Driving giants: spatial and temporal variables influencing giraffe movements in a private protected area

By

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ABSTRACT

Spatiotemporal factors play important roles in shaping interactions between species within ecosystems, influencing their behavior and survival strategies. For predator/prey interactions, survival of the prey may rely heavily on spatial and temporal characteristics of the landscape together with species-specific behavioral strategies. The fear of predation prompts antipredator responses in prey which include vigilance behavior, grouping, and shifts in habitat selection. However, these responses may incur costs, impacting energy expenditure of prey and time allocation of prey activities such as foraging, sleeping, drinking, and fleeing predators.

This study investigates spatiotemporal habitat use characteristics of southern giraffes (*Giraffa giraffa*) and lions (*Panthera leo*) within a small private protected area in South Africa where lions are the primary predator of giraffes. Giraffes are most vulnerable to predation when young, sick, or when in a splay-legged position while drinking water. In addition to direct predation risk, the presence of lions in the landscape may influence a 'landscape of fear', triggering general antipredator behaviors. Giraffe movement and landscape use within the reserve may therefore be strongly influenced by the presence of lions, together with various environmental factors such as water accessibility, habitat preferences, and the need for sufficient food intake to meet their substantial daily energy requirements.

This study uses GPS collar data collected over two years from simultaneously collared lions and giraffes in a private game reserve in South Africa's North West Province, the !Khamab Kalahari Nature Reserve. Using this data, t-LoCoH home ranges were calculated to identify patterns of seasonal change and overlap between lions and giraffes. Resource selection function models (RSFs) were then used to identify spatiotemporal variables that influence giraffe movement in a landscape with lions. Variables were resource proximity, including distance to waterholes, NDVI, land cover, landforms, a predation risk variable, and temporal variables, seasonality and time of day.

There was high overlap between all lion and giraffe home ranges (73.9 to 92.2%), suggesting a high probability of encounters between the two species in the reserve. RSFs revealed season, time of day, proximity to waterholes, NDVI, and land cover were significant predictors of giraffe habitat and resources use. Importantly, 'distance to the closest lion' was also included as a significant variable in the best-fit model. The findings suggest that, within this reserve, giraffes select for areas of higher NDVI and those closer to waterholes. Their presence in the landscape also suggests some avoidance of lions, preferring sites further from lions. In terms of land cover, giraffes selected areas with woodland and transformed land despite their lower proportion on the reserve. Grasslands, the most abundant land cover type, exhibited neither preference nor aversion.

Overall, this study identified four spatial variables and two temporal variables that influence giraffe movement within this fenced, semi-arid, small reserve. The insights gained are valuable for understanding how predators impact prey species in managed game reserves, where natural ecological processes may be disrupted to varying degrees and necessitate careful management. Furthermore, given the significance of giraffes as tourist attractions, understanding their ecological requirements is crucial for both their welfare and effective reserve management.

Keywords: predation, antipredator response, resource selection function models, t-LoCoH, home ranges, southern giraffe

Note: the spelling of words in this thesis follows the rules of American English.

INTRODUCTION

Spatial heterogeneity describes the complexity of a landscape, which in turn influences the movement and behavior of animals (Li and Reynolds 1994; Colling 2010). These movements and behaviors are assessed on spatial and temporal scales and affect ecosystem dynamics and ecological processes through nutrient cycling, energy flows, habitat modification, and trophic processes (Lacher et al. 2019). More specifically, mammals and herbivores affect the modification of plant communities through foraging patterns, local nutrients via excretions, carbon and nitrogen cycles through grazing and trampling of plants and influencing predator-prey relationships (Huntly 1991; Singer and Schoenker 2003; Sinclair 2003; Tuomi et al. 2018). The movement of animals in spatially heterogeneous environments is influenced by multiple factors, including body size and resource productivity that may be affected temporally by factors like seasonal variation in vegetation (Duncan et al. 2005), predation risk, prey density, and habitat structural complexity and seasonality (Bowman and Huffaker 1958; Harper 1969; Harris 1980). Together, these factors impact multiple ecosystem processes, such as nutrient availability, host-parasite interactions, predator-prey relationships and where cover may provide refuge for prey species (Holling 1965).

Defining spatial heterogeneity in landscapes shapes our understanding of the relationships between spatial variables and landscape function and processes (Li and Reynolds 1994). Greater spatial heterogeneity facilitates a larger number of ecological niches, fostering variation between organisms (Bazzaz 1975; Massé and Côté 2012). An increase in organisms and species leads to increased complexity in their interactions and relationships, including predator-prey relationships (McCoy and Bell 1991). Additionally, the patchiness of vegetation types within a habitat may influence behavioral changes in herbivores, promoting selective foraging in preferred food patches (Senft et al. 1987; Barraquand and Benhamou 2008). Seasonality, as a driver of forage quality, may further influence herbivore behavior, altering vegetation heterogeneity, especially during drier months when vegetation is scarce (Thouless 1995; Duncan et al. 2005). Further, topography may influence resource availability; for instance, a resource-rich patch on a cliff face may be inaccessible to megaherbivores like elephants (Kimuyu et al. 2020).

