

# Social interactions and spatiotemporal movements of cheetah (*Acinonyx jubatus*) in Selati Game Reserve



Photo: SWF (2023)

A thesis submitted to Cardiff University in accordance with the requirements for the completion of the Global Ecology and Conservation MSc

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September 2024

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#### 1. Abstract

Cheetahs (Acinonyx jubatus) are cryptic, felid predators known for their high-speed chase hunting technique. Cheetah populations are declining but there is an important metapopulation located in South Africa. The majority of this South African metapopulation is within fenced game reserves alongside other predator species. Cheetahs are considered meso-predators and exhibit avoidance behaviours towards dominant predators such as lions (Panthera leo). There are two main types of avoidance behaviours: proactive and reactive - each have their own costs but reactive is considered more costly. Therefore, understanding inter and intraspecific avoidance and movement behaviours is key for cheetah conservation. This study aimed to analyse the GPS data of 5 cheetahs and 8 lions on a small game reserve over a two-year period to infer inter- and intra-specific movement behaviours and whether movement behaviours differed between cheetah social structures. Spatial analysis was completed in RStudio and involved estimations of home and core ranges, static and dynamic interactions analyses, identification of potential contact points between individuals, movement behaviours relating to individuals, and movement behaviours after potential contact points. The results showed that cheetahs expressed both inter- and intra-specific avoidance behaviours, but the type and degree of avoidance varied based on cheetah social structure and breeding status. Male cheetahs demonstrated weaker avoidance behaviours towards lions and conspecifics than female cheetahs demonstrated, with one male showing attraction to a female. Female cheetah avoidance behaviours differed by breeding status. The less experienced mother exhibited the strongest avoidance behaviours, demonstrating both proactive and reactive responses to lions and other cheetahs. The more experienced mother also displayed avoidance behaviours but were reduced compared to the less experienced mother. The non-breeding cheetah female displayed the weakest avoidance behaviours and exhibited mostly reactive responses. These differences were inferred to be linked to energy expenditure and the risk associated with differing social structures, with mothers displaying less risky strategies than non-breeding females and males. Generally, cheetahs appeared to avoid conspecifics more strongly than lions via proactive avoidance behaviours, potentially due to their scent-marking behaviours facilitating olfactory communication of spatial and temporal information. Despite cheetah density being high and home range sizes being small on the game reserve, results do not suggest that this has resulted in abnormal inter- or intra-specific conflict. This is positive news for small game reserves and cheetah conservation.

- 2. Abbreviations
- **SWF** Selati Wilderness Foundation
- IUCN International Union for the Conservation of Nature
- **GPS** Global Positioning System
- VHF Very High Frequency
- **EWT** Endangered Wildlife Trust
- LoRa Long Range
- MCP Minimum Convex Polygon
- KUD Kernel Utilisation Density
- **CRS** Coordinate Reference System
- **GLMM** Generalised Linear Mixed Model
- **CV** Likelihood Cross-validation
- **LSCV** Least-squares Cross-validation
- aKDE Autocorrelated Kernel Density Estimator

#### 3. Introduction

#### 3.1. Predator Conservation

Top-down pressures from carnivores are most commonly recognised as the influence carnivores exert on prey populations (Soule 2014). However, competition and interactions amongst predators can significantly impact prey species but also the population dynamics and distributions of subordinate- or meso-predator species (Palomares and Caro 1999; Caro and Stoner 2003; Ripple et al. 2014; Swanson et al. 2016). These pressures can lead to broader and cascading effects on the surrounding ecosystem (Davis et al. 2011; Pasanen-Mortensen et al. 2013; Swanson et al. 2016) by affecting prey population dynamics and movement (Linnell and Strand 2000; Soule 2014) of meso-predator species, as well as influencing nutrient dynamics through processes such as carcass provisioning (Schmitz et al. 2010) or herbivore control (Soule 2014). These influences support the suggestion that top carnivores act as keystone species (Palomares and Caro 1999; Hayward and Slotow 2009), a topic that is becoming increasingly relevant as several predator species are declining across the globe (Ripple et al. 2014; Swanson et al. 2016)(e.g. Tigers (*Panthera tigris*) in Asia (Harihar et al. 2020); Lions (*Panthera leo*) in Africa (Bauer et al. 2022); Fosa (*Cryptoprocta ferox*) in Madagascar (Gerber et al. 2012); Snowy Owl (*Bubo scandiacus*) in the Arctic (Gousy-Leblanc et al. 2023)).

One of the biggest threats that large predators face is from human persecution. This was particularly true in South Africa during the mid-20<sup>th</sup> Century where large predators were actively shot and displaced to protect livestock and game animals (Marker et al. 2018). Now, almost all conservation areas that contain dangerous animals (large predators and megaherbivores) in South Africa are enclosed by predator-proof fences (Hayward et al. 2009). The vast majority of cheetahs (*Acinonyx jubatus*) in southern Africa occur across a transboundary strip encompassing Angola, Botswana, Namibia, Mozambique, and South Africa (Durant et al. 2017; Weise et al. 2017). In South Africa, the cheetah population is split into three units: free-roaming, unmanaged subpopulations, a managed metapopulation consisting of cheetahs within fenced reserves, and population, this allows for large-scale management providing a framework for conservation initiatives to maintain connectivity and long-term action (Magliolo et al. 2023). The majority of the cheetah population is soft high importance for cheetah conservation in South Africa.

#### 3.2. Cheetah Conservation

Cheetahs are classed as Vulnerable by the International Union for the Conservation of Nature (IUCN 2023) and currently occupy only 9% of their historical range which is also severely fragmented (Durant et al. 2017; Weise et al. 2017). Cheetahs face several threat from humans such as persecution, land management change, and agriculture expansion (Durant et al. 2017; Weise et al. 2017; IUCN 2023), but also face major threats from the natural world as a meso-predator. Cheetahs are considered subordinate predators to lions (*Panthera leo*) facing direct competition via killings of both adults and cubs, as well as indirect competition via killings of both adults and cubs, as well as indirect competition via killings of both adults and cubs, as well as indirect competition via killings of both adults and cubs, as well as indirect competition via killings of both adults and cubs, as well as indirect competition via killings of both adults and cubs, as well as indirect competition via killings of both adults and cubs, as well as indirect competition via kileptoparasitism (the behaviour of food theft by an individual from a separate individual that acquired the food (Hamilton 2002; Scantlebury et al. 2014)). This dynamic is attributed to the cheetah's smaller size and more solitary nature compared to the more socially-cohesive lions (Broekhuis et al. 2013; Swanson et al. 2016; Cornhill et al. 2022). As such, they are a prime example of the top-down pressures larger carnivores can have on meso-carnivores.

#### 3.3. Cheetah Ecology

Cheetahs are diurnal (Owen-Smith and Mills 2008), cryptic (Weise et al. 2017) felids known for their stalk and ambush hunting techniques (Durant 1998). They are able to reach speeds of ~100km per hour when hunting (Mills et al. 2004; Wilson et al. 2013) and are found in a variety of habitats, but show a preference for mostly woodland savannas and open plains (Broomhall et al. 2003; Weise et al. 2017). Their diet consists largely of medium-sized prey displaying preferences for Thomson's Gazelle (Eudorcas thomsonii) and Impala (Aepyceros melampus)(Durant 1998; Owen-Smith and Mills 2008; Wilson et al. 2013), however this varies depending on location, prey species abundance, and the individual's demographic parameters (i.e. sex, age, breeding status)(Mills et al. 2004). They occur at low densities (Durant 1998; Linnell and Strand 2000; Weise et al. 2017) with estimates of 0.48 cheetahs per 100km<sup>2</sup> in southern Africa (Weise et al. 2017) and are considered to be solitary predators, however males will form guilds called 'coalitions' consisting of usually two to four related or unrelated males (Melzheimer et al. 2018; Broekhuis et al. 2019). Territories are maintained via scent marking which also conveys reproductive information to the opposite sex (Broomhall et al. 2003; Broekhuis et al. 2019) however not all males maintain territories (known as 'floaters'; Melzheimer et al. 2018). Males will compete over territory which can result in the death of an individual, however territory boundaries can often be fluid and shared areas are occupied by different individuals on different temporal cycles communicated through olfaction (Broekhuis et al. 2019). Cheetahs have large litter sizes compared to other felids, high growth rates, and low birth weights, suggested as a life-history strategy in response to high cub mortality rate from other species and sometimes even conspecifics (Laurenson 1994).

# 3.4. Competition and Movement Behaviour

There are two main types of avoidance behaviour: 'proactive', which is anticipatory behaviour based on previous knowledge about the competitor such as shifting spatial and temporal usage of an area; and 'reactive', which is the immediate response to real-time risk such as actively fleeing an area (Broekhuis et al. 2013; Creel 2018; Broekhuis et al. 2019; Cornhill et al. 2022).

Research has shown that cheetahs exhibit avoidance behaviours towards lions as a mechanism to minimise competition and risk associated with spatial interactions with lions (Broekhuis et al. 2013). There is evidence that cheetahs avoid lions on a fine temporal scale in a reactive response. For example, Cornhill et al. (2022) and Broekhuis et al. (2013) found cheetah avoidance response to be reactive towards lions, and Swanson et al. (2016) identified short term reactive avoidance by cheetahs towards lions when they were present in the same area. Swanson et al. (2016) also reported a degree of attraction by cheetahs towards areas with lions, however this was proposed to be due to the factor of habitat preference rather than lion presence.

There is conflicting evidence in the literature regarding differences in cheetah spatial usage between sexes. Cornhill et al. (2022) found no significant difference in space use between sexes, however suggested this could be due to the study not controlling for the factors of denning and non-denning females and the associated spatial variation between these two factors. Melzheimer et al. (2018) reported significant differences between the spatial uses of sexes and also within sex differences i.e. between male 'floaters' and 'territory holders', but not between 'solitary' and 'coalitions'. There is however evidence that coalitions will kill solitary individuals when interaction occurs, however this same behaviour is not expressed in female cheetahs (Broekhuis et al. 2019). This highlights the need to understand intraspecific social structures to be able to correctly interpret spatial data and avoidance behaviours recorded.

Movements and behaviours all come with incurred costs for individuals and subsequently the wider population. For example, the high stress incurred from a reactive avoidance response can have negative metabolic, reproductive, or survival impacts on the individual (Creel 2018; Cornhill et al. 2022) which could secondarily lead to reduced population growth. Therefore, understanding movement behaviour of cheetahs can aid in cheetah conservation by understanding the pressures and costs cheetahs face. The level of risk is not homogenous across time and space, but changes with habitat use, density, activity, and distribution of competitors or predators (Broekhuis et al. 2013). Therefore, studies need to be completed from a variety of different locations to determine differences caused by local factors.

# 3.5. GPS

Global Positioning System (GPS) collars were first used in conservation in the 1960s to study grizzly bears (*Ursus arctos horribilis*) in Yellowstone, and have since been used to greatly progress our understanding of movement ecology (Hebblewhite and Haydon 2010). GPS telemetry allows for fine-scale, precise, and 24hour spatial data acquisition (Hebblewhite and Haydon 2010; Kie et al. 2010). This is especially important as large carnivorous felines are typically elusive and occur in low densities making detailed spatial data difficult to collect via ground-based observation methods (Kortello et al. 2007; Havmøller et al. 2019). However, GPS telemetry data provides highly precise, fine-scale spatial and temporal data to a scale that methods such as very high frequency (VHF) radio telemetry and camera trapping cannot provide (Hebblewhite and Haydon 2010; Kie et al. 2010). For instance, GPS telemetry is not constrained by the daylight or weather restrictions encountered with visual observation methods, and its extensive database of highly detailed data allows for the use of numerous statistical tests while accommodating biases (Kie et al. 2010; Buk et al. 2018). Detailed knowledge of animal movements and spatial usage has several management and conservation applications (Katzner and Arlettaz 2020).

