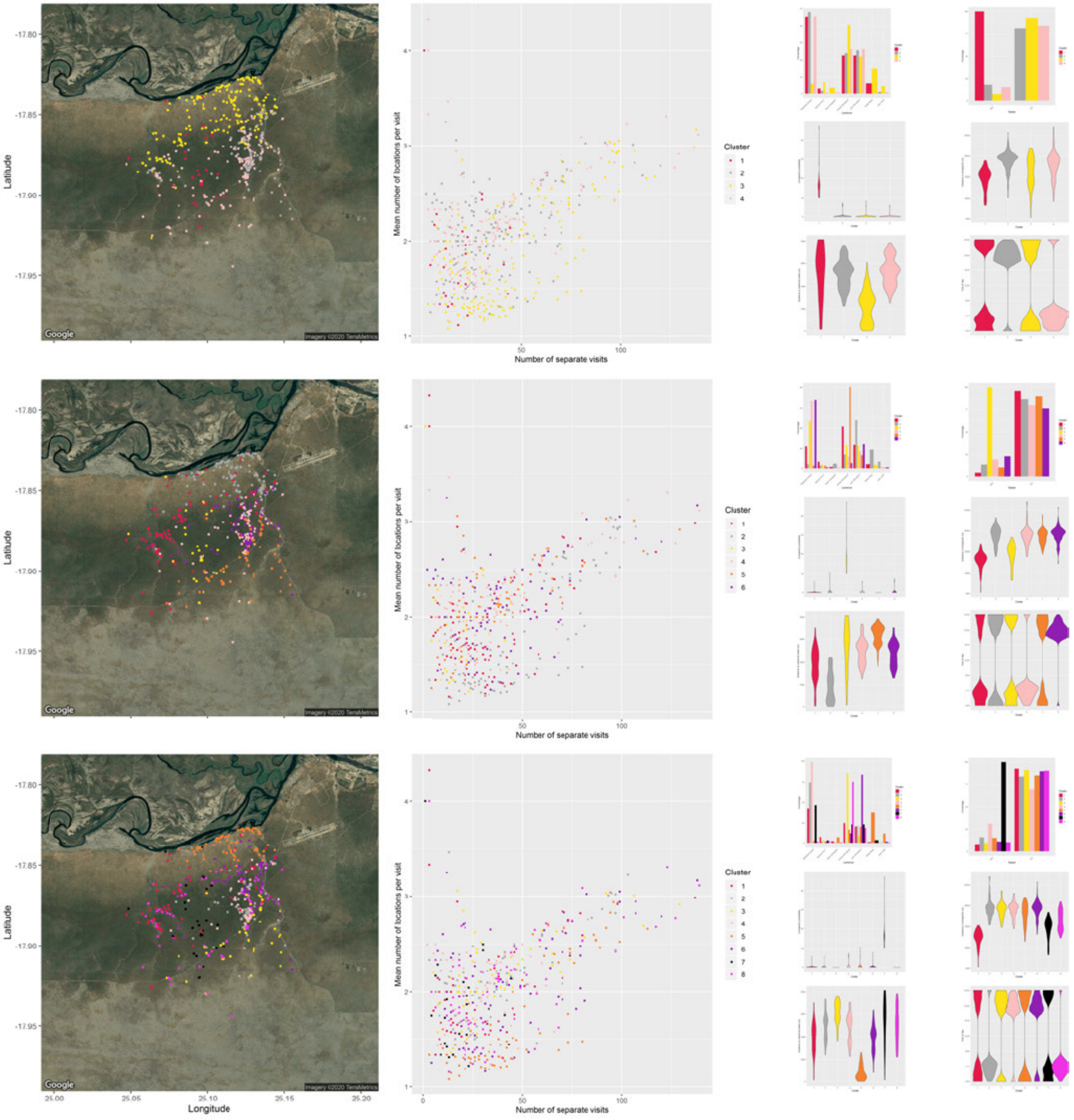


Latitude
-18.8
-18.9
-19.0
-19.1
-19.2
Google
Imagery ©2019 TerraMetrics
Longitude
15.6
15.7
15.8
15.9
16.0
Mean number of locations per visit
Number of separate visits
0
5
10
15
20
25
40
60
80
Cluster
1
2
3
4
5
6
7
8

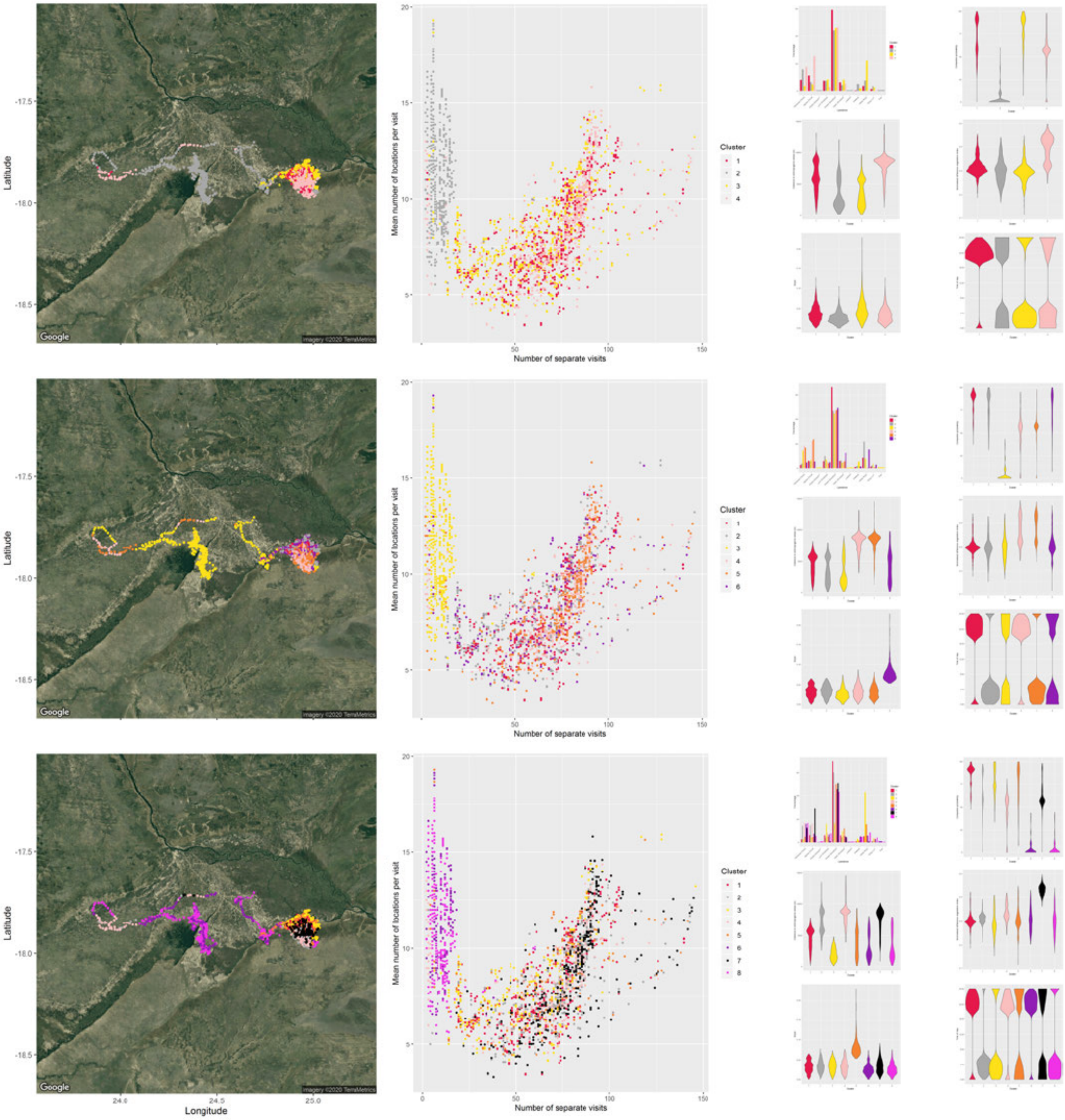
(b.1) IH-33870


Latitude
-17.80
-17.85
-17.90
-17.95
Google
Imagery ©2020 TerraMetrics
Mean number of locations per visit
1
2
3
4
5
0
100
200
300
Number of separate visits
Cluster
1
2
3
4
5
6
7
8
Longitude
24.85
24.90
24.95
25.00
25.05

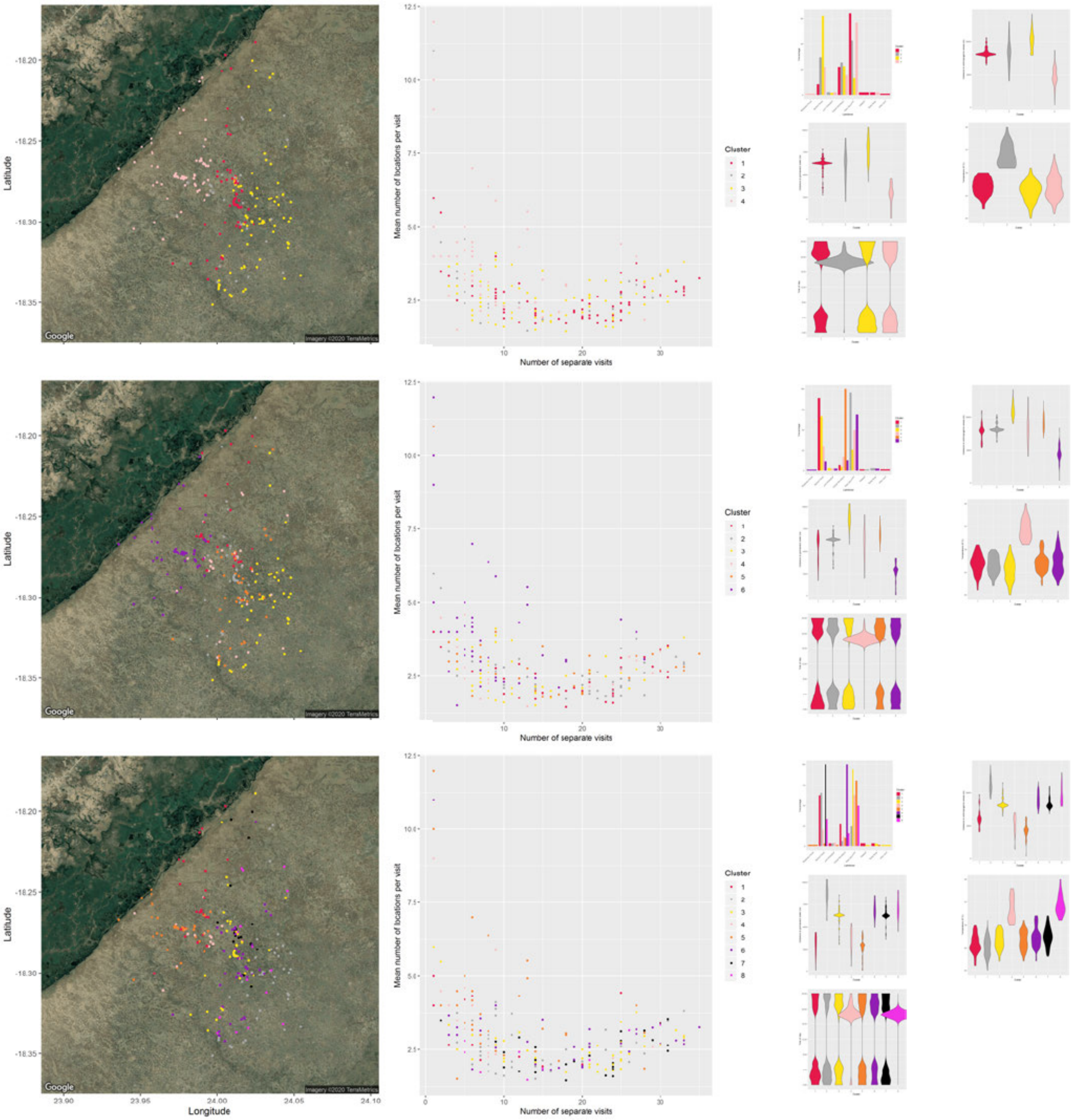
(b.2) KW-33871


-17.80
-17.85
-17.90
-17.95
Latitude
Google
Imagery ©2020 TerraMetrics
25.00
25.05
25.10
25.15
25.20
Longitude
Mean number of locations per visit
1
2
3
4
0
50
100
Number of separate visits
Cluster
1
2
3
4
5
6
7
8