The role of megaherbivores in creating spatial heterogeneity

Megaherbivores, including elephants (*Loxodonta africana*), rhinoceros (Rhinocerotidae spp.), hippopotamus (*Hippopotamus amphibius*), and giraffes (*Giraffa camelopardalis*), exhibit a preference for resource-rich patches to meet their high food-intake requirements while minimizing energy expenditure (Kimuyu et al. 2020). These animals weigh >10^3 kg and consume large quantities of vegetation with impacts on plant dynamics and ecology (Owen-Smith 1988; Fritz et al. 2002). These impacts include removal of vegetation causing competition between other smaller herbivores as well as trampling of vegetation which restructures the landscape (Owen-Smith 1988; Haynes 2012). On the other hand, these disruptions to vegetation can lead to regrowth in the understory vegetation which encourages more selective species growth (Owen-Smith 1988). A study focusing on *Acacia* species in the Serengeti found a reduction in canopy cover due to destruction by elephants, but growth was then suppressed by giraffe browsing inhibiting mature canopy recovery (Pellew 1983). A similar study near the Caprivi strip of Northern Botswana, showed reduction in canopy cover of several tree species and growth was similarly suppressed by giraffes, kudu, and impala in the area (Teren et al. 2016). Furthermore, high densities of giraffes in South Africa have led to tree mortality by intense herbivory causing local extinctions of *Acacia* species (Bond and Loffell 2001). Megaherbivores thus influence spatial heterogeneity as well as being influenced by it.

Predator-prey interactions and the landscape of fear

Predator-prey relationships constitute fundamental ecological dynamics that play a pivotal role in preserving the equilibrium of ecosystems and exerting evolutionary pressures (Holling 1965; Lima and Dill 1990; Polis and Strong 1996; Sih et al. 1998; de Boer et al. 2010). An overabundance of predators can trigger a decline in prey species, precipitating a subsequent collapse in predator population (Hairston et al. 1910; Preisser et al. 2007). Predators instill fear in their prey, prompting behavioral adaptations and giving rise to what is referred to as ‘landscapes of fear’ (Brown et al. 1999; Laundré et al. 2001; Laundré et al. 2010). While this concept is debated in large herbivores owing to limited experimental data (Riginos 2014), it is supported by evidence, such as increased vigilance in elk in Yellowstone following the reintroduction of wolves (Laundré et al. 2001). The landscape of fear has been shown to be dynamic in the South African savanna context, depending on environmental context such as predation risk, and if forage was preferred or available (Davies et al. 2020).

The dynamics of the landscape of fear are influenced by the physical landscape, predator biology (such as hunting mode), prey biology (such as prey size), and the distribution of both predator and prey (Gaynor et al. 2019). Moreover, risk and perception come into play, encompassing indirect and direct cues (such as refugia), sensory perception, and evolutionary history (Gaynor et al. 2019). These variables collectively contribute to the creation of the landscape of fear, eliciting responses that consider the costs and benefits of the response of prey, individual condition, and consequently impact foraging, movement, and social behaviors (Gaynor et al. 2019). While organisms contend with a multitude of habitat-related features that influence their survival, these variables can be amplified or altered within their landscapes (Hernández and Laundré 2005; Courbin et al. 2015).

Anti-predator behaviors in herbivores

Predators influence prey through two primary mechanisms: direct killing and non-consumptive effects, also termed antipredator behaviors (Preisser et al. 2007). Antipredator behaviors encompass a range of responses, including changes in prey group size, shifts in spatial distributions of prey, preferential habitat selection, modifications to prey assemblages, and heightened vigilance behaviors (Turchin and Karieva 1989; Kotler et al. 1991; Brown and Kotler 2004; Caro 2005; Périquet et al. 2010). These behaviors may take a proactive form, involving preemptive risk assessment and behavioral adjustments, or a reactive form, triggered by immediate threats that prompt prey to either flee or stay in the area (Courbin et al. 2015).

Antipredator behaviors, while crucial for survival, are not without costs. Movement away from essential resources such as food (Brown et al. 1999), water (Valeix et al. 2009a), or preferred habitats (Holt 1984; Creel et al. 2005) introduce trade-offs that shape evolutionary behavior and behavioral ecology (Brown and Kotler 2004; Courbin et al. 2015). These trade-offs not only impact energy expenditure but also influence time allocation (Brown and Kotler 2004). For instance, seeking safer habitats may decrease foraging opportunities. Evidently, these trade-offs significantly influence prey behavior (Courbin et al. 2015). Costs associated with these trade-offs are important when considering prey dynamics, as they impact body condition and health, such as decreased feeding rates, altered diets, stress, decreased body condition, and lower fecundity, with impacts on species fitness (Werner et al. 1983; Kotler et al. 1991; Clinchy et al. 2004; Christianson and Creel 2008).

Prey continually engage in behaviors that attempt to outweigh costs with benefits. Prey species consider environmental variables like cover and distance to safety (Preisser et al. 2007;

Périquet et al. 2009). The innate fear response to predators, the degree of threat posed by the predator (Makin et al. 2017), and predator cues including predator body language (Preisser et al. 2007), such as a stalking position, are also considered when making the decision to flee (Makin et al. 2017).

Which variables influence predation?

Predation, as an ecological driver, significantly influences resource selection by prey species and influences broader landscape-level movements (Fortin et al. 2005; Valeix et al. 2009a; Valeix et al. 2009b). The predator-prey relationship has been the subject of extensive study, revealing landscape-level variables that significantly impact the antipredator behavior of prey species (Huffaker 1958; Holling 1965; Harper 1969; Bowman and Harris 1980). Among the many landscape-level variables, habitat type, water availability, and anthropogenic features, such as roads, are prominent determinants of prey behavior (Fortin et al. 2005; Valeix et al. 2009a; Périquet et al. 2010; DeMars and Boutin 2018). Further, whether a habitat is open or closed can play a role in shaping the vigilance capabilities, as well as access to physical refugia for prey species (Holling 1965). In open landscapes, herds of impala, for example, can strategically scan the surroundings to detect potential predators, while closed landscapes may provide additional physical refugia for prey species seeking safety.