#### 3.6. Game Management

Fencing has both positive and negative impacts on the wildlife contained within. In one respect, fencing provides protection from threats such as poaching, a barrier to invasive species, and reduces the potential of habitat encroachment (Naha et al. 2023). Conversely, fences prevent connectivity restricting the movement of species, influencing habitats and population dynamics such as gene flow and resource access (Buk et al. 2018). Under these restrictions, fenced populations need to be closely monitored and managed as restricted movement can increase the threats of genetic diversity loss due to isolation by barriers (Naha et al. 2023). This is especially important for cheetahs as they have experienced several historic genetic bottlenecks resulting in low genetic diversity to which further fragmentation could exacerbate (O'Brien S.J. et al. 1983; Menotti-Raymond and O'Brien 1993; Schmidt-Küntzel et al. 2018; Naha et al. 2023). The Endangered Wildlife Trust (EWT) established the Cheetah Metapopulation Project in 2011 to combat this genetic diversity issue via translocation of cheetahs between game reserves in the metapopulation of South Africa (Magliolo et al. 2023; EWT 2024).

There is also evidence of differing avoidance behaviours exhibited between fenced and unfenced reserves by cheetahs (Cornhill et al. 2022). For instance, cheetah densities in

protected areas are around 0.02/km<sup>2</sup> (Durant et al. 2017) with space use estimations ranging from 37-2161km<sup>2</sup> (Cornhill et al. 2022). This considerable variation is influenced by factors such as the local population's characteristics, including sex ratio and prey availability, as well as physical barriers, threat levels in the area, and the overall size of the reserve (Cornhill et al. 2022). These fenced areas are predominately game reserves, therefore spatial usage data inferences can have implications for reserve management and cheetah conservation.

# 3.7. Aims and Objectives

The purpose of this study was to identify the specific type of avoidance behaviour cheetahs exhibit towards lions and other cheetah conspecifics, along with identifying whether sex, social structure, and habitat influence cheetah spatial movements and avoidance behaviours. This project will cover the scientific recommendations for research surrounding cheetah behaviour within fenced areas (Cornhill et al. 2022), the influence of habitat on cheetah movement and behaviour (Swanson et al. 2016), the utilisation of movement data to inform effective game reserve management (Katzner and Arlettaz 2020), and research detailing intraspecific cheetah social behaviour (Melzheimer et al. 2018). The project incorporated data derived from modern technology provided by Selati Game Reserve to analyse previously collected GPS data on cheetahs and lions from their fenced reserve. Overall, this project aimed to provide information on knowledge gaps around cheetah spatial movements that are linked with inter- and intraspecific influences.

GPS data were used to infer: **1**) home and core ranges; **2**) areas of spatial overlap between species and individuals; **3**) dynamic interactions (defined as "identifying how the movements of one individual are related to another" (Long and Nelson 2013) and whether this behaviour is proactive or reactive; and **4**) behaviour after potential encounters.

This project used GPS data from 2 male and 3 female cheetah, and 8 lion from the Selati Game Reserve (Limpopo Province, South Africa) to evidence the hypotheses: i) cheetahs exhibit a reactive avoidance response to lion in shared areas; ii) solitary female cheetah individuals proactively avoid male cheetah coalitions; iii) habitat type is an influential factor to avoidance behaviour expression, with less avoidance exhibited in densely vegetated areas compared to open areas. The specific aims and objectives to achieve this goal were:

Aim 1) To investigate cheetah social behaviour relating to,

a) male coalitions; and

b) attraction/avoidance of individuals of both sexes, by:

**Objective 1)** identifying areas of overlapping home/core ranges, and both inter- and intra-specific dynamic interactions;

**Aim 2)** Identify the type of avoidance behaviour displayed by cheetahs towards lions (i.e. proactive or reactive) by:

**Objective 2)** using spatial and temporal data to calculate proximity threshold maintenance, attraction coefficients, and frequency and extent of interactions;

Aim 3) To investigate the extent of avoidance behaviour by:

**Objective 3)** analysing cheetah movements after possible encounters (both inter- and intra-specific), and whether this differs between social groupings (coalitions, solitary individuals);

**Aim 4)** To investigate the influence of habitat type and exhibited avoidance behaviours of cheetah by:

**Objective 4)** analysing spatial usage and avoidance behaviours in different habitats;

#### 4. Methods

#### 4.1. Study Area

Selati Game Reserve (hereby referred to as 'Selati') is a small (26,907.27 ha (Peel and Martindale 2020)), enclosed game reserve located in Limpopo Province, South Africa (between longitude 30° 38' 42" E and 30° 54' 26" E and latitude 23° 54' 25" S and 24° 05' 09" S (SWF 2023)). Several roads border the reserve with the northern boundary dictated by the R526 road Gravellote-Mica and the southern boundary by the R17 Gravelotte – Phalaborwa road, however the entire reserve boundary is fenced with a 2.4m height electric fence suitable for enclosing small and large game (Comley 2019; Peel and Martindale 2020). To the north of the reserve are communal and livestock ranching areas, to the east are the protected areas of Abelana and Balule Private Nature Reserve, to the south of the reserve are the Karongwe and Makalali-Pidwa Reserves, and the town of Gravelotte borders the west (Peel and Martindale 2020)(Figure 1 and A1). Selati consists of mostly arid lowveld and mopani veld with the north, south, and west areas characterised by granite lowveld (e.g. mixed Combretum apiculatum-Sclerocarya birrea veld, Combretum apiculatum veld, Terminalia sericea veld and sodic areas, including a grass layer of Pogonarthria squarrosa), and the central and eastern areas characterised as Phalaborwa-Timbavati mopane veld (e.g. mixed Mopane-Combretum apiculatum-Acacia spp, and mixed Mopane-Combretum apiculatum), with areas of Gravelotte rocky bushveld to the north-west and south-east (Rutherford et al. 2006; Comley 2019)(Figure 2 and 3). Selati's climate is classed within the hot, arid steppe climate zone (BSh) (Kottek et al. 2006; Comley 2019) with annual rainfall averaging between 490-530mm (Comley 2019; Peel and Martindale 2020), summer temperature ranges being 18-45°C, and winter temperature ranges being 8-23°C (Peel and Martindale 2020).







# 4.2. Study Animals

Cheetahs were first introduced to Selati in 2015, with three young males brought from Mountain Zebra National Park in the Eastern Cape (SWF 2023). The reserve is now part of the EWT's cheetah metapopulations initiative, which aims to enhance genetic diversity and prevent inbreeding by simulating natural dispersal via translocation (SWF 2023; EWT 2024). During the study time there were 5 cheetahs with GPS collars and 5 without (*Table A1*). Concerning the cheetahs in this study, there were two male cheetahs that are coalition brothers (CM07 and CM08), one female who was an active mother (CF12), one female who had not yet bred (CF11),

and one female (C2.F6) who bred on the reserve in 2021 but one cub was relocated on the 16<sup>th</sup> March 2023 and one died on the 24<sup>th</sup> March 2022 in a car collision.

Selati's lion population is notable in that there is only one pride on the reserve (*Table A2*). Individuals often fragment during the day into smaller groups due to lack of competition from another pride keeping them in one tight unit (SWF 2023). Therefore, several individuals from the pride were collared to better represent the movements of lions on the reserve.

Other predators on the reserve during the study period included leopard (*Panthera pardus*), Spotted hyena (*Crocuta crocuta*), and African wild dog (*Lycaon pictus*).

# 4.3. GPS data

Selati Game Reserve and Selati Wilderness Foundation (SWF) provided Long Range (LoRa) collar GPS data from 2 male cheetahs, 3 female cheetahs, and 8 lions over a 2-year time period (1<sup>st</sup> January 2022 to 31<sup>st</sup> December 2023). The reserve maintains 3 LoRa towers achieving 95% coverage of reserve area (SWF 2023). GPS collars were programmed to ping to the reserve's local network once an hour. There were two exceptions to the ping program: lion LM2 whose collar pinged every 3 hours; and CM07 had a VHF collar during the start of the study period (1<sup>st</sup> January 2022 to 26<sup>th</sup> March 2022) but an LoRa collar later (27<sup>th</sup> July 2023 to 31<sup>st</sup> December 2023).

A final version of the dataset was produced as an excel sheet (Microsoft Excel (Microsoft-Corporation 2018)). Reserve management produced the first draft of the available data. Data were then further scrutinised during this project to produce the final dataset. GPS fixes of zero were removed from the dataset which would have been caused by inadequate ping signal due to factors such as geographic barriers (e.g. hills blocking signal). GPS fixes from individuals who were situated in bomas during the study period were also removed to avoid data skew from anthropogenic influence.

Data was split into four groups based on temporal overlap and social structure analysis (*Table 1*). Lion individuals Dela and LMC.MC were not included in the temporal analysis (*Table 2A*) as the degree of temporal overlap was too small.

CM07 has two data types (VHF and LoRa based on temporal overlap of technologies).								
Stage	Species	ID	Demography					
Stage 1	Cheetah	CM08	Male, coalition brother to CM07					
	Cheetah	CM07 (VHF)	Male, coalition brother to CM08					
	Lion	LMF.MF	Male					
Stage 2	Cheetah	CM08	-					
	Cheetah	CM07 (VHF)	-					
	Cheetah	C2.F6	Female, non-active mother					
	Lion	LE.M01	Male					
	Lion	LMA.FD	Female, mother to uncollared lions, sibling to LMA.FE					
Stage 3	Cheetah	CF11	Female, non-breeding					
	Cheetah	CM07(LoRa)	Male, coalition brother to CM08					
	Lion	LM1	Male, coalition with LM2					
	Lion	LM2	Male, coalition with LM1					
	Lion	LMA.FD	-					

*Table 1*: Information of groupings of cheetah and lion individuals that had GPS collars during the study period in Selati Game Reserve. Groupings are organised based on temporal overlap and social structure. CM07 has two data types (VHF and LoRa based on temporal overlap of technologies).

Table 1 continued									
Stage	Species ID Demography								
Stage 4	Cheetah	CF11	-						
	Cheetah	CF12	Female, active mother						
	Cheetah	CM07(LoRa)	-						
	Lion	LM1	-						
	Lion	LM2	-						
	Lion	LMA.FD	-						
	Lion	LMA.FE	Female, mother to LE.M01, sibling to LMA.FD						

#### 4.3. Data Analysis

#### 4.3.1. Spatial usage and static interaction analysis

Data analysis was conducted in the coding language R (RCore-Team 2020) in RStudio (RStudio-Team 2020). The GPS data were read from an excel sheet into RStudio and zeros/NAs were removed. Duplicate GPS records were also removed using the packages 'lubridate'(Grolemund and Wickham 2011) and 'dplyr' (Wickham et al. 2023) by first converting date format to 'year/month/day', then identifying duplicates via 'ID' and 'DateTime', and removing identified duplicates from the dataset. The package 'leaflet' (Cheng et al. 2024) was used to visualise the GPS datapoints in an interactive map format (*Figure A1*).

Home range estimates were calculated via two methods: minimum convex polygons (MCPs (Mohr 1947)) and kernel utilisation distributions (KUDs (Worton 1989))(Hayward et al. 2009; Kie et al. 2010; Cristescu et al. 2013) using the R packages 'adehabitatHR'(Calenge and Fortmann-Roe 2023), 'sf' (Pebesma and Bivand 2023), and 'sp' (Pebesma and Bivand 2005). Multiple spatial usage methods are recommended to enable comparison and improve the accuracy of inferences (Hayward et al. 2009). Home range refers to the area an individual normally traverses in search of resources or a mate (Burt 1943), whilst core range refers to the highly utilised area within the home range (Seaman and Powell 1990). Home ranges were defined as 95% thresholds of an individual's utilisation distribution to reduce the risk of overestimation of home range caused by outlying GPS points during unusual movement patterns, and core ranges at 50% to represent more concentrated area usage (Bertrand et al. 1996; Cristescu et al. 2013). The GPS data were subset into the desired grouping, the 'SpatialPoints' data were converted to a SpatialPointsDataFrame using the function 'sp::coordinates', which was then assigned the coordinate reference system (CRS) to WGS84 using the function 'sf::proj4strong', and then created a new object with UTM projection Zone 36 South using 'sp::spTransform' to allow for accurate distance results. To calculate MCPs, the function 'mcp' was applied to the UTM projected SpatialPointsDataFrame (units in = m, units out = km<sup>2</sup>) at 95% and 50% thresholds to represent home and core ranges. A distribution centroid was generated by plotting the median of GPS points to represent a central point for activity. The MCP outputs were then converted into shapefiles for visualisation using 'st\_write' and 'st\_as\_sf'. To calculate KUDs, the function 'adehabitatHR::kernelUD' was used on the UTM projected SpatialPointsDataFrame with 80% of the reference bandwidth (href) parameter being assigned to avoid over-smoothing when href was >1000 (Broekhuis et al. 2019). The function 'getverticeshr' was used to extract the shape contour at 95% and 50% ranges from rasterised data. The function 'kernel.area' was used to calculate KUD area size from vector data (units in = m, units out =  $km^2$ ). The KUD outputs were then converted into shapefiles for visualisation using 'st\_write' and 'st\_as\_sf'. Data were

visualised using the package 'ggplot2' (Wickham 2016). Static interaction was determined by calculating spatial overlap of KUDs by re-running 'kernelUD' with the addition of 'same4all=TRUE' to make each individual's object length the same, then run with the function 'kerneloverlaphr' at 95% and 50% intervals (method = HR). It must be noted the overlap output is a matrix that should be read directionally. Specifically, the percentage of Individual A's polygon overlapping with Individual B's polygon is not necessarily the same as the percentage of Individual B's polygon. This asymmetry arises because the polygons differ in size and shape, meaning that a smaller polygon may overlap a larger one differently than the larger polygon overlaps the smaller one. Therefore, interpretation of this matrix must include the direction of overlap being reported.