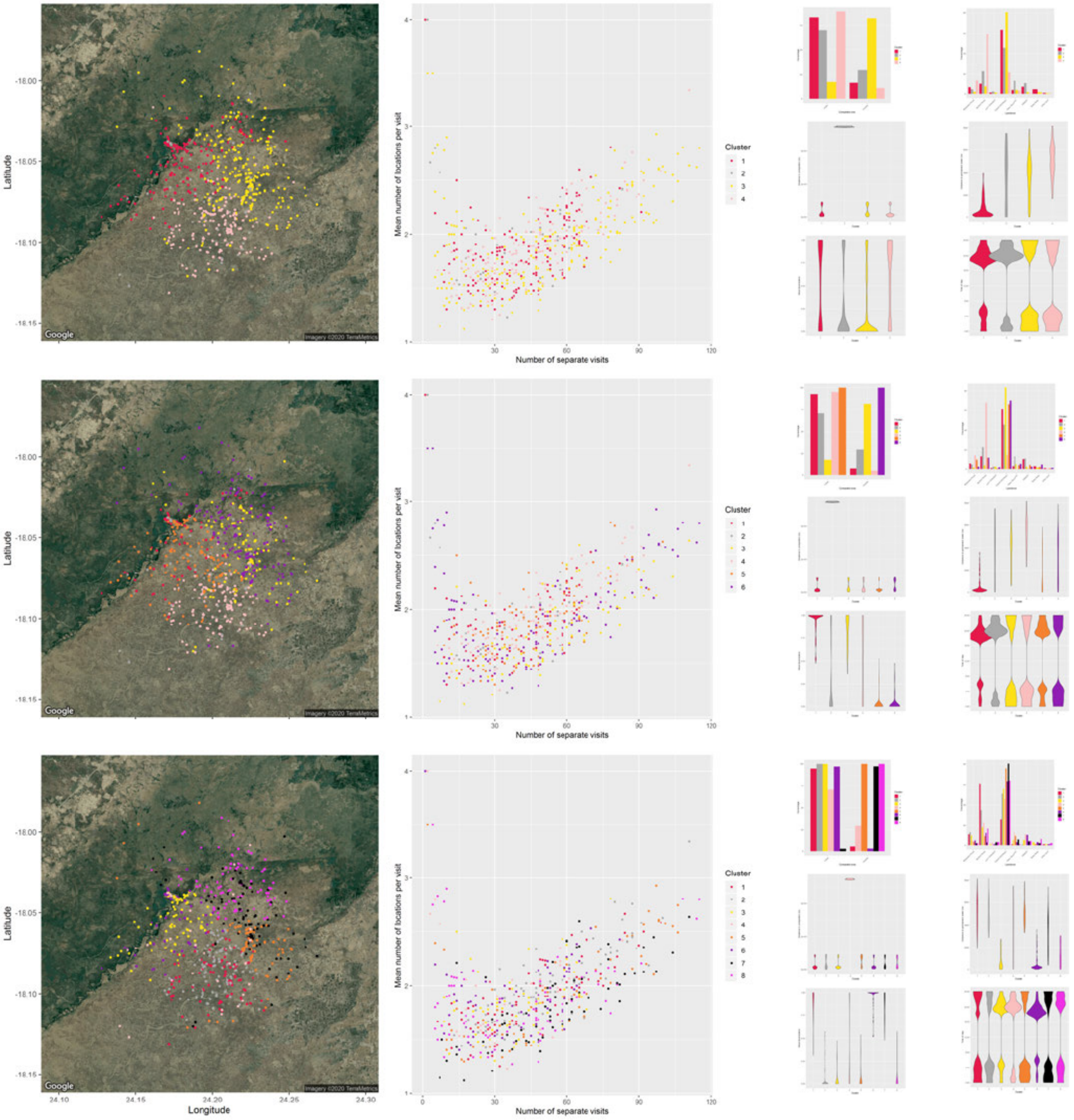
(b.3) SR-34310


Latitude
-17.5
-18.0
-18.5
Longitude
24.0
24.5
25.0
Google
Imagery ©2020 TerraMetrics
Mean number of locations per visit
Number of separate visits
0
50
100
150
5
10
15
20
Cluster
1
2
3
4
5
6
7
8

(c.1) AR-33869


Latitude
-18.20
-18.25
-18.30
-18.35
Google
Imagery ©2020 TerraMetrics
Longitude
23.90
23.95
24.00
24.05
24.10
Mean number of locations per visit
12.5
10.0
7.5
5.0
2.5
Number of separate visits
0
10
20
30
Cluster
1
2
3
4
5
6
7
8