Water availability significantly influences animal movement and, consequently, predation dynamics (Valeix et al. 2009a; Périquet et al. 2010). Given the essential need for water in the daily lives of most mammals, waterholes become focal points for their movements, especially during arid seasons when alternative water sources are scarce (Mills and Retief 1984; Valeix et al. 2009a; Périquet et al. 2010; Courbin et al. 2015). Importantly, variables such as the direct presence of predators, the likelihood of predator encounters, as well as proximity to protective cover significantly influence prey decisions at waterholes (Périquet et al. 2010). A comprehensive understanding of habitat utilization and seasonal shifts in resource availability can help optimize individuals' fitness and balance the costs and benefits of antipredator behaviors.

Study species

Southern giraffes (Giraffa giraffa)

Giraffes inhabit a diverse array of habitats including deserts, savannas, and woodlands (Fig. 1; Muller et al. 2018a; Muller et al. 2018b). As megaherbivores, they are unique in their role as obligate browsers, feeding primarily from trees, setting them apart from most other ungulates (Pellew 1984). Their preferred habitats are woodlands dominated by *Acacia* species, where they browse on plants with heights ranging from 2 to 5 meters (Cameron and du Toit 2007; Mallon et al. 2013; Deacon 2015).

Fig. 1. Southern giraffes *Giraffa giraffa*) in different habitats depicting from left to right, the desert landscape of Etosha National Park, Namibia (Renate n.d.), woodland in Kruger National Park, South Africa (Schell n.d.), and a Masai giraffe (*Giraffa tippelskirchi*) in the open savanna of the Masai Mara, Kenya (Masai Mara Travel n.d.).

While historically thought to be a single species, recent complete genome studies of geographically dispersed giraffes have challenged this belief (Bock et al. 2014; Coimbra et al. 2022; Bertola et al. 2024). Coimbra et al. (2022) identified four distinct evolutionary lineages: southern giraffes (*G. giraffa*), Masai giraffes (*G. tippelskirchi*), reticulated giraffes (*G. reticulata*), and northern giraffes (*G. camelopardalis*; Fig. 2). Despite this, the International Union for Conservation of Nature (IUCN) collectively list these species as a single species which is considered vulnerable with a decreasing population (Muller et al. 2018b). In a 2021 assessment of giraffe populations, Brown et al. (2022) estimated there to be approximately 117,173 giraffes across 21 different countries. However, when considering population size per species, estimates were lower, and some were classified as endangered rather than vulnerable (Brown et al. 2022). The recognition and division of this species into four distinct species may lead to a change in status and a reconsideration of conservation strategies, as seen in other species (Comstock et al. 2008; Cotterill et al. 2014; Taylor et al. 2019; Coimbra et al. 2022). This study focuses on southern giraffes (*Giraffa giraffa*) in the !Khamab Kalahari Nature Reserve but will refer to them as giraffes hereon. Southern giraffe numbers are estimated at ~49,867 individuals in total (Brown et al. 2022).