#### 4.3.2 Dynamic interaction and contact network analysis

For temporal and interactions analyses, distance- and time-threshold parameters needed to be set. Distance (dc) determines the distance at which a function will delineate a statistical fix, whilst time-threshold (tc) determines the time between which fixes are taken. Calculating ecologically representative thresholds are important as the results from many types of interactions analyses rely entirely on the parameters that are inputted (Joo et al. 2018). CM07's VHF data were removed due to the aforementioned data skewing and cheetah GPS data were used to provide threshold estimates relevant to the ecology of the cheetahs in this study. Threshold tc was determined by calculating the resolution gap length via average time difference in GPS pings using the 'mutate' function in dplyr. Anomalies were removed and tc was set to half the average gap length in seconds (see Long (2024); tc = 2840seconds). Distance dc was determined by calculating the average step length in the gap resolution. First, a nonnested track object was made using the function 'make\_track' from the package 'amt' (Signer et al. 2019); CRS = 2054), UTM projected cheetah coordinates, and time parameter in the format 'POSIXct' (time zone = "Africa/Johannesburg") using the function 'parse\_date\_time' from the package 'lubridate'. Step lengths were extracted from the track using 'amt::step\_lengths', then resampled at average gap length to get a result more representative to the study animals using the function 'amt::track\_resample' (rate = lubridate::minutes (95), tolerance = lubridate::minutes (20)). This resulted in an average gap step length of 3563.5m ±6176.2m (mean ±standard deviation). Distance thresholds were then set at ~0.5x, 1x, 1.5x, and 2x the step length (1,750m, 3,500m, 5,250m, 7,000m; Broekhuis et al. 2019) to encompass ecologically relevant distance thresholds.

For spatiotemporal analyses in adehabitat packages, 'ltraj' objects are required. Several steps are required to format the data to be compatible with ltraj object creation. The data were subset into two data frames: one for lions and one for cheetahs with CM07 VHF data removed. Ltraj objects do not contain UTM projection information, therefore GPS coordinates were extracted and projected to UTM format using 'sp::proj4string' (proj = longlat, datum = WGS84) and then 'sp::spTransform' (proj = utm, zone=36 south, datum = WGS84) prior to conversion to a SpatialPointsDataFrame using 'sp::coordinates' for the xy parameter for either species. The data ("year, month, day, hour, minutes", time zone = Africa/Johannesburg) for each species. Ltraj objects were created for each individual using the calculated parameters for the associated species and assigned ID name.

The package 'wildlifeDI' (Long and Nelson 2013) was used to analyse spatiotemporal movements and dynamic interaction analysis. Temporal overlap was confirmed using the 'checkTO' function and the function 'Don' was used to confirm the compatibility of Itraj data with dc, tc, and stages to confirm dynamic interaction analysis could be executed using these designations (Doncaster 1992). Global dynamic interaction refers to the analysis of related movements between two individuals (Macdonald et al. 1980; Long and Nelson 2013) which can be assessed through a combination of proximity, attraction, and displacement indices. Proximity analysis (Bertrand et al. 1996) was completed using the function 'wildlifeDI:: Prox' to identify the proportion of simultaneous fixes between two individuals within the designated dc as an indication of proactive avoidance behaviour, for threshold-dependant interpretation (Joo et al. 2018). The proximity output (prox) is a parameter indicating the percentage of GPS fixes within the set dc between the individuals within the function. Benhamou's IAB Index (Benhamou et al. 2014) was used to test direct interaction via statistical attraction and avoidance outputs at dc thresholds with the function 'IAB' as it takes into account the serially correlated nature of GPS relocation analysis that other methods do not. The IAB analysis produces a p value (alpha = 0.05) for attraction and avoidance of movements between two individuals. The dynamic interaction index (Long and Nelson 2013) was used as further analysis into the global movement cohesion, displacement, and direction of movements between two individuals using the function 'DI' (global analysis, no dc set). The main output statistic (DI) indicates the strength of the cohesion of movements between individuals. These indices allow for the inference of proactive or reactive movement behaviour for both inter- and intra-specific avoidance behaviour.

Contact network analysis was completed to infer the potential proactive nature and intensity of avoidance behaviour between individuals using the packages 'wildlifeDI' and 'adehabitatLT' (Calenge et al. 2023). First, the function 'wildlifeDI::dcPlot' (dmax = 7000) was used as an exploratory tool to visualise the distribution frequency of pairwise distances between two individuals to confirm appropriate tc and dc values. The function 'conProcess' was used to create an object of contact points and distances, then this object was run through 'conPhase' to infer points where continuous contact occurs for a set unit of time (pc) indicating a contact phase (pc = 60mins). The function 'conSummary' was used on the contact phase object to identify the number of contact points within the dc between the two individuals and the average duration of a contact phase. To visualise the contact phases, the function 'adehabitatLT::ltraj2sf' was applied to the contact phase object to create an sf object of all GPS fixes, and the function 'wildlifeDI::conSpatial' was also applied to the contact phase object (def = all, type = point) to create an sf object of contact points. These were then visualised with 'ggplot' to identify where contact phases occur on the reserve and whether they were within home or core ranges extents.

Behaviour after contacts was analysed to infer potential reactive behaviour responses by statistically analysing differences in step length between contact fixes and non-contact fixes. Behaviour after encounters can provide information on cheetah behaviour and the extent/intensity to which avoidance behaviour is expressed. This was done by using the function 'conContext' to complete randomisation analysis on the contact phase object (var = dist, nrand = 1000). The package 'nlme'(Pinheiro et al. 2023) was then used to generate a generalised linear mixed model (GLMM)(method: REML) with the independent variable of step length and the covariate of fix type with ID as a random effect (random = ~1). The function 'set.seed' was used for repeatability, and the package 'MuMIn'(Barton 2024) was used to obtain  $R^2c$  values from models for variance explained.

#### 4.3.3. Habitat Use

Habitat data were provided as a shapefile which had to be formatted for analysis. First, the shapefile was checked for geometry validity using 'sf::st\_is\_valid', and any invalid geometries were corrected using the function 'st\_make\_valid'. The shapefile was converted into a SpatialPolygonsDataFrame with the function 'sf::as'. A raster template was created using the 'raster' and 'extent' functions from the package 'raster'(Hijmans 2023)(resolution = 0.0001). The SpatialPolygonsDataFrame was then rasterised using the function 'rasterize' based on the raster template created (field = Habitat Name). The raster was then converted to a SpatialPixelsDataFrame with the function 'sf::as'.

To allow for habitat use inference, habitats data were added to the GPS data to join the correct habitat type to each coordinate point. GPS coordinate data (UTM projected, including CM07's VHF collar) were converted to an sf object with the function 'st\_as\_sf'. The fixed habitat shapefile was joined to the GPS sf object using 'st\_join' and GPS points with no habitat designation were removed to create a data frame containing only coordinates within the reserve boundary using the function 'filter' from the package 'dplyr'. This sf object was then converted into a spatial object using the function 'sf::as\_Spatial' and a data frame using 'as.data.frame', which were then used to create a SpatialPointsDataFrame suitable for statistical analysis.

Chi-squared test was used to test for statistical differences between individual ID and habitat type counts to infer initial habitat preference. This was done using a data frame containing all cheetah and lion GPS counts for interspecific inference, and with a data frame of only cheetah GPS count for intraspecific inference.

Percent habitat composition on the reserve was also calculated and visualised in the context of home and core ranges. Habitat composition on the reserve was calculated using the packages 'dplyr' and 'units' (Pebesma et al. 2016) by first calculating habitat type geometry area using 'units::set\_units' (km<sup>2</sup>), calculating the total area via the sum of geometry area, and calculating percentage for each habitat type using 'dplyr::mutate' ((total area/ study area)\*100). This was also completed for 95% and 50% MCPs to visualise differences. The MCP shapefiles were read in and habitat area encompassed within the MCP boundaries was calculated using the function 'sf::st\_intersection' with the intersection object then undergoing the area percentage analysis mentioned previously. Results were visualised using the package 'ggplot2'.

Habitat use was analysed by comparing habitat use vs availability on the reserve, with analysis under the assumption that higher than expected 'use' is an indicator of 'preference' (Aebischer et al. 1993), and vice versa. Individual habitat use by individuals was calculated using 'count.points' from the package 'adehabitatMA'(Calenge and Basille 2023b) using the GPS and habitat SpatialPixelsDataFrame to create a table of derived utilisation weights for each map pixel for each ID. Habitat availability was calculated by creating a table of derived utilisation weights for each map pixel on the reserve. Habitat selection ratios were analysed via Manly's selection ratio (Manly et al. 2002) using the function 'widesII'. This analysis produced the statistics 'Khi2L1' testing for identical use of habitats by individuals and a p value, and 'Khi2L2' testing for overall habitat selection by individuals and a p value. The lvlev's electivity index was used to investigate habitat utilisation compared to habitat availability. First, the data were normalised (sum of all ratios equals one) to standardise habitat area in an attempt to infer individual habitat choice behaviour in relation to abundance and alternative habitats (Lechowicz 1982). Electivity indices were calculated using the function 'ivlev\_electivity' from the package 'electivity' (Quintans 2019). The electivity output indicates the strength of avoidance or preference of an individual to a habitat type.

#### 5. Results

# 5.1. Spatial usage and static interactions

# 5.1.1. Cheetahs

Unfortunately, the VHF collar data had issues with data skewing due to its reduced ping rate and reliability with solar power. As a result, the temporal and social interaction analysis involving the two male cheetahs as a coalition was not entirely possible, as their LoRa collar data do not overlap. However, CM07's VHF data was still used for analysing the spatial home range and habitat use in order to maintain some insights into the male coalition's behaviour.

The centroid for cheetah activity is to the south-east of the reserve and total home range polygons encompass the entire reserve (*Figures 4 A&B and 5 A&B*). Core ranges appear to be more contained within reserve boundaries than home range areas, and area use does not appear to be totally contained by fencing (i.e. reserve boundary). Female cheetahs have larger core range estimates than males with both the MCP and KUD methods, and larger home ranges except for CF12 KUD method (*Table 2 and 3*). CF12 has lower home and core range estimates than the other female cheetahs.



*Figure 4*: Minimum Convex Polygon (MCP) estimations using GPS points (decimal coordinate projection) for 5 cheetahs on Selati Game Reserve. The black dot represents the distribution centroid (median) of GPS points. A) 95% MCP polygons indicating home range extent; B) 50% MCP polygons indicating core range extent.



*Figure 5*: Kernel Utilisation Density (KUD) estimations using GPS points (UTM projection) for 5 cheetahs on Selati Game Reserve. The black dot represents the distribution centroid (median) of GPS points. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent.

<i>Table 2</i> : Area estimates (km²) from Minimum Convex Polygon (MCP) estimates for 5 cheetahs on Selati Game Reserve. 95%								
MCP represents home range extent, 50% MCP represents core								
range extent.								
ID	95% MCP	50% MCP						
C2.F6	234.84	91.60						
CF11	258.03	87.70						
CF12	110.11	34.32						
CM07	156.88	31.01						
CM08	185.51	23.17						

Table 3: Area estimates (km²) from Kernel Utilisation Density									
(KUD) estimates	(KUD) estimates (80% href) for 5 cheetahs on Selati Game								
Reserve. 95% KUD represents home range extent, 50% KUD									
represents core r	ange extent.								
ID	95% KUD	50% KUD							
C2.F6	273.95	48.34							
CF11	307.63	65.92							
CF12	165.82	29.33							
CM07	197.79	29.16							
CM08	219.91	20.85							

#### 5.1.2. Lions

The centroid for lion activity on the reserve is in the centre of the game reserve (*Figure 6 A&B*). LM1 had the largest home range but Dela had the largest core range size (*Table 4*). LMA.MC had the smallest home range but LMA.FE had the smallest core range size. For lions, two individuals appeared to have core ranges that extended outside of the reserve to the east.