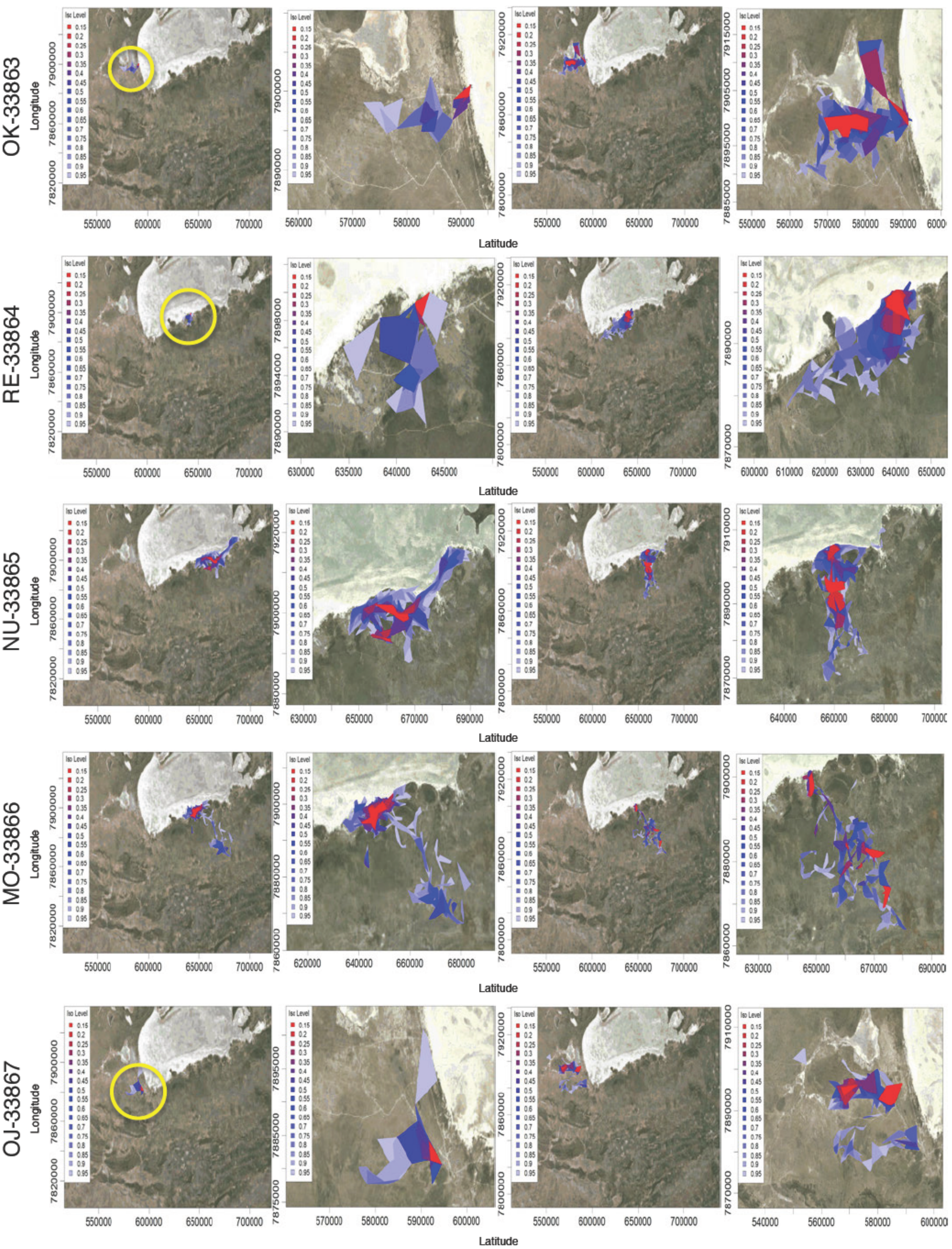
(c.2) RV-33873

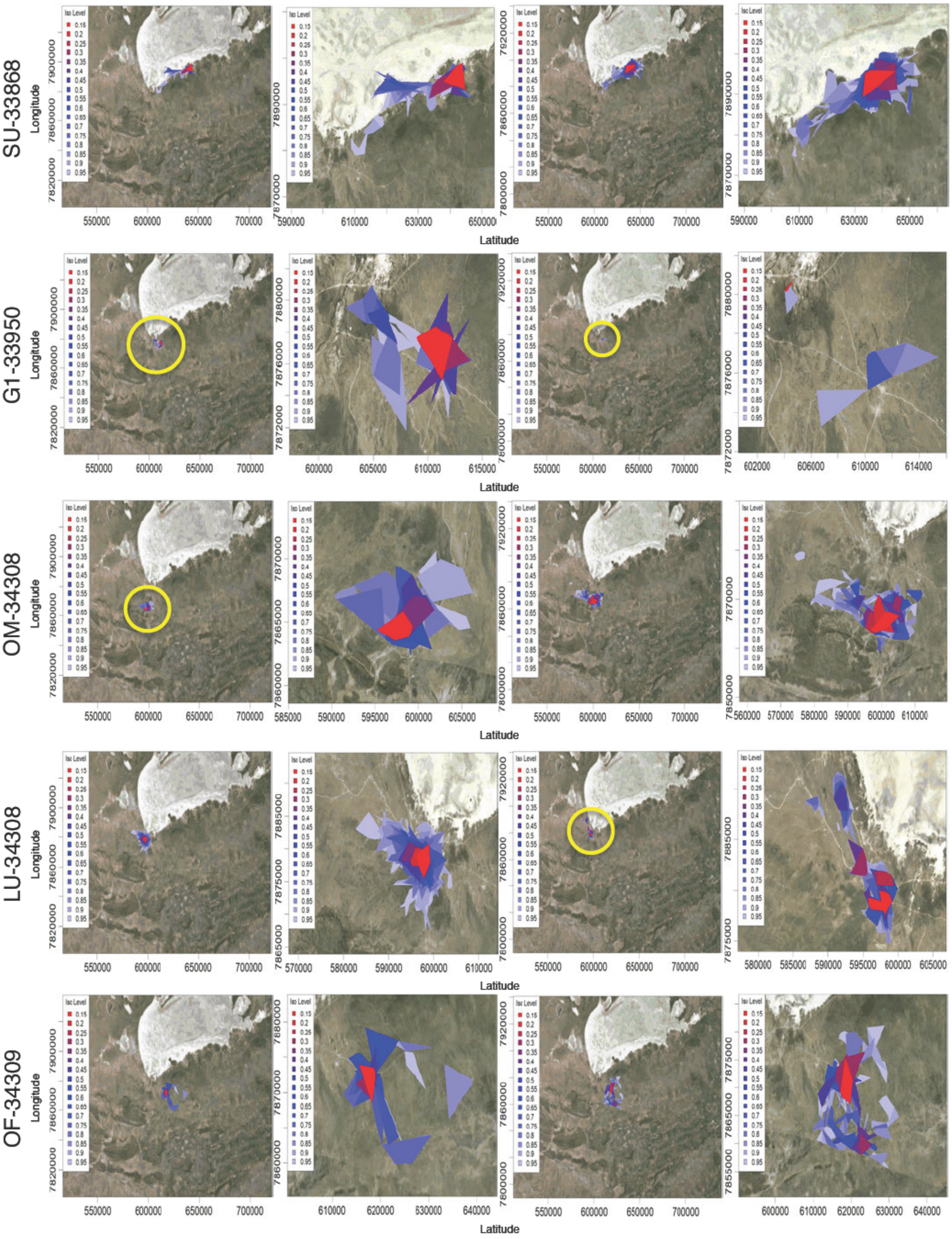


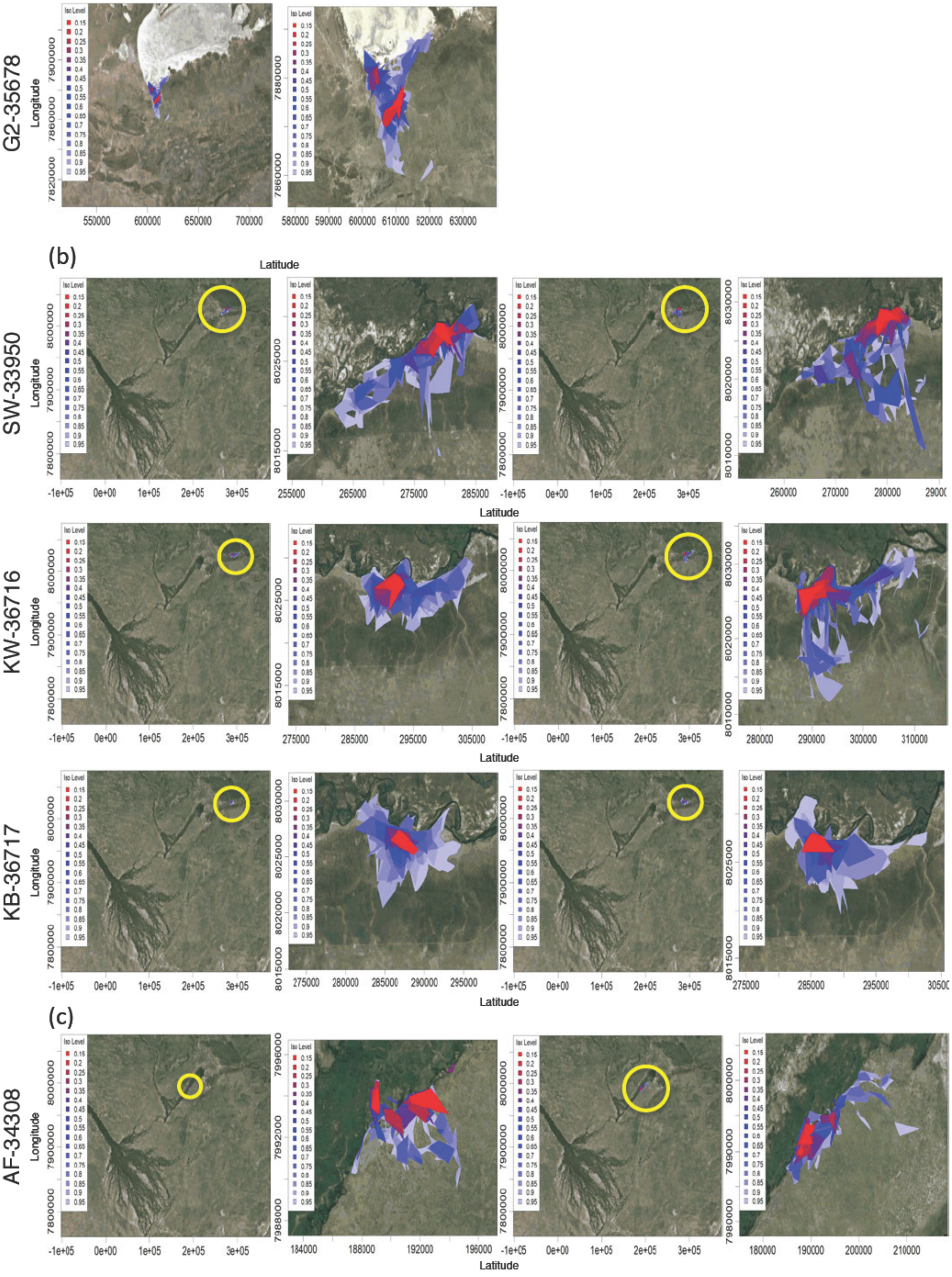
Appendix S2.5.2. Maps (left panels) depict the individual spotted hyena's relocations as four (top row), six (middle row), and eight (bottom row) clusters in the (a) Etosha National Park, Namibia; (b) Chobe National Park; and (c) Linyanti Conservancy, Botswana. Unique identifiers are depicted on top corner of each page. Relocations are colour-coded according to the clusters indicated by the range of revisitation (number of separate visits) and duration (mean number of locations per visit) values in RD space plots (shown in central panels). Clusters in the RD space were determined with the *k*-prototype algorithm and are based on ecogeographical variables attached to each relocation. The smaller plots (right panels) present the distribution and percent category of each cluster for each of the ecogeographical variables selected from the FAMD analysis.

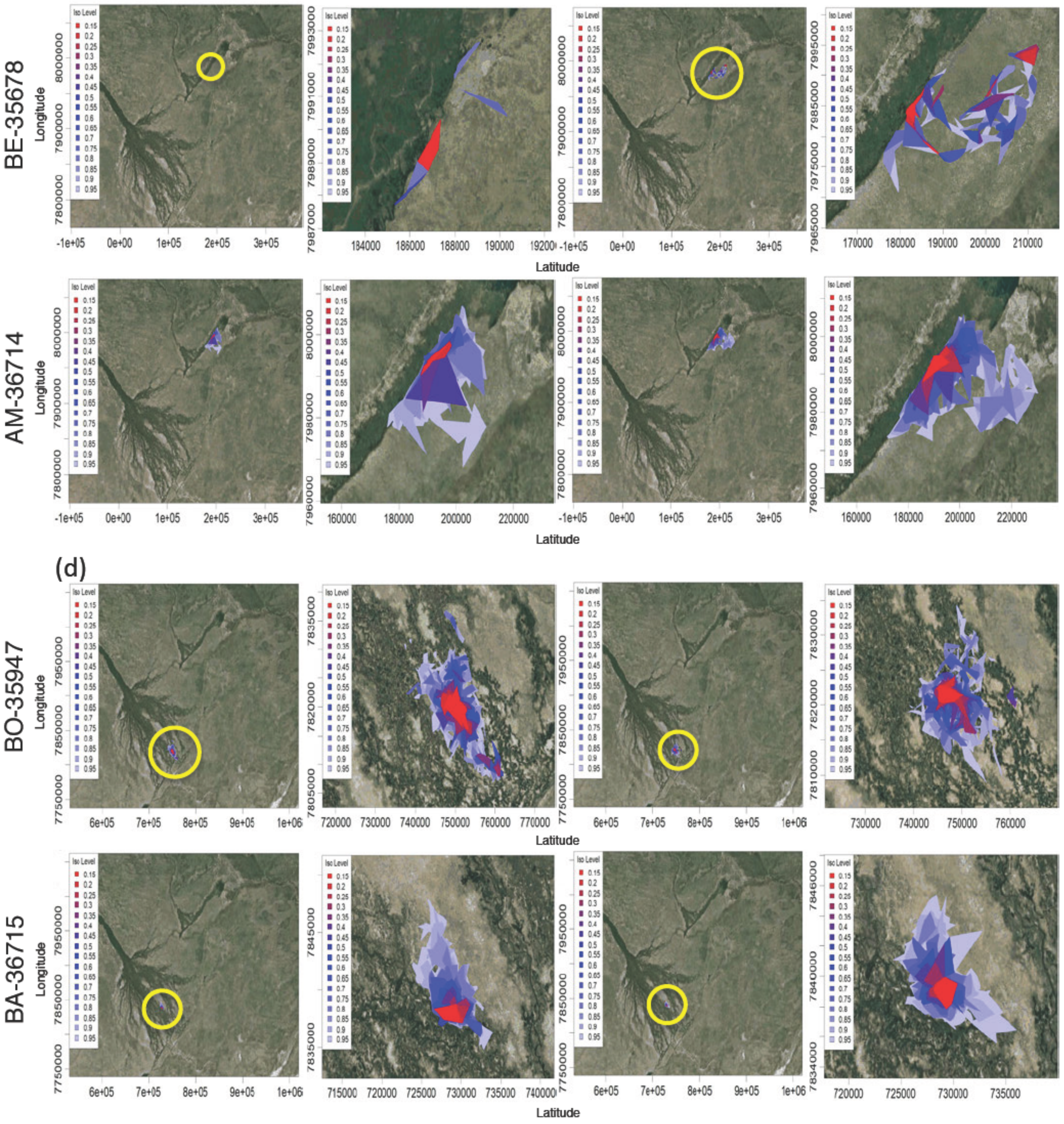
Supplementary materials to Barker et al., *Concurrent spatiotemporal ecology of African lions and Spotted hyenas and the potential for inter- and intraspecific interactions in semi-arid and wetland ecosystems*. Supplemental to Chapter 3.

(a)

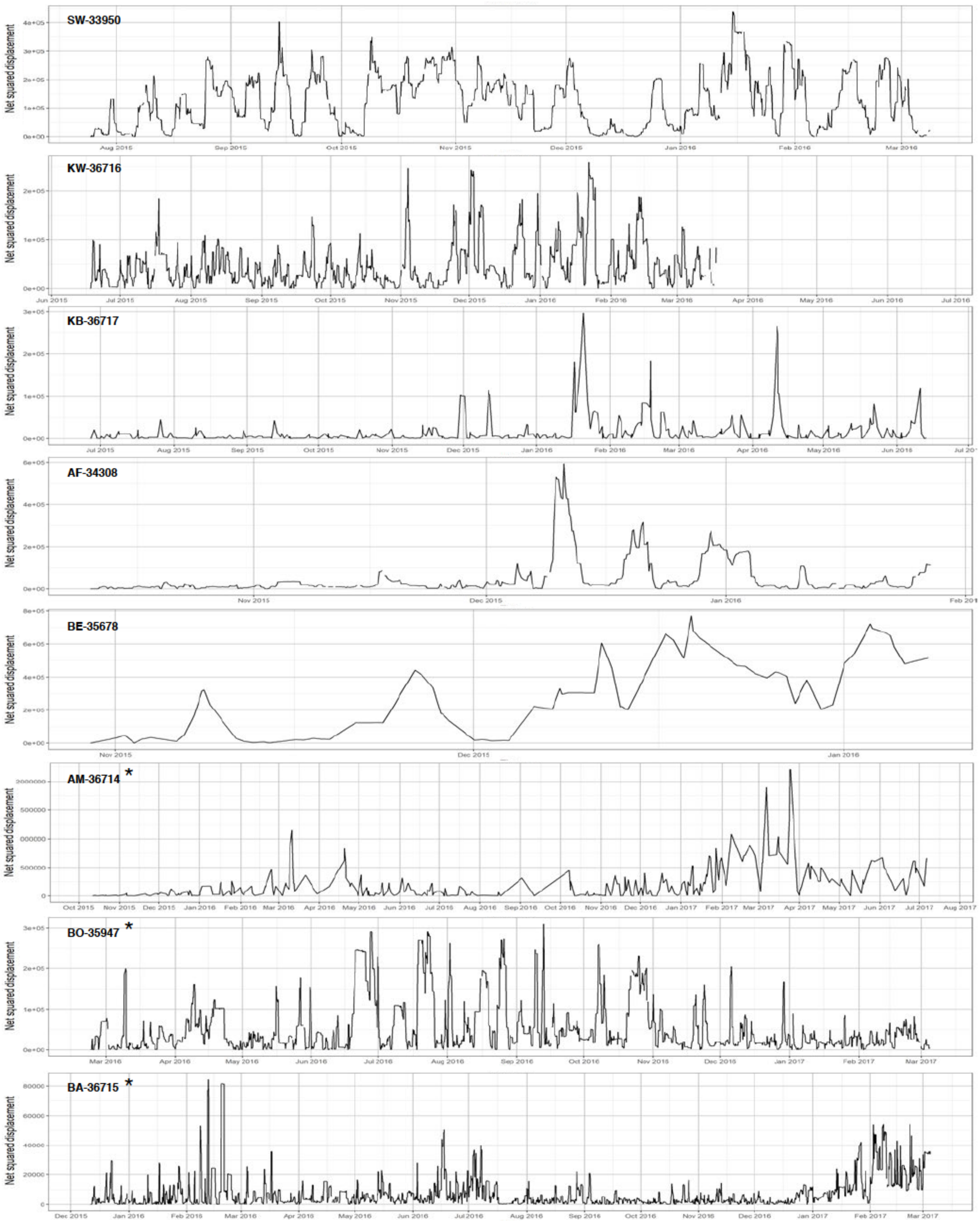



SU-33868
G1-33950
OM-34308
LU-34308
OF-34309
Longitude
Latitude
Iso Level
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
7820000
7860000
7900000
550000
600000
650000
700000
7870000
7890000
590000
610000
630000
650000
7800000
7920000
7872000
7876000
7880000
605000
615000
602000
606000
610000
614000
7860000
7865000
7870000
585000
595000
7850000
560000
570000
580000
7865000
7875000
7885000
620000
630000
640000
7855000