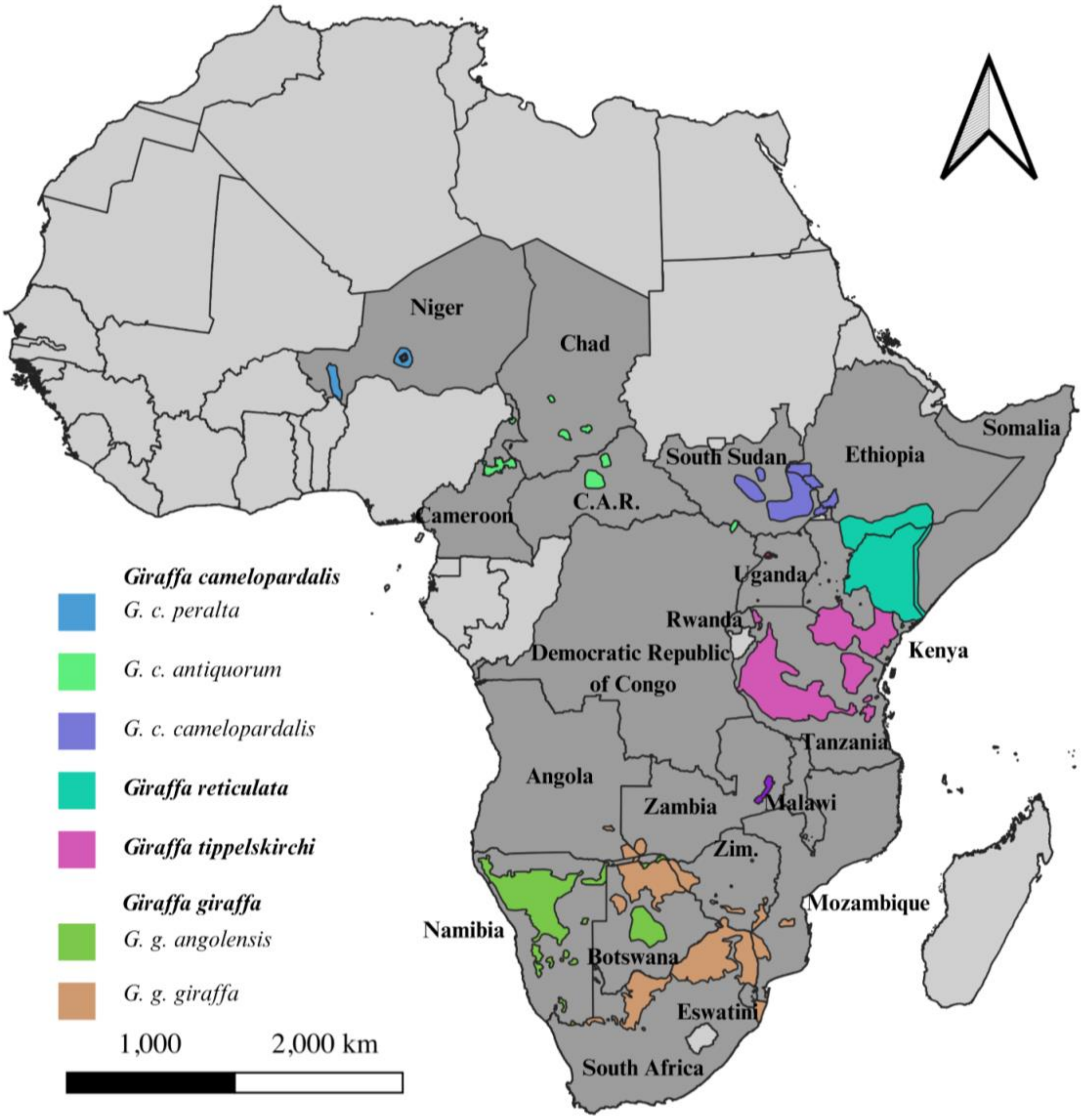


Fig. 2. A distribution map of the four currently recognized giraffe species in Africa and their subspecies (Fennessy et al. 2016), reproduced from Brown et al. (2022).

Giraffes form social groups based on linear hierarchies based on kinship, home-range overlap, social preferences, and age structure within the populations (Horová et al. 2000; Bercovitch and Berry 2013a; Bercovitch and Berry 2013b; VanderWaal et al. 2013; Carter et al. 2013;

Muller et al. 2018a). Group sizes vary from three to nine individuals, and this can vary with season, geographical location, and giraffe population density (Muller et al. 2018a). Unlike other ungulates, predation risk is not the primary determinant of grouping behaviors in giraffes (Creel et al. 2014). Lions prefer to hunt small groups of prey which giraffes form (Creel et al. 2014). Therefore, large group formation as an antipredator response seen in other species such as zebra and wildebeest are not apparent in giraffes and other antipredator behaviors are prioritized (Scheel 1993; Creel et al. 2014; Thaker et al. 2010). Small groups also form when female giraffes have calves, creating crèches which increase probability of survival (Bercovitch & Berry 2013b). Calves raised in the same cohort spend most, if not all, of their lives together. However, males do disperse to be solitary or form loose male-male associations (Bercovitch & Berry 2013a; Bercovitch & Berry 2013b).

The primary predator of giraffes is the lion (*Panthera leo*) (Cameron and du Toit 2005). Due to their large size, giraffes are vulnerable to lion predation mainly when young, sick, or while drinking water due to their splay-legged posture (Valeix et al. 2009a; Strauss and Packer 2012). Because predation risk is high around waterholes, giraffes avoid risky waterholes where safe areas may be far away, visibility is low, or where lions are present (Valeix et al. 2009a). Furthermore, they generally favor open areas where they can readily escape when threatened (Valeix et al 2009a). Giraffes also exhibit asynchronous activity patterns, predominantly diurnal, when they forage, and drink (Burger et al. 2020). Unlike smaller ungulates which often prioritize safe habitat, giraffes tend to use their favored habitat unless the presence of a predator is detected (Thaker et al. 2011). Little is known about predatory effects on giraffe resource use. However, it is essential to consider that the non-consumptive effects stemming from predator-prey interactions may outweigh the population-level consequences of direct predation (Courbin et al. 2015). This underscores the importance of understanding the complex dynamics of giraffe resource use and predator-induced responses.

Lions (Panthera leo)

Lions are the largest African predator. They are habitat generalists, inhabiting a diverse range of environments including the semi-desert of the Kalahari (Jackson and Nowell 1996; Stuart and Stuart 2000). Their presence is predominantly within protected areas due to habitat fragmentation and low human tolerance (Woodrofe 2000; Riggio et al. 2013). Lions are classified as vulnerable according to the IUCN Red List, with just a few remaining strongholds including protected areas (Riggio et al. 2013; Nicholson et al. 2023).

Lions are polygynous mammals forming fission-fusion groups known as prides (Greenwood 1980; Packer and Pusey 1987). Sexually mature male lions disperse from their natal prides, enter a nomadic phase, and then go on to establish new prides or take over existing ones (Packer and Pusey 1987). In contrast, females typically remain with their maternal pride (Packer and Pusey 1987). Female lions cooperate in raising cubs and synchronize their estrous cycles (Elliot et al. 2014).

Lions are apex predators and exert top-down pressure on food webs (Sinclair et al. 2003). They often hunt in prides which plays a critical role in hunting dynamics (Lehmann et al. 2008). This strategy allows them to hunt larger prey, including giraffes, although lions prey on a wide range of other medium to large sized mammals including wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*), gemsbok (*Oryx gazella*), Plains zebra (*Equus quagga*), and waterbuck (*Kobus ellipsiprymnus*) (Hayward and Kerley 2005; Lehmann et al. 2008). In Hayward and Kerley's (2005) identification of lion food preferences, giraffes were determined to be fourth in a review of 32 studies. However, in other studies, giraffes were not even found in their diets (Beukes et al. 2020). However, this may be explained by prey preferences in lion prides, where lion diet is influenced by prey availability and learned behavior (Hayward and Kerley 2005). Size of prey may also impact prey preference with smaller prey species selected against due to the low energy yield relative to the expended energy needed to capture the prey (Sunquist and Sunquist 1997). On the other hand, large prey species pose risks to lions due to their antipredator behaviors such as tusks or strong kicking hind legs (Makacha and Schaller 1969; Wilson 1981; Hayward and Kerley 2005). In general, lions are highly opportunistic and therefore predominantly predate on medium prey species rather than large ones such as giraffes (Schaller 1976; Hayward and Kerley 2005). They mainly hunt at night when prey species are inactive and can cover significant distances in coordinated group hunts (Schaller 1976; Eloff 1984). Furthermore, they prefer to sit and wait for prey in areas with high prey accessibility, rather than abundance (Hopcraft et al. 2005).