*Figure 6*: Minimum Convex Polygon (MCP) estimations using GPS points (decimal coordinate projection) for 8 lions on Selati Game Reserve. The black dot represents the distribution centroid (median) of GPS points. A) 95% MCP polygons indicating home range extent; B) 50% MCP polygons indicating core range extent.

(MCP) estimates for 8 lions on Selati Game Reserve. 95% MCP									
represents home range extent, 50% MCP represents core									
range extent.									
ID	95% MCP	50% MCP							
Dela	209.37	99.41							
LE.M01	159.01	18.22							
LM1	233.43	27.79							
LM2	218.59	31.54							
LMA.FD	95.52	13.25							
LMA.FE	36.07	3.61							
LMA.MC	29.93	6.16							
LMF.MF	193.80	54.87							

Table 4: Area estimates (km<sup>2</sup>) from Minimum Convex Polygon

#### 5.1.3. Stage 1

Analyses including temporal information were applied to groupings of cheetah and lion individuals referred to as stages (Table 1).

Stage 1 home range activities were spread largely across the reserve with absence from the south-east (Figure 7 A&B). When comparing overlap, results are directionally read 'row' to 'column', where overlap is considered to be percentage overlap of the individual's area (row) over the individual's area (column; e.g. Table 5: 60% of CM07's home range overlapped with CM08's, and 52.75% of CM08's home range overlapped with CM07's). Core ranges were much more segregated between lion and cheetahs than home ranges, with no overlap between CM08 and LMF.MF, and a small overlap for CM07 and LMF.MF with 9.09% of CM07's core range overlapping with LMF.MF's core range (Table 5). Cheetah coalition males had high overlap in home range areas (52.75/60%), and even higher degree of overlap in core range areas (63.64/87.50%). Cheetah~lion home range overlap was higher than lion~cheetah.



Figure 7: Kernel Utilisation Density (KUD) polygons (80% href) for cheetah and lion individuals on Selati Game Reserve. Individuals are included in the stage 1 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent.

*Table 5*: Percentage overlap of Kernel Utilisation Density (KUD) area estimates (80% href) for cheetahs and lions on Selati Game Reserve. Individuals are included in the stage 1 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent.

	95% KUD		-	50% KUD			
	CM07	CM08	LMF.MF	CM07	CM08	LMF.MF	
CM07	-	60.00	53.75	-	63.64	9.09	
CM08	52.75	-	70.33	87.50	-	0	
LMF.MF	43.88	65.31	-	4.35	0	-	

# 5.1.4. Stage 2

Stage 2 home range activities were spread largely across the reserve with absence from the south-east of the reserve (*Figure 8 A&B*). C2.F6 and LE.M01 home ranges extended past the reserve boundary to the north, and all Stage 2 cheetahs' home ranges extended past the reserve boundary to the south. Cheetah coalition males had high home range overlap (56.90/64.08%) and cheetah males had higher home range overlap with female C2.F6 (60.34/64.08%) than C2.F6 did with males (46.15/48.95%). Lion~cheetah home range overlap was higher than cheetah~lion, and the highest interspecific home range overlap was between C2.F6 and LE.M01(52.45%). Stage 2 core ranges were segregated, with no overlap between cheetahs CM07 and C2.F6, or CM08 and C2.F6, but high overlap between the coalition brothers (68.75/100%)(*Table 6*). The core range of CM08 did not overlap with any lions but coalition brother CM07 had small overlap with LE.M01 (6.25%). C2.F6 had the highest core range areas (*Figure 7*).



*Figure 8*: Kernel Utilisation Density (KUD) polygons (80% href) for cheetah and lion individuals on Selati Game Reserve. Individuals are included in the stage 2 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent.

*Table 6*: Percentage overlap of Kernel Utilisation Density (KUD) area estimates (80% href) for cheetahs and lions on Selati Game Reserve. Individuals are included in the stage 2 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent.

	95% KUD						50% KUD				
	C2.F6	CM07	CM08	LE.M01	LMA.FD	C2.F6	CM07	CM08	LE.M01	LMA.FD	
C2.F6	-	46.15	48.95	52.45	30.07	-	0	0	8.00	8.00	
CM07	64.08	-	64.08	51.46	32.04	0	-	68.75	6.25	0	
CM08	60.34	56.90	-	47.41	31.03	0	100	-	0	0	
LE.M01	80.65	56.99	59.14	-	50.54	15.38	7.69	0	-	61.54	
LMA.FD	86.00	66.00	72.00	94.00	-	22.22	0	0	88.89	-	

#### 5.1.5. Stage 3

Stage 3 home range activities covered the entire reserve, however core ranges were in the western and central areas of the reserve (*see Figure 9 A&B*). CM07 had very high home range overlap with CF11 (81.40%) and CF11 had a lower degree of overlap but it was still high (52.24%; *Table 7*). CF11's core area was split into three separate areas occupying the northern and central reserve areas (*Figure 9B*). There was no core range overlap between CM07 and lions, and CF11 had the highest interspecific core range overlap with LM2 (*Table 7*; 32.14%). Core range overlap between cheetahs was low (10.71/25%), and the highest interspecific home range overlap was between CM07 and LM1 (45.35%). Lion~cheetah home and core range overlap was generally higher than cheetah~lion (except LM2 – CM07 and LM2 – CM07 home ranges).



*Figure 9*: Kernel Utilisation Density (KUD) polygons (80% href) for cheetah and lion individuals on Selati Game Reserve. Individuals are included in the stage 3 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent. *Table 7*: Percentage overlap of Kernel Utilisation Density (KUD) area estimates (80% href) for cheetahs and lions on Selati Game Reserve. Individuals are included in the stage 3 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent: B) 50% KUD polygons indicating core range extent.

	95% KUD						50% KUD				
	CF11	CM07	LM1	LM2	LMA.FD	CF11	CM07	LM1	LM2	LMA.FD	
CF11	-	52.24	43.28	44.03	27.61	-	10.71	28.57	32.14	17.86	
CM07	81.40	-	45.35	43.02	33.72	25.00	-	0	0	0	
LM1	65.17	43.82	-	96.63	33.71	88.89	0	-	100	66.67	
LM2	64.84	40.66	94.51	-	31.87	90.00	0	90.00	-	60.00	
LMA.FD	88.10	69.05	71.43	69.05	-	71.43	0	85.71	85.71	-	

#### 5.1.6. Stage 4

Stage 4 home range activities covered the entire reserve, and core ranges were also spread with CF12 being the only individual with a core range in the south-east (*Figure 10 A&B*). CF12 had both the highest and lowest interspecific home range overlaps of Stage 4 (*Table 10*). CM07 had the highest intraspecific overlap with CF11 (81.40%) and CF11 had the lowest interspecific overlap with CF12 (24.63%). CF12 had no core range overlap with any individuals, and CM07 had no overlap with lions and low core range overlap with CF11 (25%; *Table 8*). CF11 had no core range overlap with CF11 (25%; *Table 8*). CF11 had no core range overlap with CF11 (25%; *Table 8*). CF11 had no core range overlap with CM07 (10.71%). Lion~cheetah home and core range overlap was generally higher than cheetah~lion (except for LM1 and LM2 home ranges with CM07 and CF12), but all lion~cheetah core ranges were higher than cheetah~lion. LMA.FE had either 100% or 0% overlap with the core ranges of cheetahs and in general a high home range overlap except for CF12 (32%).



*Figure 10*: Kernel Utilisation Density (KUD) polygons (80% href) for cheetah and lion individuals on Selati Game Reserve. Individuals are included in the stage 4 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent. *Table 8*: Percentage overlap of Kernel Utilisation Density (KUD) area estimates (80% href) for cheetahs and lions on Selati Game Reserve. Individuals are included in the stage 4 grouping meaning there is temporal overlap in GPS data. A) 95% KUD polygons indicating home range extent; B) 50% KUD polygons indicating core range extent.

	95% KUD						50% K	UD						
	CF11	CF12	CM07	LM1	LM2	LMA.FD	LMA.FE	CF11	CF12	CM07	LM1	LM2	LMA.FD	LMA.FE
CF11	-	24.63	52.24	43.28	44.03	27.61	17.16	-	0	10.71	28.57	32.14	17.85	14.29
CF12	45.21	-	35.62	63.01	68.49	10.96	10.96	0	-	0	0	0	0	0
CM07	81.40	30.23	-	45.35	43.02	33.72	16.28	25.00	0	-	0	0	0	0
LM1	65.17	51.69	43.82	-	96.63	33.71	28.09	88.89	0	0	-	100	66.67	44.44
LM2	64.84	54.95	40.66	94.51	-	31.87	27.47	90.00	0	0	90.00	-	60.00	40.00
LMA.FD	88.10	19.05	69.05	71.43	69.05	-	57.14	71.43	0	0	85.71	85.71	-	57.14
LMA.FE	92.00	32.00	56.00	100	100	96.00	-	100	0	0	100	100	100	-

#### 5.2. Spatiotemporal and dynamic interactions

Interaction statistics indicated no statistically conclusive avoidance or attraction behaviours between CM08 and any other cheetahs or lions with overlapping temporal data at any distance threshold or general global analysis (*Table 9*). These interaction statistics are not directional, therefore interpretation is for a relationship between two individuals, not the behaviour of one individual. Proximity analysis yields a proximity parameter (prox) indicating the percentage of GPS fixes within the set dc between the individuals (e.g. *Table 9*; 'dc = 1,750, prox = 0.05' would indicate that 5% of CM08's GPS fixes were within 1,750m of LMF.MF). Proximity analysis yielded results of <0.5 indicating that less than 50% of simultaneous GPS fixes were within the distance threshold, which showed potential avoidance behaviour, however the IAB index displayed no significant avoidance at any distance threshold for any CM08 movements. Dynamic interaction analysis further failed to identify any cohesive relationship between movements of individuals with CM08 (DI ~0), indicating movement indifference respective of the compared individual (e.g. a DI value close to 0 indicates no cohesion, 1 would indicate complete cohesion of movements, -1 would indicate repulsion of movements), except for a weak relationship with C2.F6 (DI = 0.03).

IAB interaction statistics indicated a potential attraction relationship between CM07 and CF11 when within the 1,750m threshold (attract p = 0.01), CM07 and LM1 up to 3,500m (attract p = 0.05), and CM07 and LM2 up to 1,750m (attract p = 0.01; *Table 9*). However, proximity analysis and dynamic interaction analysis failed to support these relationships, instead proximity analysis indicated avoidance (prox = <0.5). Dynamic interaction showed a potential weak cohesion of movements between CM07 and CF11 (0.03) and LM1 (0.02).

Proximity analysis of C2.F6 and LMA.FD indicates a potentially weak attraction at 7,000m (prox = 0.58), however there was evidence of avoidance behaviour at other thresholds and towards other individuals (*Table 9*). IAB index supported avoidance relationship of lions by C2.F6 at larger threshold distances with avoidance at 5,250m (avoid p = 0.05) but this was not supported by the dynamic interaction statistic (DI = -0.01).

Proximity analysis for CF11 and LMA.FD indicated a weak attraction at 7,000m (prox = 0.52) and a weak attraction with LMA.FE at 7,000m (prox = 0.66), but showed avoidance behaviour at other thresholds and with other individuals (*Table 9*). IAB index indicated a potential attraction between CF11 and CM07 at 1,750m (p = 0.01) and the strongest cohesion of movements of all individual comparisons with CF11 however the cohesion was weak (DI = 0.03).

Interaction statistics involving CF12 indicated potential avoidance behaviours. Proximity analysis yielded results of <0.5 indicating strong avoidance, however the IAB index indicated only significant avoidance behaviour for CF12-LMA.FD at 1,750m (*Table 9*). Dynamic interaction

analysis further failed to identify any cohesive relationship between movements of individuals with CF12.