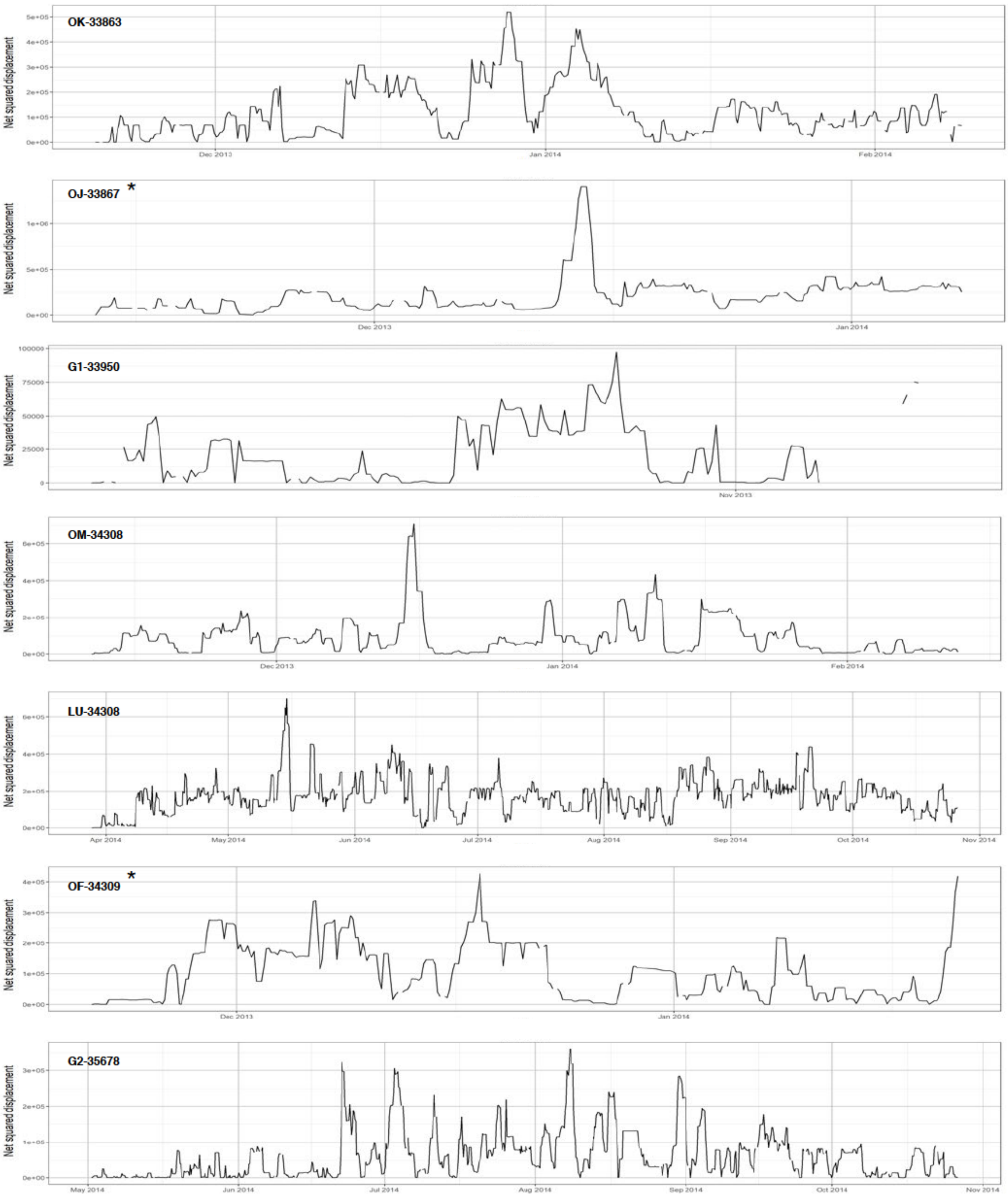
G2-35678
(b)
SW-33950
KW-36716
KB-36717
(c)
AF-34308
Longitude
Latitude
Iso Level
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
7820000
7860000
7900000
550000
600000
650000
700000
7860000
7880000
580000
590000
600000
610000
620000
630000
7800000
7900000
8000000
-1e+05
0e+00
1e+05
2e+05
3e+05
8015000
8025000
255000
265000
275000
285000
8010000
8020000
8030000
260000
270000
280000
290000
275000
285000
295000
305000
280000
290000
300000
310000
8020000
8030000
280000
295000
7988000
7992000
7996000
184000
188000
192000
196000
7980000
7990000
180000
190000
200000
210000



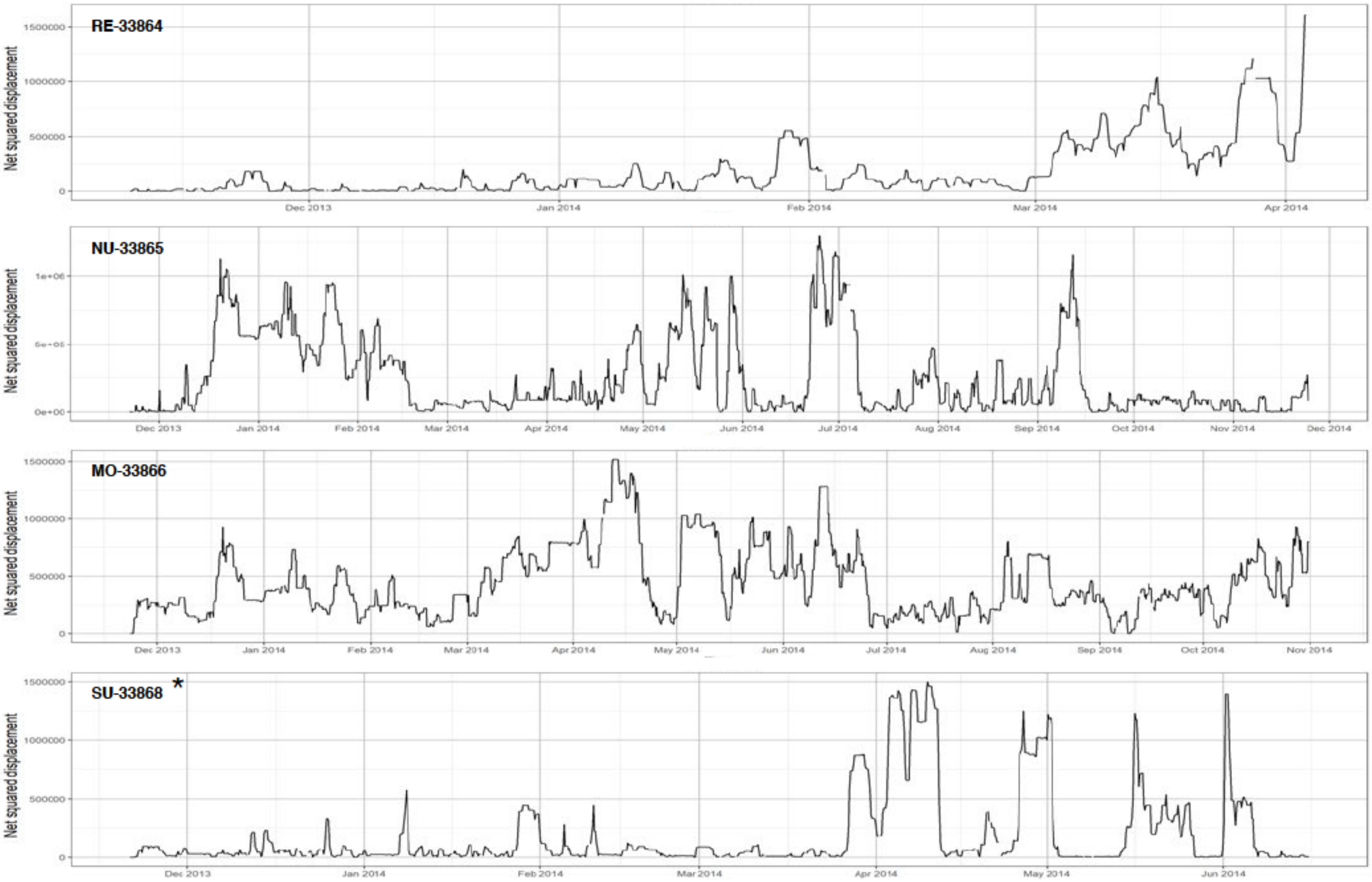
Appendix S3.1. Nocturnal space use of lion individuals from the (a) Etosha National Park, Namibia; (b) Chobe National Park; (c) Linyanti Conservancy; and (d) Okavango Delta, Botswana. Utilization distributions were constructed with the LoCoH α-method. Panels represent the 95% isopleth of the individual's home range for the dry season (left two panels) and wet season (right two panels). Far left and middle right panels indicate the individual's home range on a small scale satellite image of the (a) Etosha National Park with the salt pan to the north; (b, c, d) Botswana region with the Okavango Delta in the southwest and the Linyanti floodplains / Chobe river in the northeast. Yellow circles aid to pinpoint the individual's home range. Middle left and far right panels indicate close-ups of the individual's home range on a large scale satellite image of the reserve. Map source: Google Imagery, TerraMetrics.



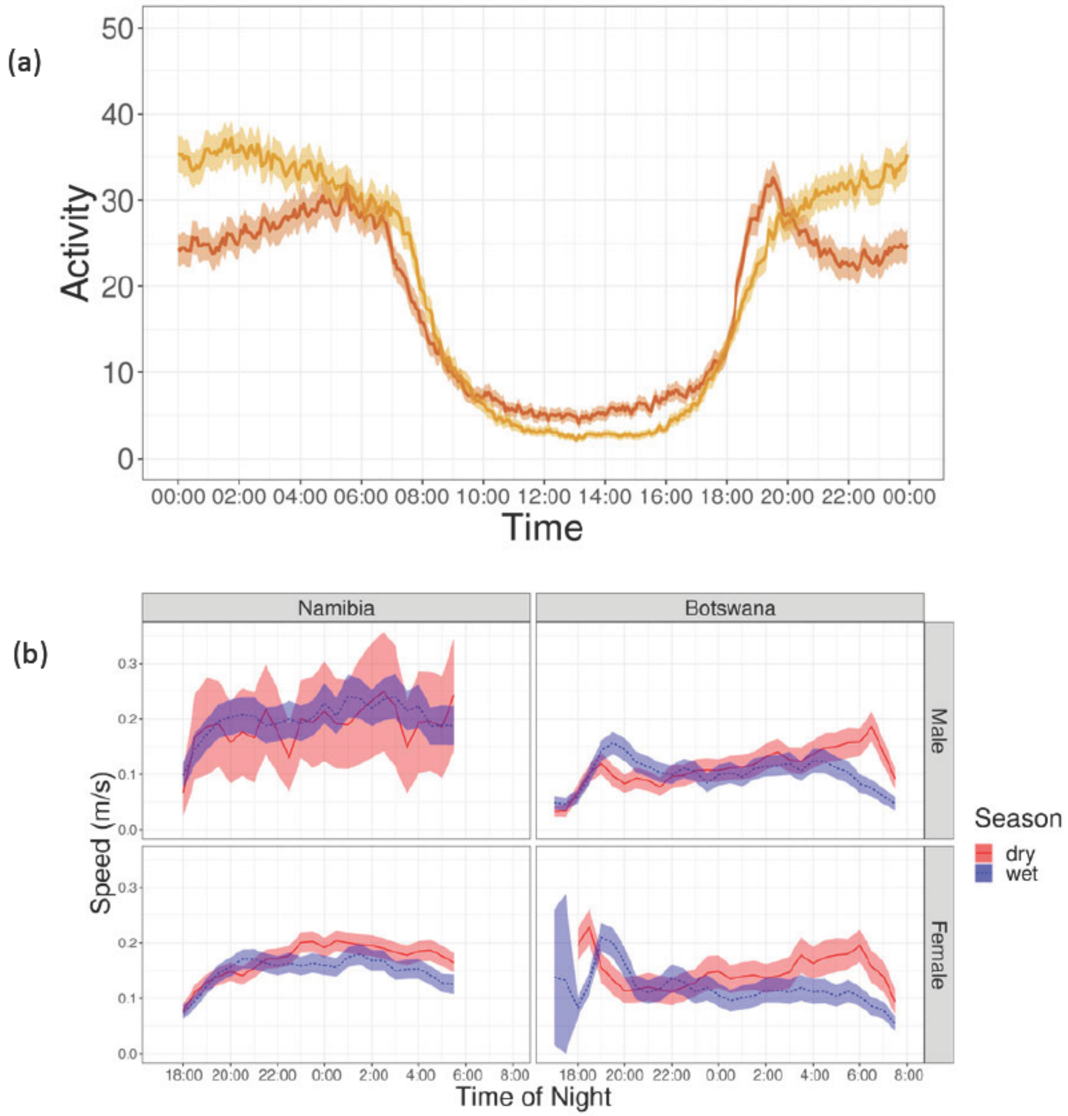
Appendix S3.2.1. Net-squared displacement of collared lion individuals from the Chobe National Park (top 3), Linyanti Conservancy (middle 3), and Okavango Delta (bottom 2), Botswana. Unique identifiers are listed on the top left of each panel, and males are denoted with an asterisk.