Lion predation is influenced by several environmental variables (Hayward and Kerley 2005). Grass and shrub cover improve hunting success especially during daytime hunts (Elliott et al. 1977; Orsdol 1984; Funston et al. 2001). Terrain and water availability also impact hunting outcomes, with prey availability typically higher in areas closer to water sources or featuring less rugged terrain (Smuts 1978; Stander and Albon 1993; de Boer et al. 2010; Creel et al. 2014). Many prey species actively avoid waterholes when lions are in proximity. Nevertheless, lion kills are often found near waterholes due to the prey's dependency on these water sources (de Boer et al. 2010). These environmental variables are interconnected with prey availability, contributing to complex dynamics of lion predation. The "landscape of fear" created by lions necessitates constant adaptations related to the presence of lions and other predators, making it essential to comprehend these relationships and their implications for habitat use in both predators and prey.

The role of ecological relationships in reserve management

Protected areas (PAs) play a crucial role in maintaining biodiversity, ecological functioning, and ecosystem services, thus functioning as social-ecological systems (Cumming et al. 2015). While counting species to measure biodiversity can be relatively straightforward, ensuring the preservation of complex ecological processes, such as predator-prey relationships, presents a significant challenge. The management of PAs extends beyond local jurisdiction, influenced by regional and global policy that significantly impact their effectiveness in sustaining ecological functioning (Cumming et al. 2015). A review of 4,000 PAs worldwide, focusing on effective management, revealed that 42% faced major deficiencies, primarily due to insufficient funding, community relations, and resource management (Leverington et al. 2010). Inadequate and inappropriate management practices, coupled with a lack of comprehensive data, have compromised ecological integrity in many PAs globally (Parrish et al. 2003; Robson et al. 2021).

As humans continue to encroach on natural landscapes, small reserves have become a common conservation solution. However, the success of these reserves depends heavily on effective management (Newmark 2008). Reduced size and poor management practices may hinder key ecosystem processes which require intensive management practices to mimic natural processes (Hayward et al. 2007; Hayward and Kerley 2009). Such practices may include culling of animals when overpopulation becomes an issue or moving individuals between parks. Moving individuals replicates natural movements, which ultimately maintains genetic diversity (Aarde et al. 1999; Trinkel et al. 2008; Ottewell et al. 2014).

Protected areas and privately owned reserves in South Africa are widespread throughout the country covering approximately 260,000 km^2 (van Hoven 2014; der Merwe and Maia 2019). Of these areas, approximately 200,000 km^2 are privately owned, creating approximately 9,000 wildlife properties (van der Merwe and Maia 2019). These properties are primarily managed for economic benefit but may have conservation goals as well. For example, many lion and giraffe reintroductions into small reserves are primarily for eco-tourism purposes (Carruthers 2008; Miller et al. 2013).

In South Africa, many lion populations are found in small reserves (< 1,000 km^2) and are intensively managed to mimic the natural processes that have broken down due to fencing (Miller et al. 2013; 2015). These natural processes normally result in natural checks so without them, predator-prey relationships may be disrupted (Hayward et al. 2007). For example, pride takeovers limit the number of cubs through infanticide which then limits population growth which reduces the pressure on prey populations (Miller et al. 2013, Miller and Funston 2014). Without management interventions, the increase in lions can strain food webs (Hayward et al. 2007; Lehman et al. 2008).

Similarly, reserve management in South Africa has led to an increase in the southern giraffe population (Deacon & Tutchings 2018). However, there are genetic concerns for these populations due to crossbreeding between Angolan giraffe and southern giraffe, especially in parks such as the Kgalagadi Transfrontier Park (Deacon & Tutchings 2018). Furthermore, lack of movement between reserves may lead to inbreeding depression (Deacon & Tutchings 2018). Reduced browse options and preferential lion predation in reserves can also cause issues in maintaining viable populations and thus they need to be managed (Brenneman et al. 2009).

Comparative studies of niche dynamics of prey species between large (> 10,000 km^2) and small reserves have revealed high dietary overlap in the latter, placing additional pressure on these herbivores including giraffes (Vogel et al. 2019). Furthermore, some PAs have observed modifications to predator-prey relationships, such as changes in hunting tactics influenced by reserve fencing (van Dyk and Slotow 2003). This example illustrates the challenges in keeping PAs natural and maintaining normal ecosystem processes.

These examples underscore the need for effective management in small reserves, where natural ecological mechanisms may not operate optimally. Ensuring that predator-prey relationships in these smaller reserves are preserved, or mimicked, is essential, as these dynamics drive vital ecological processes, including trophic cascades and food web structuring (Hayward et al. 2007). Consequently, investigating these relationships within small, managed protected areas, such as !Khamab Kalahari Nature Reserve, is crucial to ensure that heavily managed areas can successfully emulate natural processes.