*Table* 9: Global statistical interaction analyses outputs of GPS data from a cheetah (CM08) and other cheetahs and lions on Selati Game Reserve. Individuals included had temporal overlap in GPS data with CM08. Distance threshold determines the distance scale in meters that the interaction analysis was completed. The proximity analysis (prox) indicates the proportion of GPS fixes from CM08 that were within the distance threshold of the individual compared. The Benhamou's IAB index provides a *p* value (alpha = 0.05) for statistical significance of attraction and avoidance between the movements of CM08 and the individual compared. The dynamic interaction statistic (DI) provides a parameter indicating the strength of cohesion of movements between CM08 and the individual compared with 0 indicating no cohesion, 1 indicating complete cohesion, and -1 indicating complete repulsion.

Cheetah	Individual	Stage	Distance	Proximity	Benhamou	ı's IAB Index	Dynamic
	Compared		threshold (m)	Analysis	p.Attract	p.Avoid	Interaction statistic
CM08	LMF.MF	Stage 1	1750	0.05	0.21	0.79	0
			3500	0.12	0.11	0.90	
			5250	0.31	0.09	0.92	
			7000	0.45	0.09	0.91	
	C2.F6	Stage 2	1750	0	0.94	0.06	0.03
			3500	0.02	0.94	0.06	
			5250	0.06	0.91	0.09	
			7000	0.16	0.87	0.13	
	LE.M01	Stage 2	1750	0.01	0.87	0.13	-0.01
			3500	0.03	0.93	0.07	
			5250	0.13	0.92	0.08	
			7000	0.30	0.93	0.07	
	LMA.FD	Stage 2	1750	0.01	0.69	0.31	0.01
			3500	0.10	0.43	0.57	
			5250	0.30	0.35	0.65	
			7000	0.51	0.38	0.62	
CM07	CF11	Stage 3,	1750	0.12	0.01	0.99	0.03
		Stage 4	3500	0.21	0.06	0.94	
			5250	0.25	0.18	0.83	
			7000	0.36	0.35	0.83	
	LM1	Stage 3,	1750	0.03	0.02	0.98	0.02
		Stage 4	3500	0.10	0.05	0.96	
			5250	0.18	0.15	0.85	
			7000	0.30	0.29	0.72	
	LM2	Stage 3,	1750	0.04	0.01	1	0
		Stage 4	3500	0.10	0.06	0.95	
			5250	0.18	0.16	0.84	
			7000	0.27	0.37	0.63	
	LMA.FD	Stage 3,	1750	0.01	0.64	0.36	0.01
		Stage 4	3500	0.06	0.76	0.24	
			5250	0.15	0.58	0.43	
			7000	0.32	0.36	0.64	

Table 9 con	tinued							
Cheetah	Individual	Stage	Distance	Proximity	Benhamou	Dynamic		
	Compared		Threshold (m)	Analysis	p.Attract	p.Avoid	Interaction statistic	
CM07	CF12	Stage 4	1750	0	0.87	0.13	0.01	
			3500	0	0.66	0.34		
			5250	0.02	0.46	0.54		
			7000	0.10	0.27	0.73		
	LMA.FE	Stage 4	1750	0.02	0.27	0.73	0	
			3500	0.07	0.28	0.72		
			5250	0.14	0.25	0.75		
			7000	0.31	0.27	0.73		
C2.F6	CM08	Stage 2	1750	0	0.94	0.06	0.03	
			3500	0.02	0.94	0.06		
			5250	0.06	0.91	0.09		
			7000	0.16	0.90	0.13		
	LE.M01	Stage 2	1750	0.06	0.76	0.24	-0.01	
			3500	0.15	0.91	0.09		
			5250	0.30	0.95	0.05		
			7000	0.43	0.96	0.04		
	LMA.FD	Stage 2	1750	0.02	0.70	0.30	0	
			3500	0.11	0.58	0.42		
			5250	0.30	0.46	0.54		
			7000	0.58	0.38	0.62		
CF11	CM07	Stage 3,	1750	0.12	0.01	0.99	0.03	
		Stage 4	3500	0.21	0.06	0.94		
			5250	0.25	0.18	0.83		
			7000	0.36	0.35	0.83		
	LM1	Stage 3,	1750	0.09	0.56	0.44	0	
		Stage 4	3500	0.18	0.63	0.37		
			5250	0.28	0.68	0.32		
			7000	0.44	0.72	0.28		
	LM2	Stage 3,	1750	0.07	0.67	0.33	0	
		Stage 4	3500	0.15	0.75	0.25		
			5250	0.25	0.79	0.21		
			7000	0.42	0.82	0.18		
	LMA.FD	Stage 3,	1750	0.11	0.05	0.95	-0.02	
		Stage 4	3500	0.22	0.13	0.87		
			5250	0.36	0.29	0.71		
			7000	0.52	0.40	0.61		
	CF12	Stage 4	1750	0	0.58	0.42	0	
			3500	0	0.38	0.62		
			5250	0.01	0.32	0.68		
			7000	0.04	0.21	0.80		
	LMA.FE	Stage 4	1750	0.16	0.79	0.22	-0.01	
			3500	0.33	0.89	0.11		
			5250	0.49	0.86	0.14		
			7000	0.66	0.81	0.20		
CF12	CM07	Stage 4	1750	0	0.87	0.13	0.01	
			3500	0	0.66	0.34		
			5250	0.02	0.46	0.54		
			7000	0.10	0.27	0.73		

Table 9 contii	nued						
Cheetah Individual		Stage	Distance	Proximity	Benhamou's	BIAB Index	Dynamic
	Compared		threshold (m)	Analysis	p.Attract	p.Avoid	interaction
							statistic
CF12	CF11	Stage 4	1750	0	0.58	0.42	0
			3500	0	0.38	0.62	
			5250	0.01	0.32	0.68	
			7000	0.04	0.21	0.80	
	LM1	Stage 4	1750	0	0.95	0.05	0
			3500	0.04	0.87	0.14	]
			5250	0.10	0.69	0.31	
			7000	0.18	0.36	0.64	
	LM2	Stage 4	1750	0	0.94	0.06	0.01
			3500	0.04	0.88	0.12	
			5250	0.11	0.73	0.27	
			7000	0.19	0.49	0.51	
	LMA.FD	Stage 4	1750	0	0.98	0.02	-0.01
			3500	0.02	0.98	0.02	
			5250	0.05	0.91	0.09	
			7000	0.08	0.70	0.30	
	LMA.FE	Stage 4	1750	0	0.98	0.02	0
		-	3500	0.03	0.87	0.14	]
			5250	0.07	0.67	0.33	]
			7000	0.08	0.41	0.59	

# 5.3. Contact Analysis

CM07, CM08, C2.F6, and CF11 came into potential contact with all the other individuals within their stage grouping except for with CF12 (*Table 10*). The longest mean contact phase duration was between CF11 - CM07 (17hours, 30minutes) and the shortest was between CM08 – LMA.FD and CF12 – LMA.FD (1hour 30minutes), however CF11 had the greatest overall number of potential contact phases (n = 44) with LMA.FD. CF12 had the least and shortest duration of potential contact phases of all cheetahs.

*Table 10*: Analysis of potential contact points of cheetahs and lions on Selati Game Reserve using GPS data. Individuals included as the interaction individual had temporal overlap in GPS data with the listed cheetah. Contact fixes and contact phases (contacts lasting >60mins) were derived between the reference cheetah and an interaction individual within a 1750m distance threshold

Cheetah	Interaction	Number of	Number of	Mean contact phase
	individual	contact fixes	contact phases	duration
CM08	LMF.MF	79	12	6hrs 39mins 11secs
	C2.F6	0	0	0
	LE.M01	16	3	7hrs 30mins 30ses
	LMA.FD	20	9	1hr 30mins
C2.F6	CM08	0	0	0
	LE.M01	29	6	10hr 0mins 48secs
	LMA.FD	16	5	6hrs 30mins 30secs
CM07	CF11	94	24	3hrs 47mins 57secs
	CF12	0	0	0
	LM1	55	8	7hrs 19mins 9secs
	LM2	38	9	5hrs 31mins 30secs
	LMA.FD	12	3	5hrs 1min 30secs
CF11	CM07	81	11	17hrs 30mins
	LM1	159	27	11hrs 27mins 28secs
	LM2	66	32	2hrs 59mins 48secs
	LMA.FD	193	44	8hrs 41mins 52secs
	CF12	0	0	0
	LMA.FE	175	37	9hrs 23mins 20secs
CF12	CF11	0	0	0
	CM07	0	0	0
	LM1	10	6	1hr 12mins 24secs
	LM2	4	5	0
	LMA.FD	3	3	1hr 30secs
	LMA.FE	0	0	0

CM07 only had potential contact phases with CF11 in his core range area, whereas all other potential contact phases occurred with lions within CM07's home range area (*Figure 11*). CM07 potential contact phases occurred mostly in the south-western and central reserve areas.



cheetah individuals on Selati Game Reserve. Polygons of CM07 KUD home and core range estimates are included and ID individuals are cheetahs and lions with temporal overlap of GPS data with CM07. Contact phases are limited to within a 1,750m distance threshold. Contact points have some colour transparency to view overlapping identified points.

CM08 had lots of potential lion contact phases within his home and core range areas, and also two potential contact phases outside either of these areas (*Figure 12*). CM08 potential contact phases were located largely across the western side of the reserve.



*Figure 12*: Potential contact phases identified of cheetah CM08 with other lion and cheetah individuals on Selati Game Reserve. Polygons of CM08 KUD home and core range estimates are included and ID individuals are cheetahs and lions with temporal overlap of GPS data with CM08. Contact phases are limited to within a 1,750m distance threshold. Contact points have some colour transparency to view overlapping identified points.

Many C2.F6 potential contact phases occurred within her core range area, several in the home range area, and one potential phase potentially occurred outside of the home range area (*Figure 13*). Potential contact phases were located mostly in the northern-central area of the reserve.



Most potential contact phases with CF11 happened within CF11's core range with almost all potential phases with LMA.FE occurred in a core area (*Figure 14*). Potential contact phases with CM07 and other lions occurred within both CF11 core and home range areas.



*Figure 14*: Potential contact phases identified of cheetah CF11 with other lion and cheetah individuals on Selati Game Reserve. Polygons of CF11 KUD home and core range estimates are included and ID individuals are cheetahs and lions with temporal overlap of GPS data with CF11. Contact phases are limited to within a 1,750m distance threshold. Contact points have some colour transparency to view overlapping identified points.

Only one potential contact phase potentially occurred within the core range of CF12 with LM1, all other potential lion contact phases occurred in the home range area (*Figure 15*). Potential contact phases were located across the central and south-eastern areas of the reserve.



individuals on Selati Game Reserve. Polygons of CF12 KUD home and core range estimates are included and ID individuals are cheetahs and lions with temporal overlap of GPS data with CF12. Contact phases are limited to within a 1,750m distance threshold. Contact points have some colour transparency to view overlapping identified points.

GLMMs of step length behaviour after contact points and non-contact points indicated statistically significant differences in step length behaviour. CM08 showed differences in step length after contact with LMA.FD ( $R^2c = 0.016$ , df = 1018, p = 0.002). CM07 displayed step length differences after contact with CF11 ( $R^2c = 0.013$ , df = 1099, p = 0.009). C2.F6 displayed differences after contact with LMA.FD ( $R^2c = 0.011$ , df = 1014, p = 0.048). CF11 showed differences in step length after contact with LM1 ( $R^2c = 0.012$ , df = 1164, p = <0.001), LM2 ( $R^2c = 0.014$ , df = 1077, p = 0.004), and LMA.FD ( $R^2c = 0.009$ , df = 1209, p = 0.047). CF12 displayed differences after contact with LM1 ( $R^2c = 0.020$ , df = 1009, p = <0.001), LM2 ( $R^2c = 0.012$ , df = 1002, p = 0.021), and LMA.FE ( $R^2c = 0.013$ , df = 1079, p = 0.009).

#### 5.4. Habitats

Percentage of habitat cover on the reserve was calculated and indicated mixed woodland comprising *C.mopane*, *C.apiculatum*, and *Acacia* sp. to have the highest percent coverage, and *Sporobolus nitens* saline areas to have the least cover (*Figure 16*). Chi squared analysis of habitat use indicated statistically significant differences in habitat use between all cheetah and lion individuals (X-squared = 26477, df = 120, p = < 2.2e-16), and between cheetah individuals (X-squared = 7510.7, df = 40, p = < 2.2e-16) (*Figures 17 and 18*).