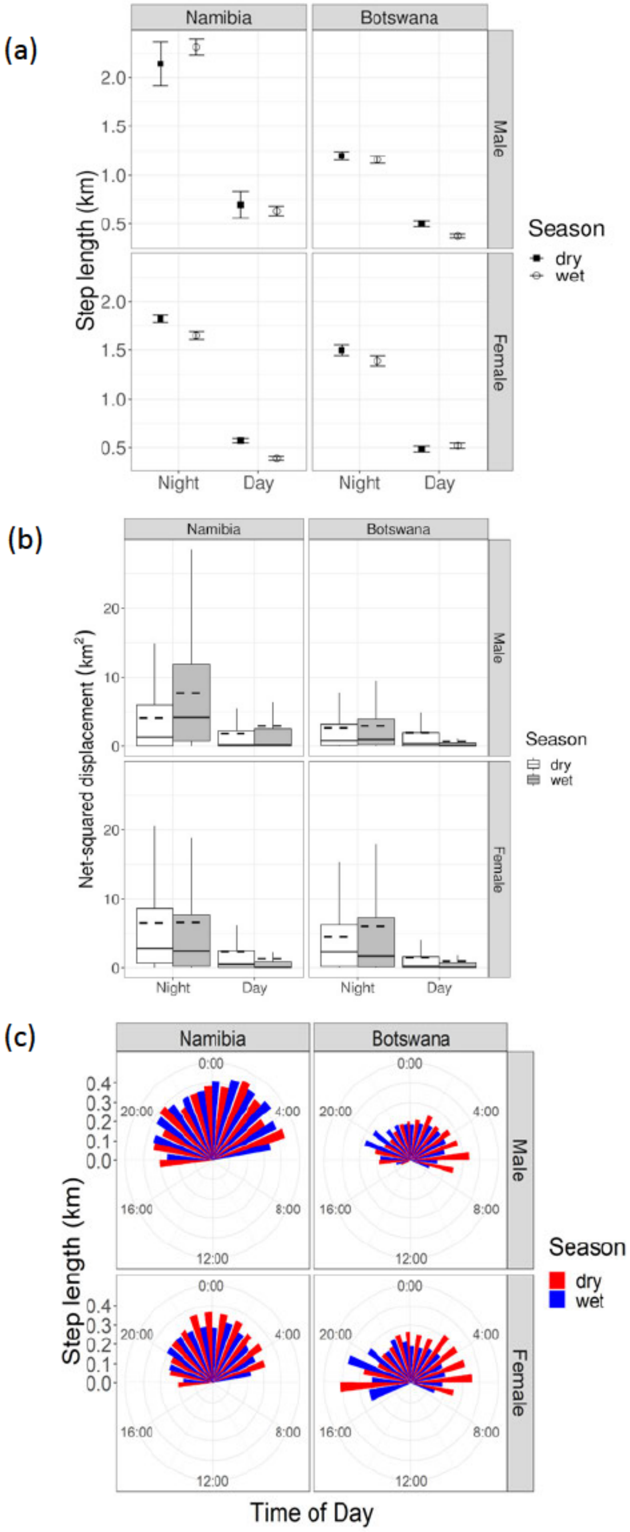
Appendix S3.2.2. Net-squared displacement of collared lion individuals from the Okaukeujo region of the Etosha National Park, Namibia. Unique identifiers are listed on the top left of each panel, and males are denoted with an asterisk.



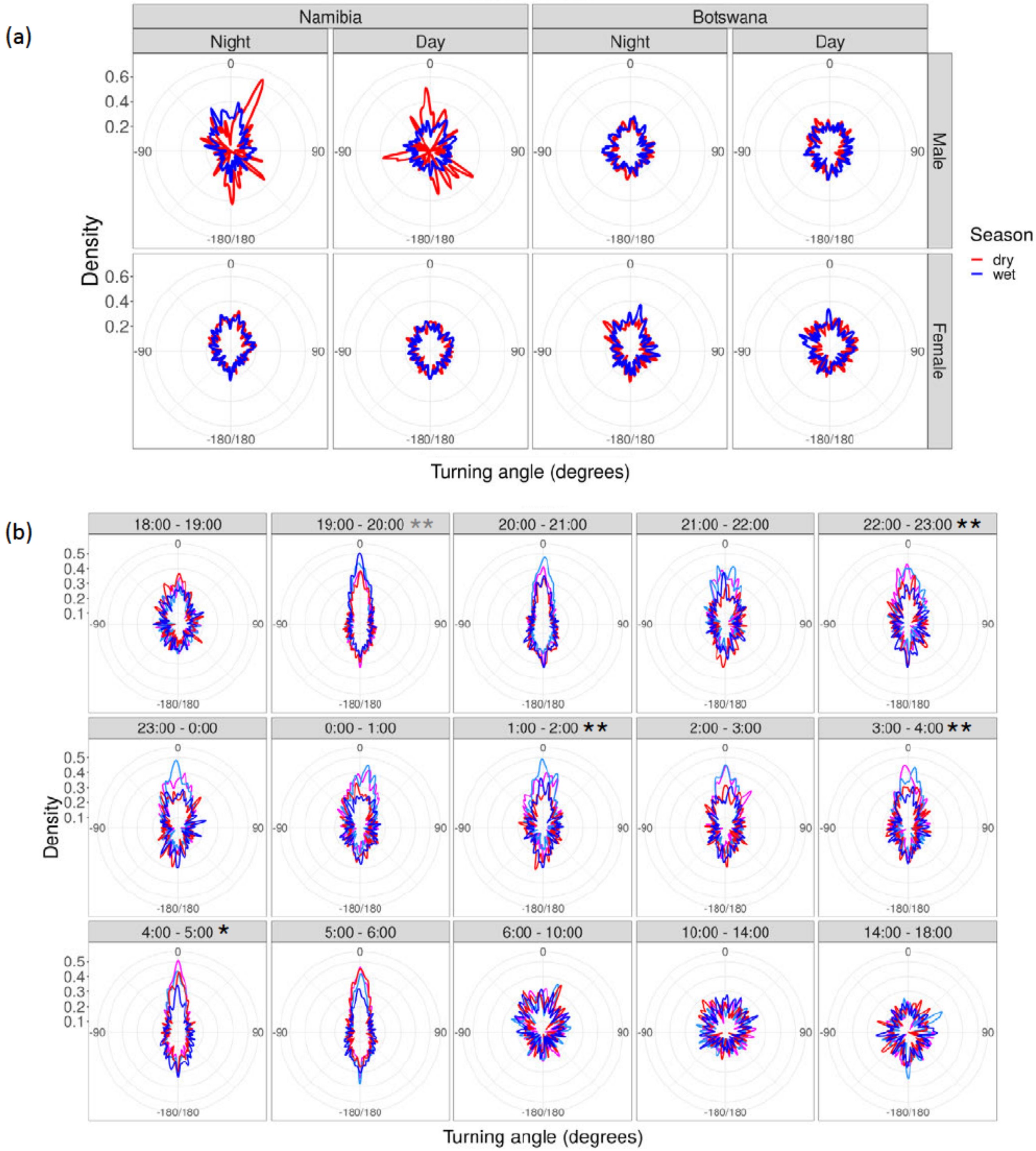
Appendix S3.2.3. Net-squared displacement of collared lion individuals from the Halali region of the Etosha National Park, Namibia. Unique identifiers are listed on the top left of each panel, and males are denoted with an asterisk.



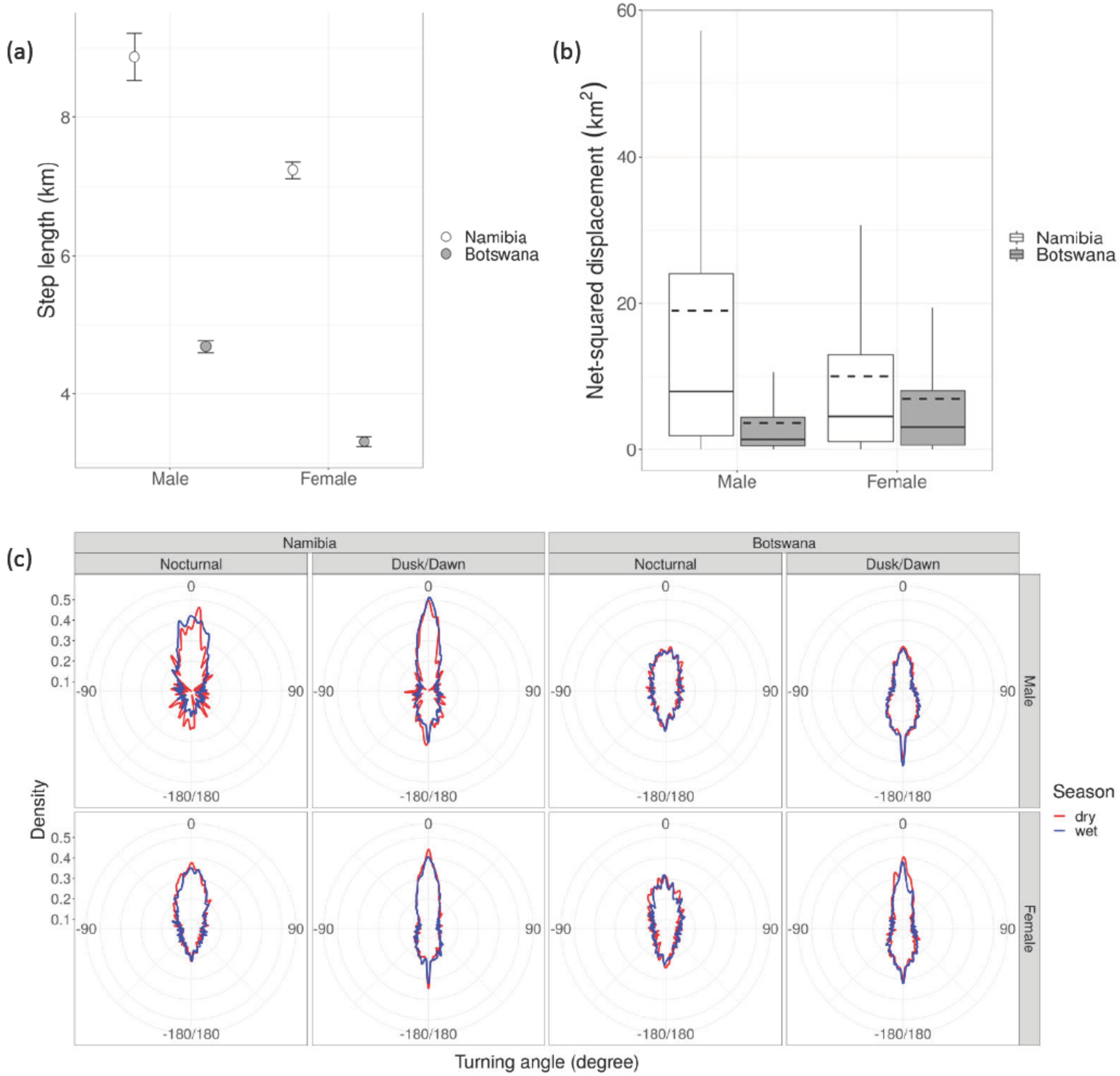
Appendix S3.2.4. (a) Mean activity of lions from the Etosha National Park, Namibia (gold colour), and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (orange colour) during the 24-hour cycle. Solid lines represent the mean and the shaded band the 95% confidence intervals for both figures. (b) Average speed (m/s) of male (upper panels) and female (lower panels) lions during nocturnal periods (sunrise - sunset) of the dry and wet seasons from the Etosha National Park, Namibia (left panels) and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (right panels).



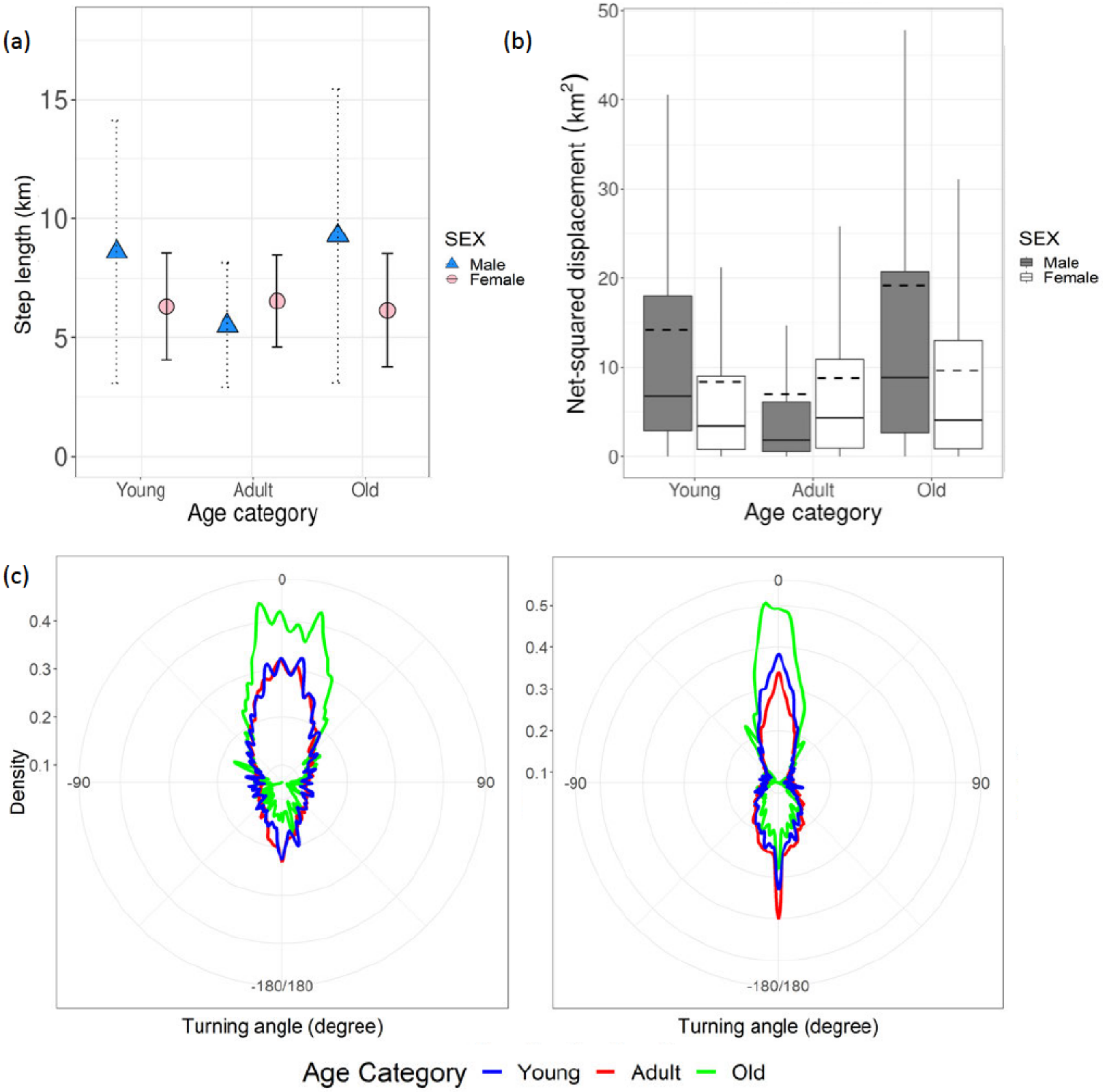
Appendix S3.2.5. Movement parameters of male (top row all figures) and female (bottom row all figures) lions from Namibia (left panels all figures) and Botswana (right panels all figures) during nocturnal (sunset – sunrise) and diurnal (sunrise – sunset) periods. (a) Lion step lengths. Points represent the mean and error bars the SE. (b) Lion mean net-squared displacements. Boxplots show medians, 25% and 75% quartiles. Dashed lines indicate means. Whiskers indicate the IQR range. (c) Seasonal step length of lions shown at different times of the nocturnal period. Bars represent the mean, and error bars were not included for easier visualization.