Aims & Objectives

This study explores resource selection by a population of southern giraffes in a small, fenced reserve and assesses how the presence of lions may influence habitat selection. Resource selection function models (RSFs) were explored using both environmental and predation risk variables to characterize the landscape and assess selection or avoidance by giraffe relative to their availability. Using simultaneous GPS collar data obtained from individuals of both species in the private fenced reserve, the !Khamab Kalahari Nature Reserve, the objectives were to (i) quantify the seasonal and overall home ranges of giraffes and lions, (ii) assess seasonal overlap among giraffes, and spatial overlap between lions and giraffes, (iii) employ resource selection functions to assess selection of habitat variables based on their availability in the landscape, and (iv) determine whether proximity to predators influences movement patterns of giraffes across landscapes. Here, I hypothesize that predation risk will influence giraffe resource use in the semi-arid private reserve !Khamab Kalahari Nature Reserve and that these trends can be applied to the relationship between megaherbivores and their predators in similar systems throughout Africa. The findings contribute to our understanding of how megaherbivores prioritize resources in small managed areas and provide valuable information of how predators impact prey species in managed game reserves where natural ecological processes may be disrupted and necessitate careful management.

METHODS

The data in this study comprise GPS collar data gathered from four lions and eight giraffes within the !Khamab Kalahari Nature Reserve (KKNR) and remain the property of KKNR. The GPS data was provided by F. Deacon (University of the Free State, South Africa), originally collected in 2012 - 2013 (Deacon 2015). The relevant methodological sections, along with an example of the raw data used in this study, are included in the Appendix for reference. A summary of the field sampling is reported here, together with detailed statistical methodology used in this study.

Study site

KKNR is located in the North West province of South Africa (25º29′S 23º15′E) and spans 95,538 hectares. It falls within the Eastern Kalahari Bushveld Bioregion and is classified as semi-arid savanna (Mucina and Rutherford 2006). There is approximately 330 mm of rainfall annually, and temperatures between 0ºC to 22ºC in winter and 18ºC to 34ºC in summer. For the purposes of this study, four seasons were considered and are represented throughout the analysis. These seasons are the wet and hot season between December and February, the wet and cool season between March and May, the dry and cool season between June and August, and the dry and hot season between September and November (Collinson 2008).

The KKNR is classified into four main vegetation types and is located in Molopo Bushveld (Mucina and Rutherford 2006). These vegetation types include grassland, *Grewia retinervis-Acacia erioloba* Woodland, *Acacia erioloba-Acacia mellifera* Woodland, and forbland (Deacon 2015). The vegetation is predominantly woodland (Fig. 3). The reserve lacks perennial surface water and KKNR management has created waterholes throughout the reserve (Fig. 3; Deacon and Smit 2017). This has influenced the distribution of indigenous plant and animal species found on the reserve (Deacon and Smit 2017).

The herbivore species on the reserve include giraffes (*Giraffa giraffa*), white rhinoceros (*Ceratotherium simum*), gemsbok (*Oryx gazella*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), red hartebeest (*Acelaphus buselaphus caama*), Plains zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), and buffalo (*Syncerus caffer*). The primary carnivores are lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), black-backed jackal (*Canis mesomelas*), wild dogs (*Lycaon pictus*), and brown hyaena (*Hyaena brunnea*). This study focused on interactions between lions and giraffes.