Manly's selection ratios indicated habitat preference of both lions and cheetahs (overall habitat selection; Khi2L2 = 45794.95, df = 130, p = 0), between lion and cheetah individuals (identical use of habitat; Khi2L1 = 23334.64, df = 120, p = 0), and between cheetah individuals (identical use of habitat; Khi2L1 = 7771.645, df = 40, p = 0)(*Table A3 and A4*).

Ivlev's electivity indices indicate the strength of preference or avoidance of a habitat along a scale of 1 indicating strong preference, >0.5 indicating preference, 0 indicating indifference, <-0.5 indicating avoidance, and -1 indicating strong avoidance. Indices showed that CM07 strongly avoided 'Sporobolus nitens saline areas' and 'T.sericia, P.squarrosa woodland' habitats, and also avoided 'C.apiculatum, S.birrea mixed woodland', 'C.mopane woodland', 'disturbed areas', 'inselberghs', and 'riverine', while preferring 'C.apiculatum woodland' (Table 11). Electivity indices indicated that CM08 strongly avoided 'disturbed areas with natural drainage' and 'T.sericia, P.squarrosa woodland', avoided 'C.apiculatum, S.birrea mixed woodland', 'inselberghs', 'riverine', and 'Sporobolus nitens saline areas', whilst preferring 'C.apiculatum woodland', 'disturbed areas with natural drainage' and 'T.sericia, P.squarrosa woodland', avoided 'C.apiculatum, S.birrea mixed woodland', 'inselberghs', 'riverine', and 'Sporobolus nitens saline areas', whilst preferring 'C.apiculatum woodland' and 'C.mopane, C.apiculatum mixed woodland'. Ivlev's indices showed that LMF.MF strongly avoided 'Sporobolus nitens saline areas', avoided 'C.apiculatum woodland', 'disturbed areas with natural drainage', 'inselberghs', and 'T.sericia, P.squarrosa woodland', whilst preferring 'disturbed areas' and 'riverine' habitats.

Ivlev's electivity indices show C2.F6 strongly avoided 'C.apiculatum woodland' and 'Sporobolus nitens saline areas', avoided 'C.apiculatum, S.birrea mixed woodland', 'C.mopane, C.apiculatum mixed woodland', 'C.mopane, C.apiculatum, Acacia sp. mixed woodland', 'disturbed areas with natural drainage', 'inselberghs', 'riverine', and 'T.sericia, P.squarrosa woodland', but displayed no habitat preference (Table 11). Electivity indices suggested LE.M01 strongly avoided 'Sporobolus nitens saline areas', avoided 'C.apiculatum woodland', 'C.mopane

woodland', 'disturbed areas with natural drainage', 'inselberghs', and '*T.sericia, P.squarrosa* woodland', but showed no preference for a habitat. Indices showed LMA.FD strongly avoided '*Sporobolus nitens* saline areas', and '*T.sericia, P.squarrosa* woodland', avoided '*C.apiculatum* woodland', '*C.mopane* woodland', and 'disturbed areas with natural drainage', but preferred '*C.apiculatum, S.birrea* mixed woodland', '*C.mopane, C.apiculatum* mixed woodland', 'disturbed areas', and 'riverine' habitats.

Indices indicated CF11 strongly avoided 'Sporobolus nitens saline areas' and 'T.sericia, *P.squarrosa* woodland', avoided 'disturbed areas with natural drainage', and 'inselberghs', but preferred 'disturbed areas' (*Table 11*). Indices for LM1 indicated avoidance of 'inselberghs' and preference for 'disturbed areas', 'riverine', and 'Sporobolus nitens saline areas'. Indices for LM2 showed no strong avoidance for any habitats, but avoidance of 'C.apiculatum woodland', 'C.mopane woodland', and 'inselberghs', with a preference for 'disturbed areas' but no strong preference.

Electivity indices indicated CF12 strongly avoided 'Sporobolus nitens saline areas', and 'T.sericia, P.squarrosa woodland', avoided 'C.mopane, C.apiculatum mixed woodland', and 'C.mopane woodland', and showed no habitat preference (Table 11). Indices indicated that LMA.FE showed strong avoidance for 'C.apiculatum woodland', 'disturbed areas with natural drainage', 'Sporobolus nitens saline areas', and 'T.sericia, P.squarrosa woodland', avoidance of 'C.mopane woodland' and 'inselberghs', but a preference for 'disturbed areas' and 'riverine' habitats.

*Table 11*: Ivlev's electivity indices for habitat preference and avoidance of cheetahs and lions on Selati Game Reserve. Ivlev's electivity indices indicate the strength of preference or avoidance of a habitat along a scale of 1 indicating strong preference, >0.5 indicating preference, 0 indicating indifference, <-0.5 indicating avoidance, and -1 indicating strong avoidance.

avoluance.											
Habitat	CM07	CM08	C2.F6	CF11	CF12	LMF.MF	LE.M01	LMA.FD	LM1	LM2	LMA.FE
C.apiculatum,	-0.74	-0.72	-0.78	-0.31	-0.46	-0.18	-0.48	0.56	0.48	0.04	0.10
S. <i>birrea</i> Mixed											
Woodland											
C.apiculatum	0.53	0.85	-1	-0.07	0.46	-0.84	-0.81	-0.99	-0.08	-0.58	-1
Woodland											
C.mopane,	0.3	0.70	-0.90	-0.35	-0.69	-0.05	-0.39	0.56	0.07	-0.45	0.10
C.apiculatum											
Mixed Woodland											
C.mopane	-0.7	-0.29	-0.29	0.06	-0.98	-0.05	-0.84	-0.62	-0.48	-0.75	-0.95
Woodland											
C.mopane,	-0.40	-0.33	-0.50	-0.29	0.31	-0.05	-0.47	0.43	0.26	-0.25	-0.33
C.apiculatum,											
Acacia sp. Mixed											
Woodland											
Disturbed Areas	-0.57	0.16	0.43	0.71	-0.18	0.87	0.02	0.94	0.95	0.87	0.85
Disturbed Areas	-0.33	-1	-0.67	-0.97	0.22	-0.75	-0.90	-0.90	-0.12	-0.30	-1
with Natural											
Drainage											
Inselberghs	-0.72	-0.81	-0.93	-0.82	0.32	-0.75	-0.86	-0.37	-0.52	-0.79	-0.99
Riverine	-0.71	-0.75	-0.90	-0.27	-0.10	0.54	0.27	0.84	0.66	0.15	0.71
Sporobolus	-1	-0.80	-1	-1	-1	-1	-1	-1	0.67	0.33	-1
<i>nitens</i> Saline											
Areas											
T.sericia,	-1	-1	-0.84	-1	-1	-0.84	-0.84	-1	0.30	-0.31	-1
P.squarrosa											
Woodland											

#### 6. Discussion

This study showed that there are differences in avoidance behaviours of cheetah social structures expressed in both inter- and intra-specific analyses. Males demonstrated weaker avoidance behaviours than females. The newer mother (CF12) expressed the strongest avoidance behaviours employing both proactive and reactive avoidance. The non-breeding female cheetah (CF11) displayed the weakest avoidance behaviour towards lions, however there was still evidence of reactive avoidance via step length analysis and reduced core range overlap with lions. Interestingly, cheetahs seemed to avoid conspecifics more strongly than lions, evidenced by the low to zero core range overlap with conspecifics, and lack of identified contact points except for between CM07 and CF11.

#### 6.1. Spatial usage

Despite extensive electric fencing around the reserve, both lions and cheetahs escaped the reserve boundary on multiple occasions during the study period. Cheetahs exited the reserve to the south via the Selati River fence line towards the small hunting and game breeding farm of Mazunga. The Selati team was often able to push cheetahs back onto the reserve without veterinary intervention (Madeline Siegel, pers. comm). An explanation for cheetahs exiting the reserve could be found in the small home range size estimates of Selati cheetahs. There are numerous reports highlighting the variability of cheetah home range sizes (e.g. Melzheimer et al. (2018) reported male territory holders average home range at 475km<sup>2</sup> and floaters at 1710 km<sup>2</sup>; Marker et al. (2008) reported average home ranges in Namibia at 1651km<sup>2</sup>; Weise et al. (2015) reported home range at 126km<sup>2</sup> and 171km<sup>2</sup> for a female cheetah). Despite this, home range estimates for cheetahs in Selati can be considered as small using these scales. Therefore, movements outside of the reserve boundary could be an expression of greater land use requirements of the species.

Within the reserve, analysis of spatial usage indicated differences in both inter- and intraspecific spatial usage. Female cheetahs displayed larger core and home range estimates compared to males, with the exception of one individual (CF12 KUD method). Larger female home ranges compared to males was also recorded in Caro (1994) and Melzheimer et al. (2018). As proposed in Durant (1998), this could be attributed to the high motility of female cheetahs, allowing them to exploit and successfully hunt smaller prey groups in areas less favoured by other predators where prey and competitor densities are lower ('competition refuges'; Durant 1998). This idea is further corroborated by the finding that lion home and core range overlap is greater with cheetahs than cheetah range overlap is with lion ranges. This suggests female cheetahs may utilise areas not occupied by lions, potentially as a competition refuge.

Male cheetah territories have been described in literature as not only 'smaller than females" but outright 'small' in size (see Durant et al. (2004); Weise et al. (2017); Melzheimer et al. (2018); Broekhuis et al. (2019); Cornhill et al. (2022)) which is also demonstrated in this study. This could be linked to the reported tendency of male cheetah coalitions to repeatedly hunt larger prey compared to female cheetahs (Caro 1994; Mills et al. 2004), potentially requiring less area to meet their hunting needs. In contrast, Hayward et al. (2009) suggest that higher energy input may allow for the maintenance of larger territory sizes. As this study did not measure the influence of prey, inferences regarding spatial usage and hunting strategy in relation to prey are limited. Nonetheless, the findings demonstrate notable differences in spatial utilisation between male and female cheetahs.

This study observed considerable variation in the degree of home range overlap among cheetahs, with a general pattern of substantial overlap in home ranges but reduced overlap in core areas, except for coalition brothers whose spatial overlap increased from home to core range. This coalition overlap was expected as coalition males spend a significant amount of time together as a nature of this social structure (Caro 1994; Marnewick and Cilliers 2006). All cheetahs maintained minimal to no overlap with lions in their core range areas, indicating a degree of proactive spatial avoidance (Cristescu et al. 2013; Cornhill et al. 2022). However, one cheetah (CF11) had a significant 32.14% core range overlap with a lion, the highest observed in the study. The degree of overlap observed did not consistently correlate with cheetahs' sex but seemed to be influenced by breeding status. For example, the inexperienced mother CF12 had no core range overlap with lions, while the non-breeding female CF11 and the more experienced mother C2.F6 showed partial overlap. Cheetah mothers CF12 and C2.F6 also avoided overlapping core ranges with male cheetahs, unlike CF11, who had some overlap. These findings align with previous research in Broomhall et al. (2003), where home range overlap between cheetah males and females was observed, but not within core ranges, which is also mostly seen here. Potential explanations for these spatially overlapping behaviours include reactive avoidance by breeding females towards males and lions to minimize the threat of cub mortality posed by lions and male cheetahs (Laurenson 1994; Durant 2000a; Durant et al. 2004). Cheetah cub mortality rates are high, with reports of up to 75% of cheetah cub deaths being attributed to lion predation (Laurenson 1994; Laurenson 1995b; Durant et al. 2004). Therefore, it would be expected that cheetah mothers would be more vigilant to avoid cub predators whilst with dependant cubs (Durant 2000a).

Further, the metabolic costs of cub rearing might influence spatial behaviour. The data analysis for CF12 included a mating event with CM07 and the birth of three cubs, covering the stages of pregnancy and early motherhood. Inexperienced mothers must expend additional energy to lactate and feed their young cubs along with metabolic demands of denning behaviour which requires the mother to regularly return to the den after feeding, whereas mothers with older, emerged cubs do not need to make this journey as often (Laurenson 1995a). C2.F6 was still caring for a single, adolescent cub that was less dependent, able to feed on kills and learn to hunt (Caro 1994; Durant et al. 2004) reducing the metabolic costs for C2.F6. Moreover, CF12 exhibited smaller home and core range sizes compared to the other females, supporting the link between predator home range size, metabolic costs, and the impact on survival and reproduction (Hayward et al. 2009; Creel 2018; Cornhill et al. 2022).