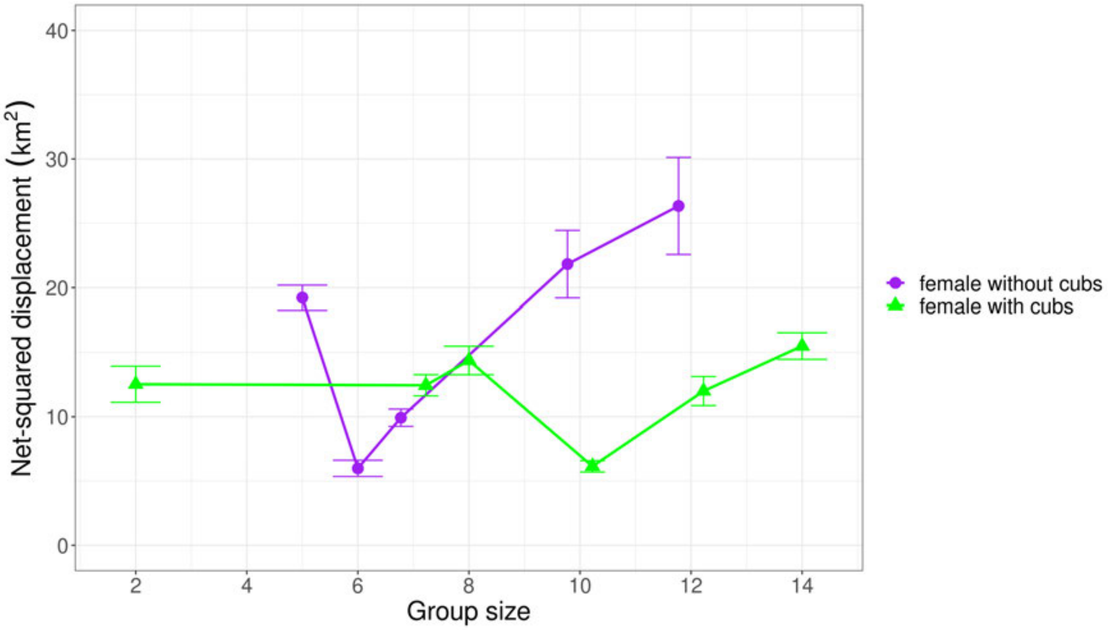
Appendix S3.2.6. Frequency density of seasonal turning angles of lions (a) from Etosha National Park, Namibia (left panels), and Chobe National Park, Linyanti Conservancy, and NG32 in Okavango Delta, Botswana (right panels); and (b) during each hour of the nocturnal period (18h00 – 6h00) and during 4-hour blocks of the diurnal period (6h00 – 18h00). Magenta lines = Namibia dry season, cyan lines = Namibia wet season, red lines = Botswana dry season, blue lines = Botswana wet season. A double asterisk indicates a significant difference in the Watson's Two-Sample Test of Homogeneity at $p < 0.05$, and a single asterisk approaches significance at $0.5 < p < 0.10$. Placement of the asterisk(s) at the panel's time label denotes the relatively more tortuous group for that time interval, with grey asterisk(s) for Namibia lions and black asterisk(s) for Botswana lions.



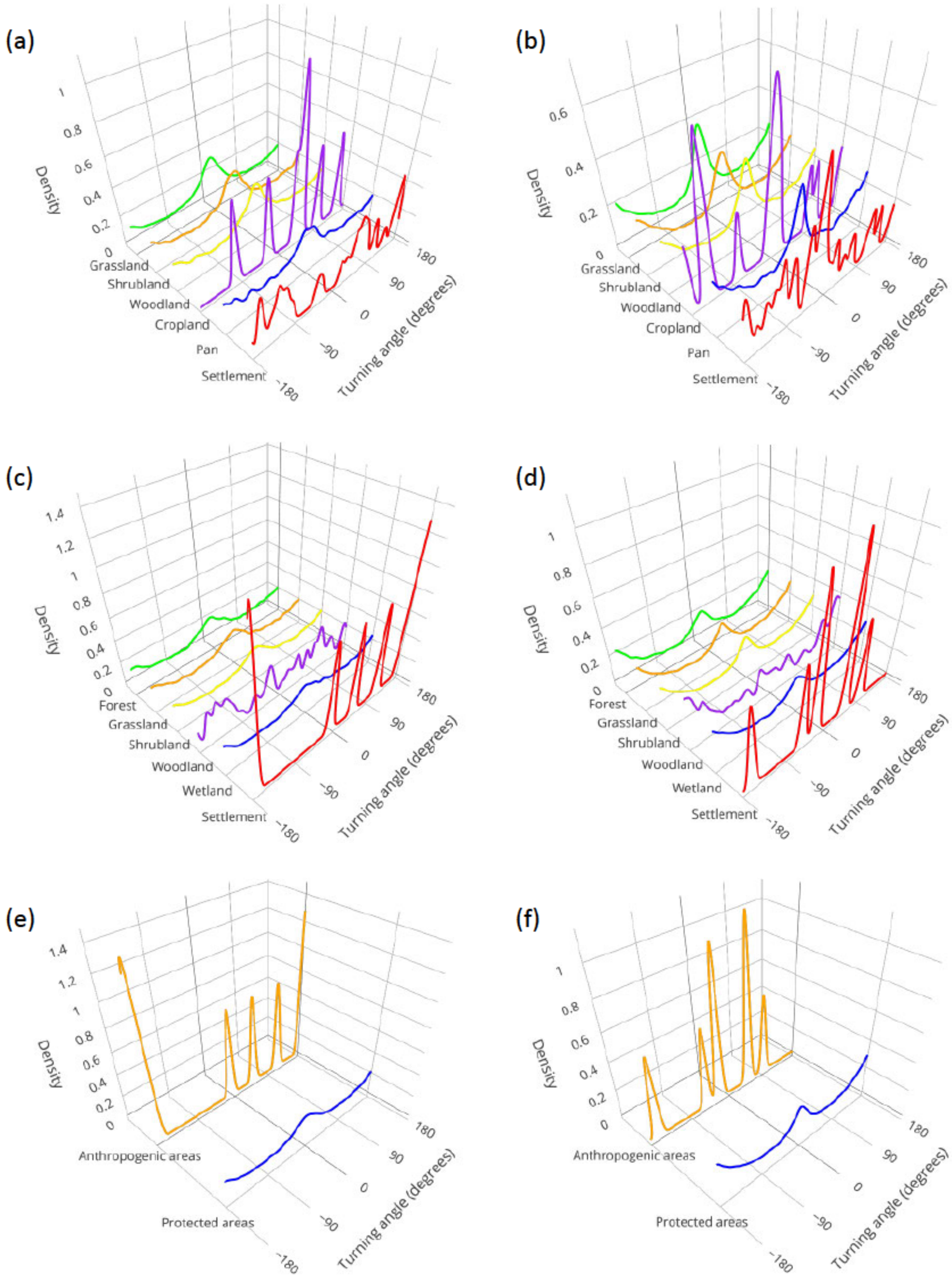
Appendix S3.2.7. Lion movement parameters of male and female lions from the Etosha National Park, Namibia and Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana. (a) Lion step lengths from Namibia (white circles) and Botswana (grey circles). Points represent the mean and error bars the SE. (b) Net-squared displacement of lions from Namibia (white boxes) and Botswana (grey boxes). Boxplots show medians, 25% and 75% quartiles. Dashed lines indicate means. Whiskers indicate the IQR range. (c) Frequency density of turning angles of lions from Namibia (left panels) and Botswana (right panels) during nocturnal (18h00-6h00 and 17h00-8h00) and dusk/dawn (19h00-21h00 and 4h00-6h00) periods. Red lines = dry season, and blue lines = wet season.



Appendix S3.2.8. Movement parameters of lions from the Etosha National Park, Namibia and Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana according to young (< 5yrs), adult (5-10yrs), and old (> 10yrs) age classes. (a) Step length of male (blue triangles) and female (pink circles) lions based on age classes. Points represent the mean and error bars the SE. (b) Mean net-squared displacement of male (grey boxes) and female (white boxes) lions based on age classes. Boxplots show medians, 25% and 75% quartiles. Dashed lines indicate means. Whiskers indicate the IQR range. (c) Frequency density of turning angles of lions from both ecosystems according to age classes, using 30 minute sampling intervals (left panel) and 5 minute sampling intervals (right panel).