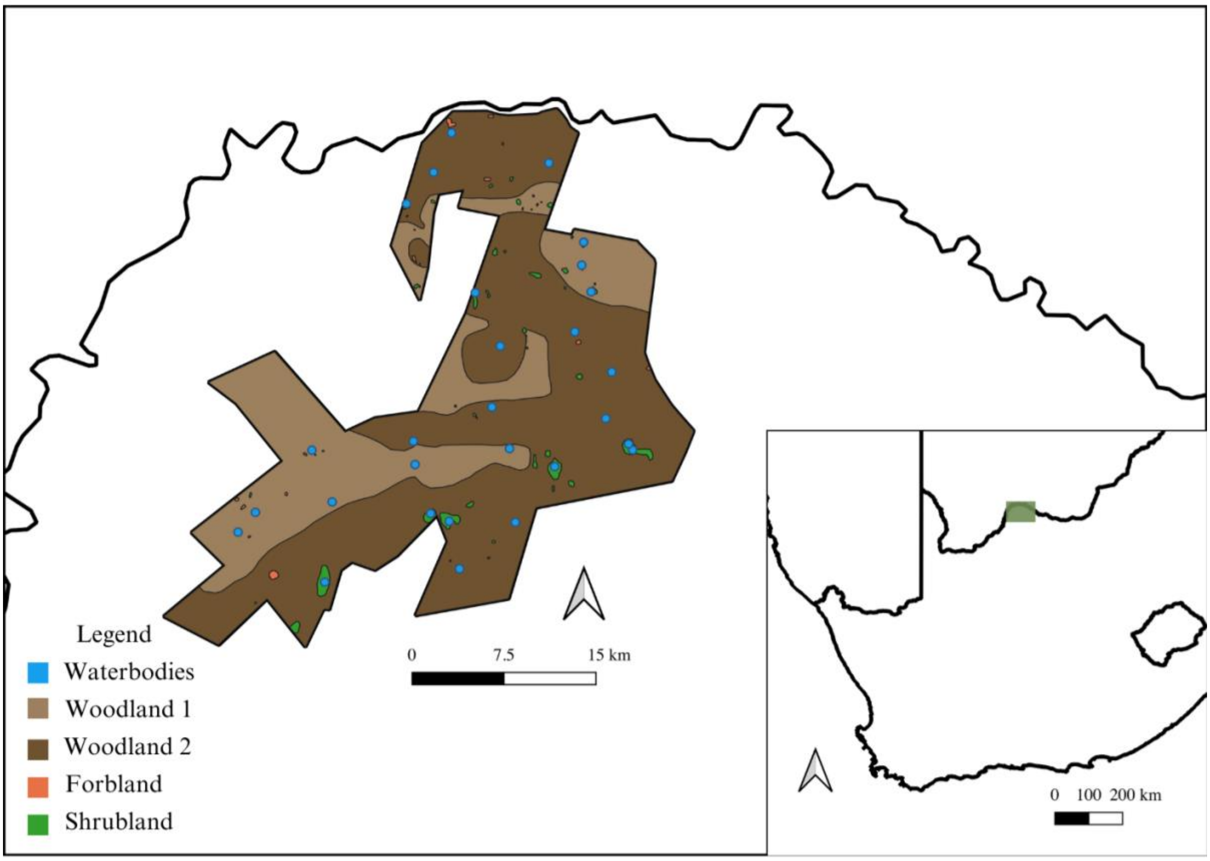


Fig. 3. !Khamab Kalahari Nature Reserve in the North West province of South Africa (see inset)showing waterholes and vegetation type.

Study animals and field collection of GPS collar data

GPS data were collected from both collared lions and giraffes over a two-year period from 2012 to 2013 (see Deacon 2015 for full details). Eight female giraffes were collared between 4 April to 8 April 2012. These individuals were originally translocated to KKNR from the North West and Limpopo provinces (Deacon and Bercovitch 2018). Each of the females belonged to one of eight different herds at the time of collaring and were chosen based on their physical health (Deacon and Smit 2017). Each giraffe was equipped with a custom-made head harness fitted with a satellite GPS tracking device manufactured by Africa Wildlife Tracking (Deacon and Smit 2017). More detailed information on immobilization and collaring can be found in Appendix I. Data collected included the GPS location and details on date, time, ambient temperature, and the speed and direction of animal movement (Deacon and Smit 2017). GPS units recorded data every four hours, with an accuracy between 2.5 and 5 meters.

Each of the eight giraffes had a unique name for distinction which consisted of "Sat", a number indicator, and two to three letters (ex: Sat305Ca; Table 1). The giraffe with ID Sat305Ca was collared prior to April 4th, 2012, and all data before this time was excluded from the analysis. Additionally, GPS coordinates outside of KKNR were removed as giraffes were unable to move outside of the reserve and these were considered to be satellite errors.

The four lions collared in this study were translocated from Tswalu Game Reserve, South Africa, in 2010. Among the collared lions, there were two females and two males. These were the only lions on the reserve at the time of collaring. However, the females gave birth to cubs during the two-year period. Lions were identified through a numbering system and based on their sex. Immobilization and collaring of the lions was overseen by KKNR management and their ground team in January 2012 following the method outlined in Donaldson et al. (2023; Appendix I). GPS tracking devices on collars were manufactured by Africa Wildlife Tracking. The units recorded location data at two-hour intervals, with an accuracy ranging from 2.5 to 5 meters. Due to collar failure the second female's GPS data was inconsistently spaced and thus excluded from the analysis of this study (Table 2). However, it is pertinent to note that the two female lions were part of the same pride and likely would have moved in close proximity to one another (Packer et al. 2001; Mosser and Packer 2009). Because lions were collared prior to the giraffes, all data collected prior to the giraffe collaring was removed from the analysis.

GPS coordinates of the 2012 - 2013 waterholes were provided by F. Deacon and KKNR to identify possible points of water use and availability for animals (Fig. 3).

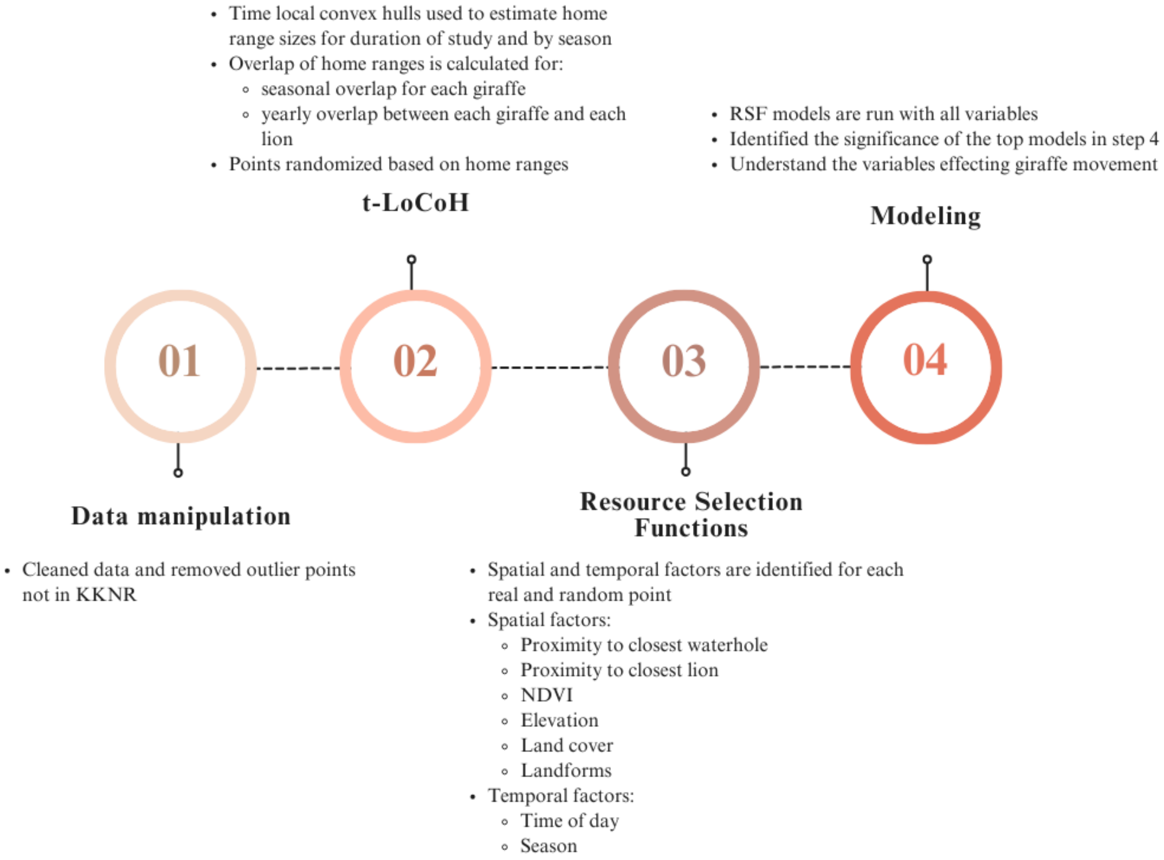
Table 1. Details of the individual giraffes (n = 8) collared in this study with animal ID, collaring information, sex, herd structure, and reproductive status (i.e., if the animal was pregnant or lactating when collared)