#### 6.2. Habitat

Male cheetahs displayed a varied response to granite lowveld habitats. Their apparent preference for *C.apiculatum* woodland may be explained by evidence that it is browsed on by impala (Berström et al. 2000), a favoured prey species of cheetahs (Broomhall et al. 2003; Owen-Smith and Mills 2008; Broekhuis et al. 2013; Wilson et al. 2013). In contrast, they avoided *C.apiculatum*, *S.birrea* mixed woodland, *T.sericia*, *P.squarrosa* woodland, and *Sporobolus nitens* saline areas which are also found within the granite lowveld (Rutherford et al. 2006). The granite lowveld is highly variable ranging from areas of tall shrubland to areas of low, dense

woodland (Rutherford et al. 2006; Comley 2019). Open areas are considered conducive to cheetahs' hunting strategy allowing them to reach and maintain high chasing speeds without many landscape obstacles (Mills et al. 2004). Therefore, if the granite lowveld habitats are more densely vegetated, they may be less favoured by cheetahs for hunting, leading to inferred avoidance. Males also appeared to avoid inselberghs and riverine habitats, likely due to the rocky environment of inselberghs creating obstacles (Migoń 2022), while obstacles in riverine habitats could be present as dense areas of vegetation (Naiman et al. 2005). In addition, riverine habitats were demonstrated to be a preferred habitat of several lions during this study, perhaps due to their associated hunting strategy of ambush hunting from vegetation (Broekhuis et al. 2013). Therefore, avoidance of riverine habitats by male cheetahs could be inferred as either unsuitable hunting habitat and/or lion avoidance.

Cheetah mothers (C2.F6, CF12) did not show a habitat preference and also avoided Sporobolus nitens saline areas and T.sericia, P.squarrosa woodland, similar to the male cheetahs. Additionally, both cheetah mothers avoided C.mopane and C.apiculatum mixed woodland (Phalaborwa-Timbavati Mopane Veld), a vegetation type associated with dry, open tree savanna situated on undulating plains (Rutherford et al. 2006). Typically, an open habitat such as this would be considered ideal for cheetah hunting, however there is the suggestion that a moderate level of vegetation cover is advantageous for cheetahs, allowing them to stalk closer to prey undetected, reducing chase distance, and concealing a kill reducing the risk of kleptoparasitism (Purchase and Du Toit 2000; Mills et al. 2004; Bissett and Bernard 2007). In fact, Wilson et al. (2013) found cheetah had higher hunting success in vegetated habitats compared to open habitat. Conversely, increased vegetation has also been reported to hinder hunting success (Mills et al. 2004). For female cheetah mothers, this vegetation can also provide cover to conceal cubs whilst hunting (Bissett and Bernard 2007). Phalaborwa-Timbavati Mopane veld are highly variable habitats (Rutherford et al. 2006), and the results suggest that the composition of these habitats in Selati may not meet the balance cheetah mothers need for cub hiding and hunting efficacy, leading to their apparent avoidance of these areas.

This study did not find that cheetah mothers preferred a habitat, despite suggestions in the literature that female cheetahs choose more densely vegetated areas than males due to stronger avoidance behaviour (Durant 2000b; Broomhall et al. 2003; Bissett and Bernard 2007). The lack of a detected habitat preference could be an indication of avoidance behaviour as Davis et al. (2011) suggested that when a dominant predator is present (lions), the dominant species may occupy its preferred areas while the subordinate species (cheetahs) focuses on avoiding those areas. Nevertheless, analysis did not indicate CF12 extensively avoided preferred lion areas. Further, female cheetah CF11 displayed a preference for disturbed areas, which was also true for lions LM1, LM2, and LMA.FE. These habitat inferences could indicate that non-breeding female cheetahs exhibit weaker avoidance of lion compared to breeding females.

It should be noted that statistical habitat analysis was only applied to first order selection (habitat use compared to the entire study area), and not second order (habitat in home range related to study area) or third order habitat selection (habitat use within the home range area). Habitat selection can be variable at different levels of analysis, so second and third order analysis may provide more insight into individual habitat selection and use (Aebischer et al. 1993; Börger et al. 2020).

#### 6.3. Interactions

GLMMs of cheetah step length behaviour revealed that cheetahs most frequently exhibited reactive avoidance to lions than between cheetahs. Female cheetahs exhibited more frequent significant post-contact responses to lions, with males only exhibiting one significant result in response to lion contact. In addition, the IAB index indicated a degree of attraction between CM07 and lions, and several potential contact points with lions occurred within the core ranges of both male cheetahs. This could be evidence of male coalitions being less fearful of other predators due to group size making them less vulnerable than solitary individuals, such as the females (Caro 1994; Palomares and Caro 1999; Broomhall et al. 2003; Bissett and Bernard 2007).

Avoidance behaviours between female cheetah individuals is less expected as there have been no recordings of fatal interactions between two female cheetahs (Broekhuis et al. 2019). Therefore, the separation in spatial use is more likely to be a factor of habitat quality or competition between females. In contrast, male cheetah movements are often largely influenced by female cheetah movements (Melzheimer et al. 2018). Spatial overlap between male and female cheetah has been proposed as a strategy to increase mating potential, with splitting of coalitions observed as a male investigates females in oestrus (Caro 1994; Broomhall et al. 2003; Marnewick and Cilliers 2006). Evidence of this can be seen in contact analysis where CM07 and CF11 had the greatest number of potential contacts and the longest contact phase duration between the cheetahs, along with IAB index analysis between CM07 and CF11 indicating significant attraction at <1750m. In contrast, no other interspecific contact phases were identified between other cheetahs.

CF12 displayed the strongest evidence of avoidance behaviour with evidence of proactive avoidance. Proximity analysis revealed that CF12 never exceeded 18.6% of GPS points within distance thresholds with lions. Additionally, the IAB index identified statistically significant avoidance patterns by CF12 towards two lions within 1750m. Due to the vulnerable nature of cubs, cheetah mothers conceal cubs in a fixed place and are vigilant to not reveal their location by lying down and often returning to the hiding spot at night (Laurenson 1994). Therefore, it would be expected that CF12 displayed avoidance behaviours to avoid revealing the location of her young cubs. However, the DI statistic may not be suitable for identifying avoidance behaviours expressed as hiding, as it involves the analysis of turn angles which are less likely to occur during hiding behaviours.

Analysis of non-breeding female cheetah CF11 indicated a large number of potential contact points with lions within one of her core range areas and the most overall contact phases between cheetahs and lions. The GLMM analysis also indicated significant differences in step lengths after potential contact with lions, suggesting a reactive avoidance response. Avoidance behaviours incur costs that impact survival, reproduction, or growth, therefore the individual must perceive the level of risk and alter responses accordingly (Ruxton and Lima 1997; Creel et al. 2007; Broekhuis et al. 2013; Creel 2018). Reactive avoidance responses are considered riskier with higher costs than proactive avoidance (Cornhill et al. 2022), and this evidence of reactive avoidance by CF11 may relate to the energy costs. For instance, the ability to exhibit riskier behaviours due to increased energy availability without the constraints of dependent cubs or pregnancy. Additionally, C2.F6, which occupied a similar area of the reserve to CF11, had fewer potential contacts and degree of overlap with lions than CF11, providing evidence that riskier strategies may be exhibited by females without dependent offspring.

#### 6.4. Game Management

Understanding spatial usage and behaviours of species has direct reserve management applications (Seaman and Powell 1990). Combining spatial usage, social structure, and related sex differences can be extrapolated to infer mortality, mating systems and subsequent reproductive strategies and interactions of a species (Melzheimer et al. 2018). Maximum cheetah density in Selati was around the highest of reported densities found in protected areas (~0.02km<sup>2</sup> (Durant et al. 2017); Selati max. density = 0.019 (n = 5)) and estimated home range sizes in the study are reportedly low. Home range estimations are a tool used by management to inform species management and removal requirements (Börger et al. 2020). Despite this, analysis here does not seem to indicate conflict for space or unusual avoidance behaviours by cheetahs on Selati. Spatial conflict between cheetahs can lead to negative population impacts, such as death as male conspecifics fight over territory (Caro 1994; Melzheimer et al. 2018) and high levels of stress cane reduce reproductive success (Cornhill et al. 2022). The spatiotemporal partitioning observed in this study between cheetahs and lions is positive for small game reserves and cheetah conservation as it indicates healthy cheetah populations can be sustained on small reserves. Despite this, this study adds to inferences that cheetah habitat and spatial usage is highly variable, and results should be interpreted at the local scale.

#### 6.5. Methods

Inferences must be considered under several methodological notations. Firstly, the chosen sampling rate of GPS data acquisition (i.e. GPS gap length) is extremely important as it determines the resolution and scale at which the analysis can be conducted (Pépin et al. 2004; Noonan et al. 2019; Signer and Fieberg 2021). Given this, the calculated standard deviation of step length analysis using the given gap length was ±6176.2m (mean step length = 3563.5m). This level of variability is not uncommon given the inherent challenges of GPS data, and the known limitations of step length and dynamic movement analysis methods, which often include significant 'noise' in their estimations (Frair et al. 2010). However, it does mean that inferences presented in this study should be interpreted with caution.

Accurate bandwidth calculations in spatial analysis methods are also important (Hemson et al. 2005; Börger et al. 2020). Here, KUD bandwidth (href) was chosen at 80% href based on recommendations from Broekhuis et al. (2019), however visualisation of results revealed consistent spillover beyond reserve boundaries, indicating the smoothing factor was too large leading to potential over-estimation (Hemson et al. 2005). Other methods for choosing an appropriate smoothing factor for home range estimates include using likelihood cross-validation (CV) or least-squares cross-validation (LSCV) (Hemson et al. 2005; Börger et al. 2020). Nevertheless, all methods have limitations, for example the LSCV method does not cope well with repeated data points which is a likely occurrence in territorial animals, denning individuals, and large data sets (Hemson et al. 2005).

The methodology used for calculating KUD and the KUD overlap varied slightly resulting in minor differences in the conclusions drawn from KUD estimations across individuals. This was necessary to compare across individual object lengths which had to be restricted to the same grid parameter using the argument 'same4all' (Calenge 2023). The argument was not used in KUD estimations for individuals in an attempt to provide more ecologically relevant results. This highlights the sensitivity and importance of using accurate and relevant thresholds and parameters in spatial data analysis.

Additionally, statistical analysis of habitats in this study was not entirely ecologically representative as analysis assumed definite lines of habitat boundaries which is not strictly true. Methods proposed to address this are to add a smoothing factor to boundary lines of habitats, or calculating a proximity measurement to all habitat types to avoid the assumption of only one habitat association (Frair et al. 2010). However, due to the high degree of variability of the spatial data, basic definitive habitat boundary lines seemed appropriate here.

The MCP and KUD methods used in this study did not include a temporal aspect. Including a temporal factor allows for a dynamic approach to spatial analysis (Kie et al. 2010) which is much more ecologically representative, and also allows for mitigation against the autocorrelation issues (non-independence of spatial points) associated with spatial data (Noonan et al. 2019). Methods such as also KDE assume GPS points are independent, which is not strictly true (Noonan et al. 2019). Therefore, methods such as Autocorrelated Kernel Density Estimators (aKDE) may be more appropriate as a smoothing factor is used based on the degree of autocorrelation in the data to reduce any impacts temporal bias (Fleming et al. 2015; Börger et al. 2020; Signer and Fieberg 2021).

#### 6.6. Further Work

This study inferred movement pattern differences on the basis of avoidance and habitat use, however other factors are acknowledged that could motivate predator movements. For example, the movements of prey populations have been demonstrated in literature to influence predator movements. Broekhuis et al. (2013) attributed the observed differences in habitat use between lions and cheetahs in their study to the related hunting strategies of each species. Broomhall et al. (2003) reported a significant positive correlation between the spatial distribution of female cheetahs and the distribution of impala, with the inferred driver being the heightened nutritional requirements of female cheetahs during critical reproductive stages such as pregnancy, lactation, and cub rearing (Laurenson 1995b). Additionally, Hayward et al. (2009) and Spong (2002) state prey availability as an explanatory factor for variations observed in home range sizes. Therefore, inclusion of a prey factor into future analysis may allow for more accurate inference of the motivator behind cheetah movement behaviours, such as inference to the occurrence and degree of the theory of competition refuge utilisation by cheetahs (Durant 1998).