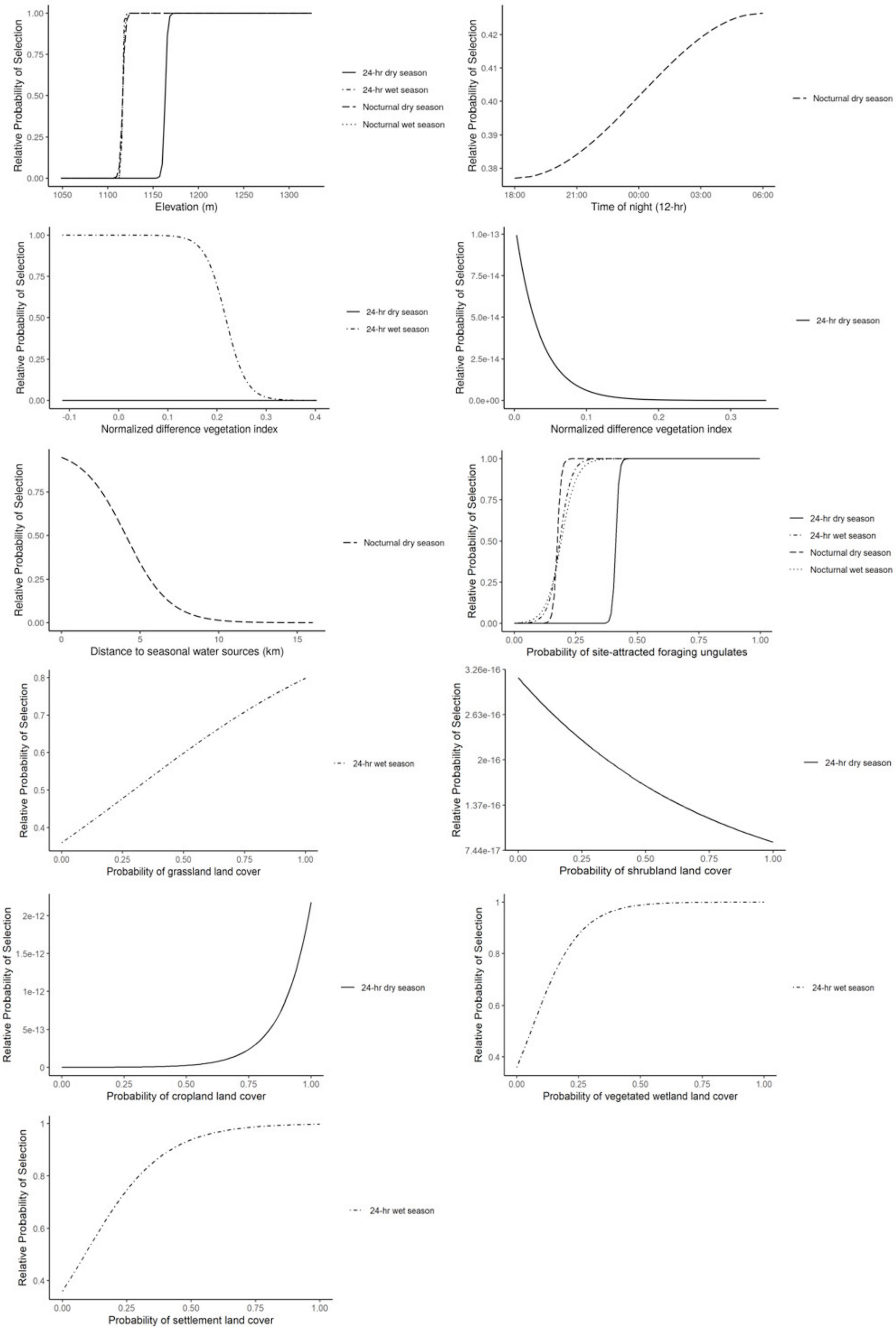


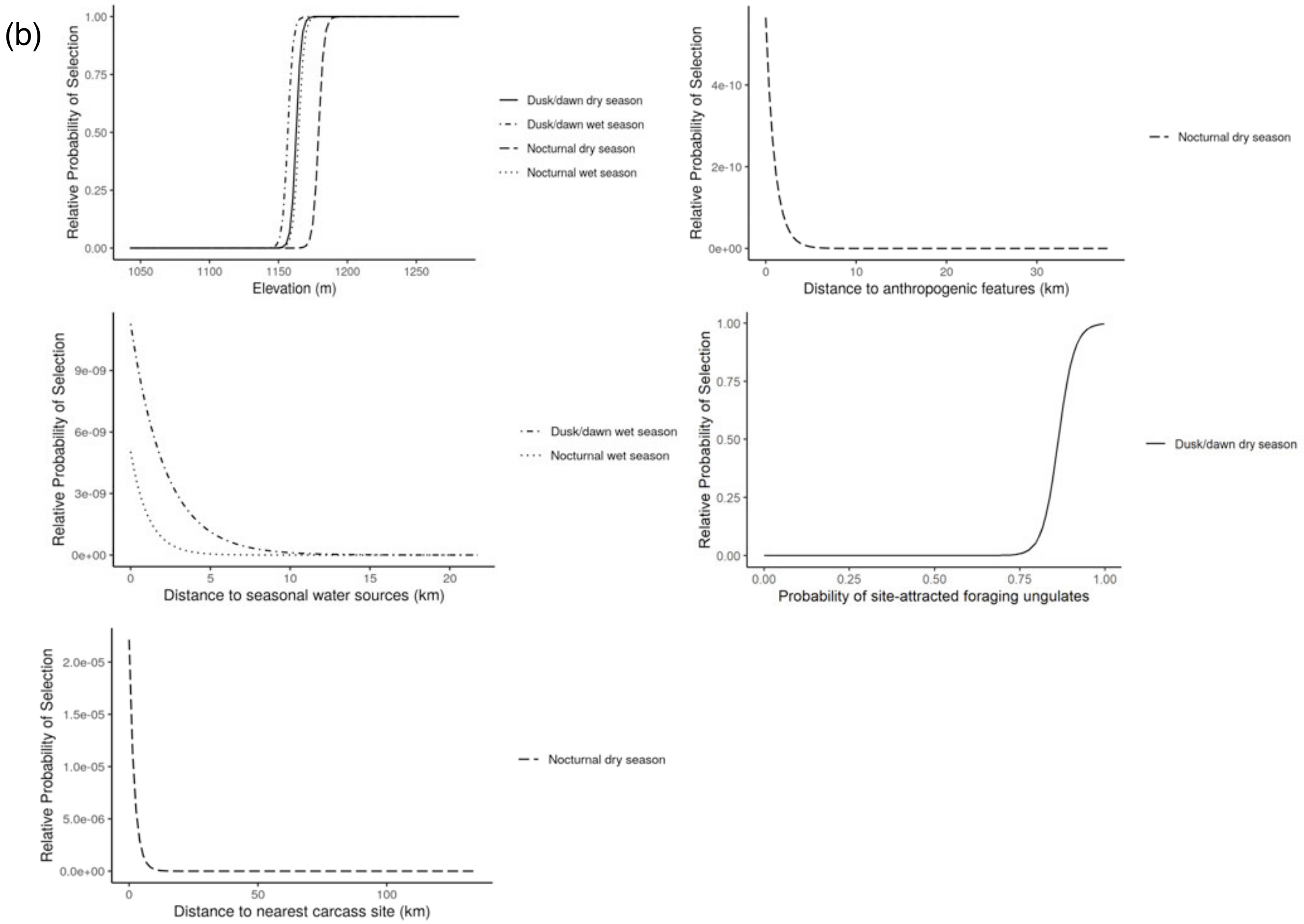
Appendix S3.2.9. Mean net-squared displacement of female lions (n = 13) from different pride sizes with (green lines, n =7) or without (purple lines, n = 6) cubs. Points represent the mean and error bars the SE.



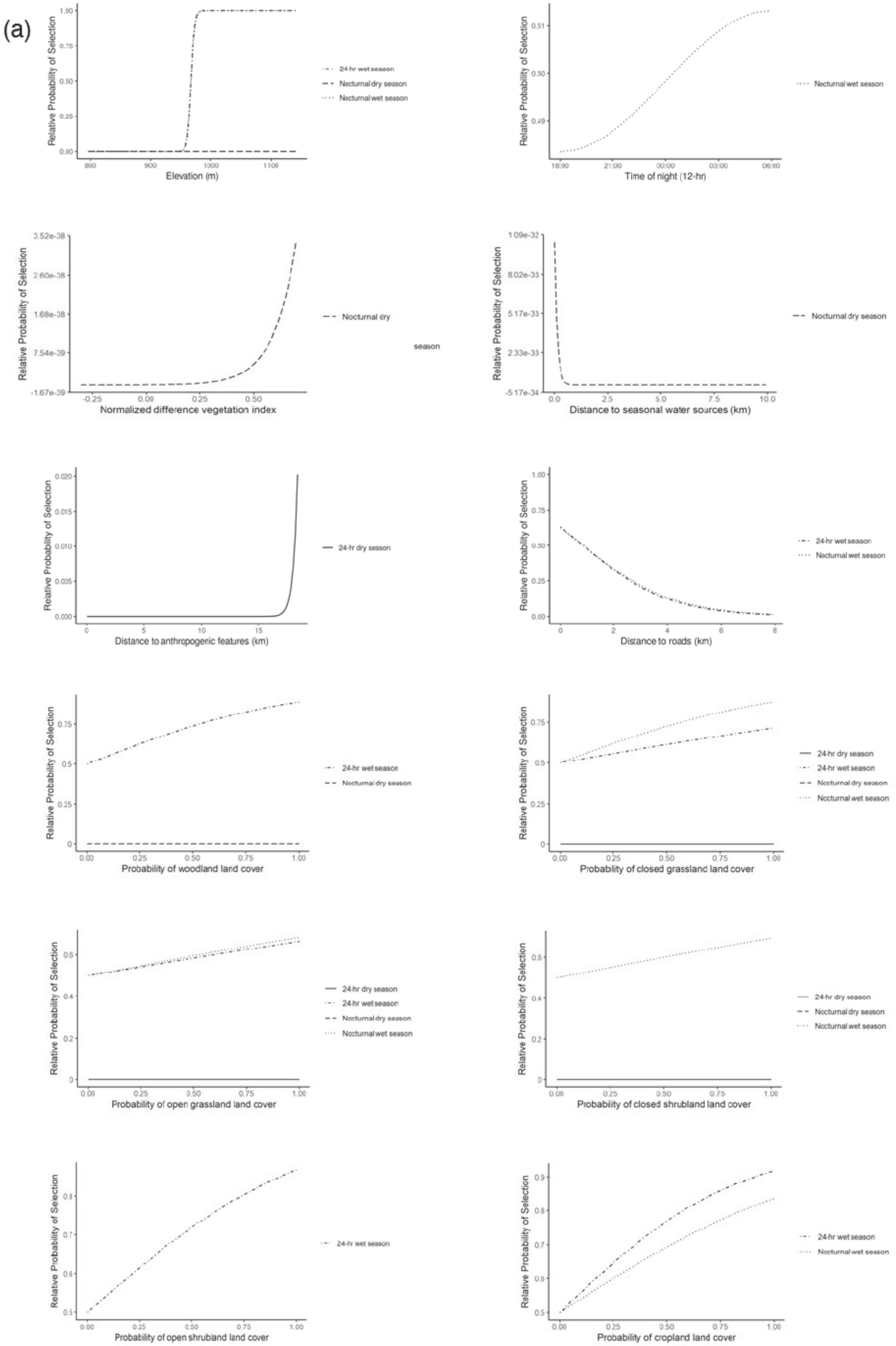
Appendix S3.2.10. Tortuosity of lions according to land cover categories during nocturnal (left side figures) and dusk/dawn (right side figures) periods. Lions from the Etosha National Park, Namibia (a & b), and the Chobe National Park, Linyanti Conservancy, and Okavango Delta, Botswana (c & d). Comparison of overall lion tortuosity between anthropogenic and protected areas (e & f).

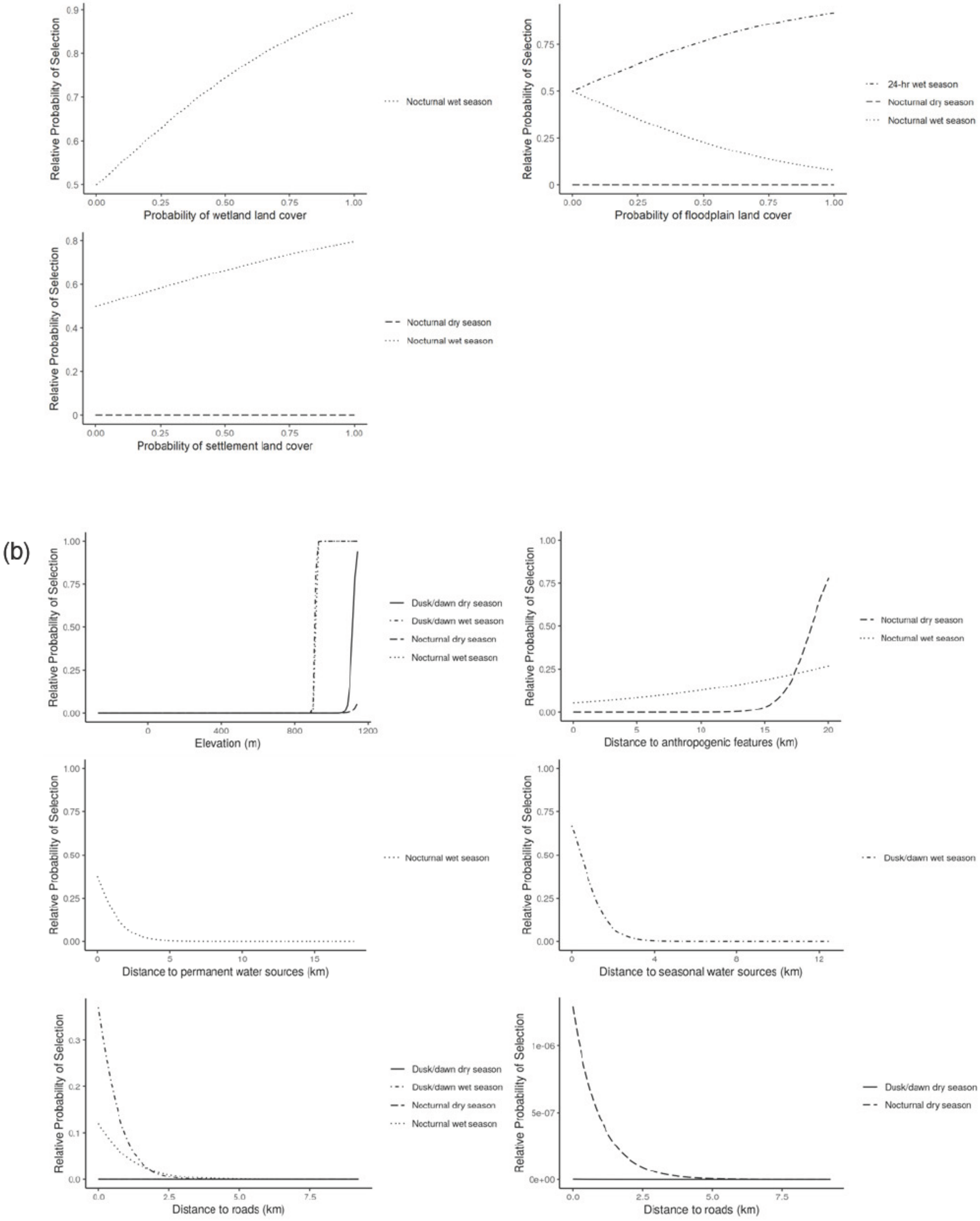
(a)


Relative Probability of Selection
Elevation (m)
1050
1100
1150
1200
1250
1300
0.00
0.25
0.50
0.75
1.00
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season
Time of night (12-hr)
18:00
21:00
00:00
03:00
06:00
0.38
0.39
0.40
0.41
0.42
Nocturnal dry season
Normalized difference vegetation index
-0.1
0.0
0.1
0.2
0.3
0.4
24-hr dry season
24-hr wet season
0.0e+00
2.5e-14
5.0e-14
7.5e-14
1.0e-13
24-hr dry season
Distance to seasonal water sources (km)
0
5
10
15
Nocturnal dry season
Probability of site-attracted foraging ungulates
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season
Probability of grassland land cover
0.4
0.5
0.6
0.7
0.8
24-hr wet season
Probability of shrubland land cover
7.44e-17
1.37e-16
2e-16
2.63e-16
3.26e-16
24-hr dry season
Probability of cropland land cover
0
5e-13
1e-12
1.5e-12
2e-12
24-hr dry season
Probability of vegetated wetland land cover
0.4
0.6
0.8
1
24-hr wet season
Probability of settlement land cover
24-hr wet season

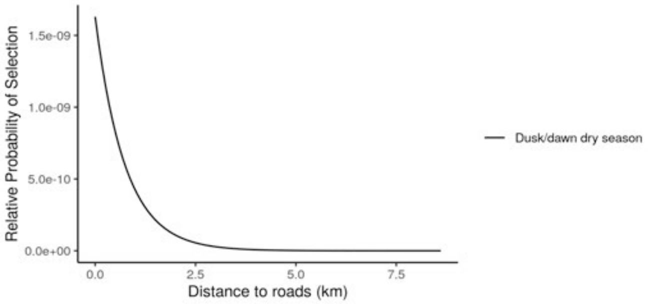


Appendix S3.3.1. Relative probability of selection indicated from RSF models (a) during 24-hour (18h00-18h00) and nocturnal (18h00-6h00) periods; and indicated from SSF models (b) during nocturnal (18h00-6h00) and dusk/dawn (19h00-21h00 / 4h00-6h00) periods by lions in the Etosha National Park, Namibia.

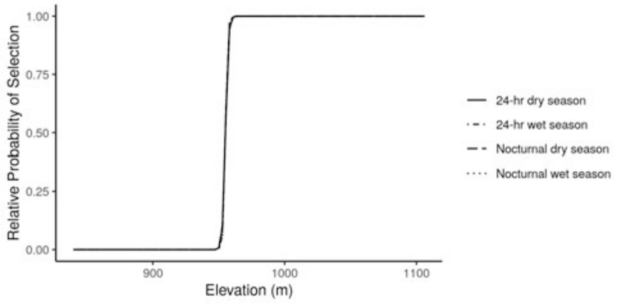

(a)
Relative Probability of Selection
Elevation (m)
24-hr wet season
Nocturnal dry season
Nocturnal wet season
Time of night (12-hr)
Nocturnal wet season
Normalized difference vegetation index
Nocturnal dry season
Distance to seasonal water sources (km)
Nocturnal dry season
Distance to anthropogenic features (km)
24-hr dry season
Distance to roads (km)
24-hr wet season
Nocturnal wet season
Probability of woodland land cover
24-hr wet season
Nocturnal dry season
Probability of closed grassland land cover
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season
Probability of open grassland land cover
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season
Probability of closed shrubland land cover
24-hr dry season
Nocturnal dry season
Nocturnal wet season
Probability of open shrubland land cover
24-hr wet season
Probability of cropland land cover
24-hr wet season
Nocturnal wet season

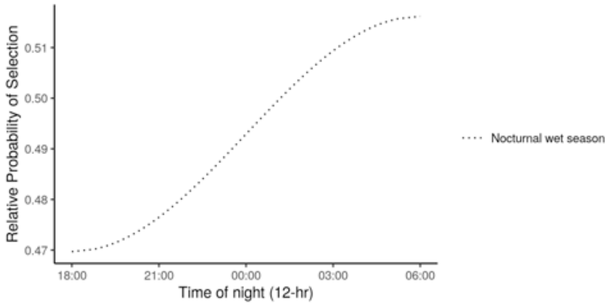


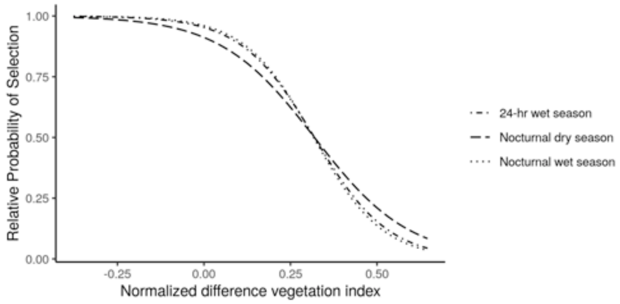
Relative Probability of Selection
Probability of wetland land cover
Nocturnal wet season
Probability of floodplain land cover
24-hr wet season
Nocturnal dry season
Nocturnal wet season
Probability of settlement land cover
Nocturnal dry season
Nocturnal wet season
(b)
Elevation (m)
Dusk/dawn dry season
Dusk/dawn wet season
Nocturnal dry season
Nocturnal wet season
Distance to anthropogenic features (km)
Nocturnal dry season
Nocturnal wet season
Distance to permanent water sources (km)
Nocturnal wet season
Distance to seasonal water sources (km)
Dusk/dawn wet season
Distance to roads (km)
Dusk/dawn dry season
Dusk/dawn wet season
Nocturnal dry season
Nocturnal wet season
Distance to roads (km)
Dusk/dawn dry season
Nocturnal dry season

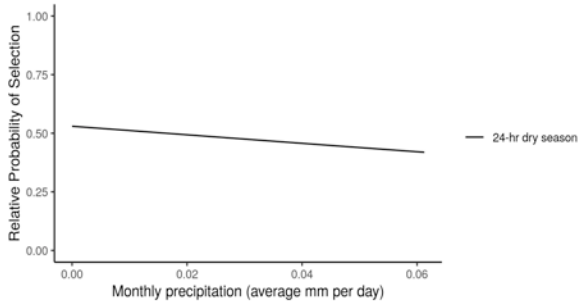


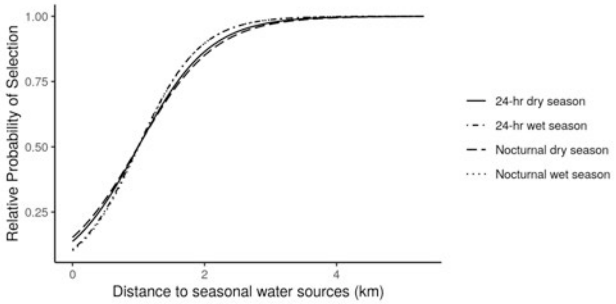
Appendix S3.3.2. Relative probability of selection indicated from RSF models (a) during 24-hour (18h00-18h00) and nocturnal (18h00-6h00 and 17h00-8h00) periods, and indicated from SSF models (b) during nocturnal (18h00-6h00 and 17h00-8h00) and dusk/dawn (19h00-21h00 / 4h00-6h00) periods by lions in the Chobe National Park and Linyanti Conservancy, Botswana.

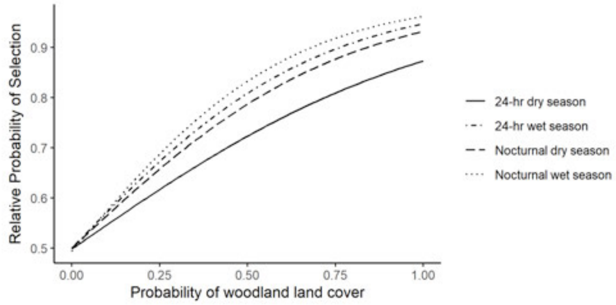

Relative Probability of Selection
1.00
0.75
0.50
0.25
0.00
900
1000
1100
Elevation (m)
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season

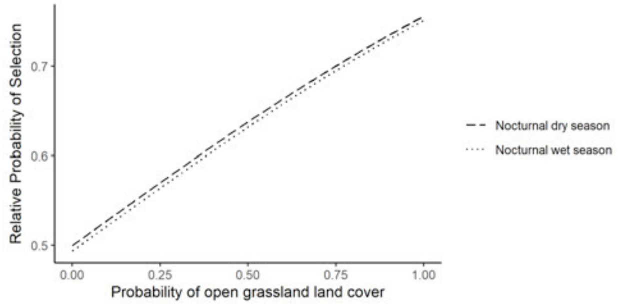

Relative Probability of Selection
0.51
0.50
0.49
0.48
0.47
18:00
21:00
00:00
03:00
06:00
Time of night (12-hr)
Nocturnal wet season

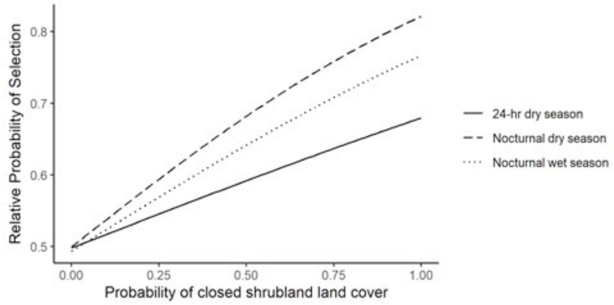

Relative Probability of Selection
1.00
0.75
0.50
0.25
0.00
-0.25
0.00
0.25
0.50
Normalized difference vegetation index
24-hr wet season
Nocturnal dry season
Nocturnal wet season

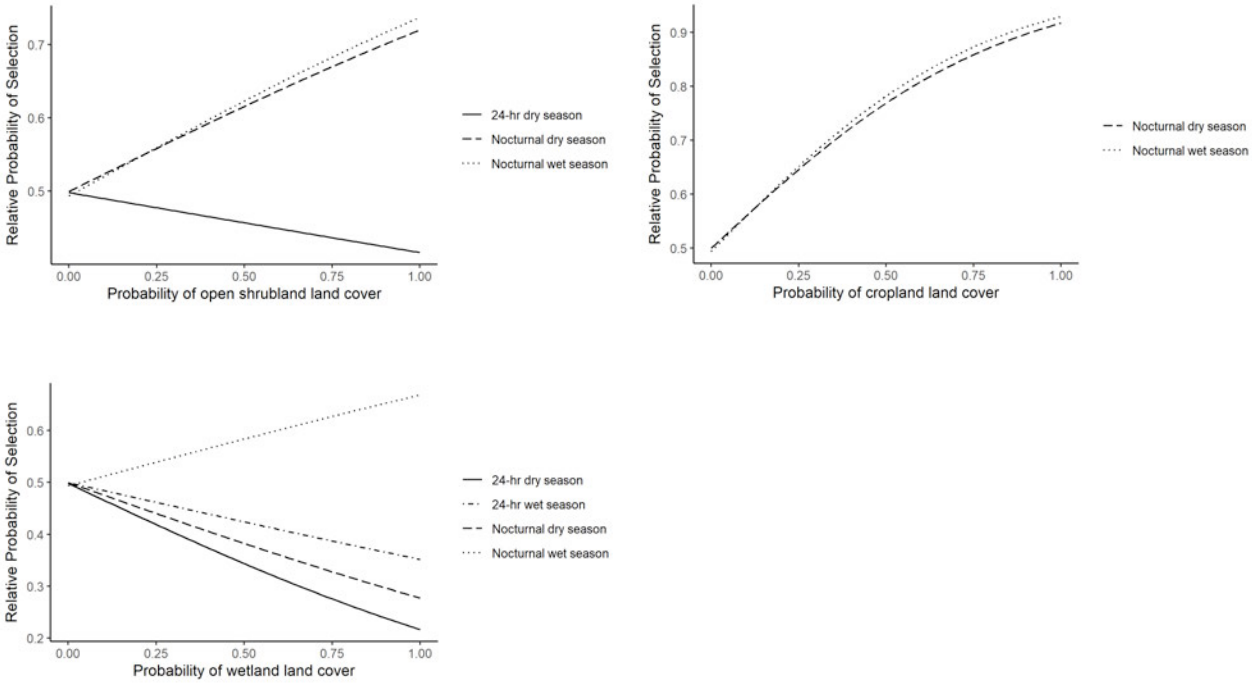

Relative Probability of Selection
1.00
0.75
0.50
0.25
0.00
0.00
0.02
0.04
0.06
Monthly precipitation (average mm per day)
24-hr dry season


Relative Probability of Selection
1.00
0.75
0.50
0.25
0
2
4
Distance to seasonal water sources (km)
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season


Relative Probability of Selection
0.9
0.8
0.7
0.6
0.5
0.00
0.25
0.50
0.75
1.00
Probability of woodland land cover
24-hr dry season
24-hr wet season
Nocturnal dry season
Nocturnal wet season


Relative Probability of Selection
0.7
0.6
0.5
0.00
0.25
0.50
0.75
1.00
Probability of open grassland land cover
Nocturnal dry season
Nocturnal wet season


Relative Probability of Selection
0.8
0.7
0.6
0.5
0.00
0.25
0.50
0.75
1.00
Probability of closed shrubland land cover
24-hr dry season
Nocturnal dry season
Nocturnal wet season



Appendix S3.3.3. Relative probability of selection indicated from RSF models during 24-hour (18h00-18h00) and nocturnal (17h00-8h00) periods by lions in the NG32 concession of the Okavango Delta, Botswana.