The factors of metabolic and energy expenditure were discussed frequently in this study, therefore a measure of energy expenditure could provide more insight. This can be achieved via the analysis of movement speed and path straightness indicating activities such as walking, running, and resting which can be extrapolated to infer hunting, hiding, or travelling activities (Morales et al. 2004; Merrill et al. 2010; Wilson et al. 2013). Analysing the activity type along with additional habitat use details could provide insights into the motivators behind habitat selection and related activities (Wilson et al. 2013). However, this type of data analysis would require more regular GPS pings (reduced gap length) to achieve fine-scale data for activity inference (Feng and Timmermans 2015) which would result in a shorter study duration due to increased GPS unit power consumption (Pépin et al. 2004).

Scent marking is an integral part of cheetah ecology providing spatial, territorial, and reproductive indicators to conspecifics (Broomhall et al. 2003; Broekhuis et al. 2019). This study's findings of spatial overlap but lack of potential contact points could be an indication of olfactory communication by cheetahs in Selati. Static landscape features such as trees,

shrubs, logs, or termite mounds are often utilised by cheetahs as scent marking posts, (Broomhall et al. 2003; Broekhuis et al. 2019). Accordingly, analysing the spatial distribution and frequency of visits by cheetahs to such marking locations could provide insights into cheetah social structures and behavioural motivations for movement. Including scent marking posts in spatial analysis could help identify cheetah movement patterns or indicate important olfactory communication areas on the reserve. If important areas are identified, they could be protected to enhance cheetah conservation by maintaining cheetah social dynamics.

This study did not include any non-coalition males within the population. As mentioned, solitary males have been shown to demonstrate different spatial use behaviours than coalition males (Durant et al. 1988; Marker et al. 2008; Melzheimer et al. 2018). Therefore, to be able to inform reserve management decisions alongside cheetah conservation, further studies with the inclusion of all social structures should be analysed to inform viable population structures and translocation efforts between game reserves.

#### 7. Conclusion

Understanding intra- and inter-specific interactions is an important aspect of population dynamics as interactions drive components of competition, sociality, disease transfer, mating events, and mortality (Broekhuis et al. 2019). This study provides evidence of differing spatial use between cheetah sexes but also within sexes expressed via breeding status. Avoidance behaviours in this study are expressed as core range area overlap reduction and temporal partitioning, however the degree and type of avoidance expression differs between social structures. Explanations for differences in avoidance behaviours were inferred to be due to the differences in energy expenditure budgets between social structures. In Selati, cheetah density is higher than the natural average and home range sizes are small, however this study's results indicate this is not causing abnormal inter- or intra-specific conflict with natural behaviours still being exhibited by cheetahs on Selati.

# <u>8. Appendix</u>

Table A1: Individual information of cheetahs on Selati Game Reserve including ID, sex, date of birth, place of birth, parents (if known), date of introduction to the game reserve (GR), date collared with a Long Range GPS collar (LoRa), date relocated from the reserve (if applicable), date of death (if applicable), and comments on the death (if applicable).

Cheetah	Sex	Date of	Place of	Mother	Father	Date of	Date Collared	Date	Date of	Death Comments
ID		Birth	Birth			Introduction	(LoRa)	Relocated	Death	
C2.F6	Female	23/11/2018	Selati GR	CF01	CM01	-	12/06/2022	16/03/2023		
CM07	Male	01/08/2018	Nambiti GR	-	-	03/06/2020	27/07/2023	-	-	
CM08	Male	01/08/2018	Nambiti GR	-	-	03/06/2020	01/04/2022	-	26/02/2023	Euthanised after
										being hit by a car on
										R526
C6.F9	Female	01/08/2021	Selati GR	C2.F6	CM07/CM08	-	-	01/03/2023	-	
C6.M10	Male	01/08/2021	Selati	C2.F6	CM07/CM08	-	-	-	24/03/2022	Hit by a car on R71
CF11	Female	25/08/2021	Mabula GR	Blue Canyon	Mabula GR	17/04/2023	17/04/2023	27/02/2024	-	-
				PGR						
CF12	Female	01/02/2021	Tswalu GR	-	-	09/06/2023	08/06/2023	-	-	-
C12.F13	Female	16/10/2023	Selati GR	CF12	CM07	-	-	-	-	-
C12.F14	Female	16/10/2023	Selati GR	CF12	CM07	-	-	-	-	-
C12.M15	Male	16/10/2023	Selati GR	CF12	CM07	-	-	-	-	-

Table A2: Individual information of lions on Selati Game Reserve including ID, date of birth, place of birth, parents (if known), date of introduction to the game									
reserve (GR), date collared with a Long Range GPS collar (LoRa), date relocated from the reserve (if applicable), date of death (if applicable), and additional									
comments	(if applicable).								
Lion ID	Date of	Place of	Mother	Father	Date of	Date Collared	Date	Date of	Comments
	Birth	Birth			Introduction	(LoRa)	Relocated	Death	
Matumi	01/01/2009	Makalai GR	-	-	2012	-	-	14/06/2023	-
Acacia	01/03/2009	Makalai GR	-	-	2012	-	-	06/06/2023	-
Mfuti	01/07/2011	Makalai GR	Acacia	Mburri	2012	-	-	26/05/2022	-
Dela	05/02/2015	Selati GR	Acacia	Mbhurri	-	11/03/2022	-	16/06/2022	-
LMA.MC	01/10/2017	Selati GR	Matumi	Mbhurri or Dela	-	24/10/2022	01/10/2022	-	-
LMA.FD	01/10/2017	Selati GR	Matumi	Mbhurri or Dela	-	10/08/2022	-	-	-
LMA.FE	01/10/2017	Selati GR	Matumi	Mbhurri or Dela	-	20/07/2023	-	-	-
LMF.MF	01/09/2019	Selati GR	Mfuti	Dela	-	23/11/2021	-	11/06/2022	-
LE.M01	01/01/2020	Selati GR	LMA.FE	Dela	-	12/08/2022	04/10/2022	-	-
LE.M02	01/01/2020	Selati GR	LMA.FE	Dela	-		-	11/06/2022	-
LE.M03	01/01/2020	Selati GR	LMA.FE	Dela	-		04/10/2022	-	-
LMA.M04	21/06/2020	Selati GR	Matumi	Dela	-		-	05/12/2022	-
LD.F21	15/02/2022	Selati GR	LMA.FD	Dela or LMA.MC	-		-	-	-
LD.F22	15/02/2022	Selati GR	LMA.FD	Dela or LMA.MC	-		-	-	-
LM1	2013	Kwande GR	-	-	01/03/2023		-	-	In boma 01/03/2023 – 20/03/2023
LM2	Aug 2013	Lalibela GR	-	-	01/03/2023		-	-	In boma 01/03/2023 – 20/03/2023
LE.F23	15/03/2022	Selati GR	LMA.FE	-	-		-	-	Disappeared 2023
LE.M24	15/03/2022	Selati GR	LMA.FE	-	-		14/10/2023	-	-
LE.M25	15/03/2022	Selati GR	LMA.FE	-	-		14/10/2023	-	-
LD.M31	11/08/2023	Selati GR	LMA.FD	-	-		-	-	-
LD.F32	11/08/2023	Selati GR	LMA.FD	-	-		-	-	-
LD.F33	11/08/2023	Selati GR	LMA.FD	-	-		-	-	-
LE.F34	25/102023	Selati GR	LMA.FE	-	-		-	-	-
LE.M35	25/10/2023	Selati GR	LMA.FE	-	-		-	-	-



(RStudio-Team 2020) using the package 'leaflet'(Cheng et al. 2024).

Table A3: Output table from Manly's Selection Raito in RStudio (RStudio-Team 2020) using the package 'adehabitatHS' (Calenge and Basille 2023a) based on habitat information and GPS data from 5 cheetahs and 8 lions on Selati Game Reserve from 1<sup>st</sup> January 2022 to 31<sup>st</sup> December 2023. Columns are the habitat types found on Selati Game Reserve, the proportion of habitat available (Available), the proportion of habitat used (Used), the Manly's Selection measure (Wi), the standard error (SE), the lower limit of confidence intervals for selection ratios (IClower), and the upper limit (ICupper).

Habitat	Available	Used	Wi	SE	IClower	ICupper
C.apiculatum, S.birrea mixed woodland	0.088	0.075	0.852	0.159	0.401	1.302
C.apiculatum woodland	0.054	0.084	1.565	0.944	-1.114	4.242
C.mopane, C.apiculatum mixed woodland	0.087	0.108	1.246	0.367	0.204	2.289
C.mopane woodland	0.158	0.050	0.318	0.121	-0.026	0.663
C.mopane, C.apiculatum, Acacia sp. mixed	0.413	0.328	0.794	0.097	0.519	1.068
woodland						
Disturbed areas	0.010	0.099	9.726	2.289	3.232	16.220
Disturbed areas and natural drainage	0.020	0.006	0.298	0.135	-0.085	0.680
Inselberghs	0.066	0.018	0.267	0.141	-0.132	0.666
Riverine	0.098	0.229	2.356	0.538	0.828	3.883
Sporobolus nitens saline areas	0.003	0.002	0.546	0.378	-0.527	1.620
T.sericia, P.squarrosa woodland	0.004	0.001	0.205	0.136	-0.181	0.590

Table A4: Output table from Manly's Selection Raito in RStudio (RStudio-Team 2020) using the package 'adehabitatHS' (Calenge and Basille 2023a) based on habitat information and GPS data from 5 cheetahs on Selati Game Reserve from 1<sup>st</sup> January 2022 to 31<sup>st</sup> December 2023. Columns are the habitat types found on Selati Game Reserve, the proportion of habitat available (Available), the proportion of habitat used (Used), the Manly's Selection measure (Wi), the standard error (SE), the lower limit of confidence intervals for selection ratios (IClower), and the upper limit (ICupper).

Habitat	Available	Used	Wi	SE	IClower	ICupper		
C.apiculatum, S.birrea mixed woodland	0.088	0.028	0.312	0.116	-0.018	0.643		
C.apiculatum woodland	0.054	0.239	4.441	1.730	-0.469	9.351		
C.mopane, C.apiculatum mixed woodland	0.087	0.174	1.998	0.977	-0.776	4.771		
C.mopane woodland	0.158	0.088	0.558	0.296	-0.286	1.402		
C.mopane, C.apiculatum, Acacia sp. mixed	0.413	0.358	0.868	0.300	0.018	1.718		
woodland								
Disturbed areas	0.010	0.026	2.522	1.524	-1.803	6.846		
Disturbed areas and natural drainage	0.020	0.011	0.532	0.331	-0.407	1.472		
Inselberghs	0.066	0.036	0.553	0.395	-0.569	1.675		
Riverine	0.097	0.040	0.412	0.171	-0.074	0.897		
Sporobolus nitens saline areas	0.003	0	0.026	0.022	-0.035	0.087		
T.sericia, P.squarrosa woodland	0.004	0	0.021	0.025	-0.049	0.091		



*Figure A2*: GPS tracks of cheetah C2.F6 on Selati Game Reserve during 25<sup>th</sup> August 2022 to 29<sup>th</sup> November 2022 . GPS tracks were created using RStudio (RStudio-Team 2020) using the package 'adehabitatLT' (Calenge et al. 2023) and plotted on top of a colour-coded habitat maps on the game reserve.



tracks were created using RStudio (RStudio-leam 2020) using the package 'adehabitatLI' (Cale and plotted on top of a colour-coded habitat maps on the game reserve.



*Figure A4*: GPS tracks of cheetah CF11 on Selati Game Reserve during 17<sup>th</sup> April 2023 to 18<sup>th</sup> December 2023. GPS tracks were created using RStudio (RStudio-Team 2020) using the package 'adehabitatLT' (Calenge et al. 2023) and plotted on top of a colour-coded habitat maps on the game reserve.





*Figure A6*: GPS tracks of cheetah CM07 on Selati Game Reserve during 27<sup>th</sup> July 2023 to 31<sup>st</sup> December 2023. GPS tracks were created using RStudio (RStudio-Team 2020) using the package 'adehabitatLT' (Calenge et al. 2023) and plotted on top of a colour-coded habitat maps on the game reserve.

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