Animal ID	Time period collared dd/mm/yy	GPS relocations	Days collared	Sex	Location within reserve	Herd structure	Pregnant or lactating	
Sat305Ca	11/03/12-31/12/13	3938	660	F	East	4 adult females, 2 sub-adult males, 4 sub-adult females	Y	N
Sat308Da	08/04/12-31/12/13	3817	633	F	North	5 adult females, 2 juveniles	N	Y
Sat310He	08/04/12-5/12/13	3648	607	F	South	1 adult female, 1 juvenile	N	Y
Sat306Kem	08/04/12-17/12/13	3741	619	F	North	6 adult females, 2 sub-adult males, 4 sub-adult females, 2 juveniles	N	Y
Sat312Ke	08/04/12-31/12/13	3821	633	F	Central	7 adult females, 2 sub-adults males, 2 sub-adult females, 1 juvenile	N	N
Sat309Ni	08/04/12-01/11/13	3458	602	F	East	2 adult females, 1 juvenile	N	Y
Sat307Pi	08/04/12-31/10/13	3460	601	F	West	3 adult females, 1 sub-adult male, 1 sub-adult female, 1 juvenile	N	N
Sat311Wi	08/04/12-31/12/13	3580	633	F	South	7 adult females, 1 sub-adult male, 3 sub-adult females, 2 juveniles	N	Y

Statistical analyses of GPS collar data

Statistical analysis framework

To identify the variables influencing giraffe movement in the semi-arid Kalahari reserve of KKNR, time-local convex hull (t-LoCoH) home ranges and resource selection functions (RSF) were employed. To do so, t-LoCoH were constructed to estimate giraffe and lion home ranges, which delineated boundaries for applying third order RSFs (i.e., assessing habitat selection at a home range level). RSFs evaluate habitat selection by animals using spatially informed, predictive models that explore the relationship between landscape features and the probability of an animal's presence (Manly et al. 1993). The statistical analyses conducted are summarized in Fig. 4. The variables used in the RSF models were categorized into spatial and temporal variables. Spatial variables included proximity to the nearest waterhole, normalized difference vegetation index (NDVI), elevation, landform types, land cover, and proximity to the nearest lion. Temporal variables include time of day (divided into dawn, day, dusk, and night), and season (categorized by temperature and rainfall into wet and cool, wet and hot, dry and cool, dry and hot). R version 4.2.2 (2022-10-31) (R Core Team 2022) was used for statistical analysis.



- Time local convex hulls used to estimate home range sizes for duration of study and by season
- Overlap of home ranges is calculated for:
  - seasonal overlap for each giraffe
  - yearly overlap between each giraffe and each lion
- Points randomized based on home ranges

- RSF models are run with all variables
- Identified the significance of the top models in step 4
- Understand the variables effecting giraffe movement

- Cleaned data and removed outlier points not in KKNR

- Spatial and temporal factors are identified for each real and random point
- Spatial factors:
  - Proximity to closest waterhole
  - Proximity to closest lion
  - NDVI
  - Elevation
  - Land cover
  - Landforms
- Temporal factors:
  - Time of day
  - Season

Fig. 4. Summary flowchart of the statistical methods performed in this study

Estimating giraffe and lion home ranges using t-LoCoH

The time local convex hulls (t-LoCoH) method was used to generate home ranges for giraffes and lions over the duration of the study and seasonal giraffe home ranges. This analysis aimed to identify if seasonal changes were found in habitat distribution among the giraffes. Using the T-LoCoH home ranges, I identified the percentage of giraffe home ranges that overlapped with lions, as well as the seasonal overlap of individual giraffes. The *tlocoh* package was used in R (Lyons et al. 2019, R Core Team 2021) for constructing home ranges from GPS data. t-LoCoH takes time into consideration and hard boundaries such as fence lines, enabling the analysis of spatio-temporal patterns in animal movements unlike alternative methods such as Maximum Convex Polygons (MCP) and Kernel Density Estimation (KDE). The 95% t-LoCoH-a (‘adaptive’ Local Convex Hulls) method was used which incorporates space and time to define isopleths that accounts for areas of different intensities. A scaling parameter (s) of 0.05 was used as a starting point but Lyons et al.’s (2013) multistep approach to optimize parameters was followed to optimize parameters and choose the best a-value for each individual. These home ranges were then clipped to the reserve fence. Home ranges were also generated for the four seasons and by year, resulting in eight seasonal home range maps for each giraffe. Three of the eight giraffes had less data in the final wet, hot season and therefore the seasonal home range could not be estimated (Table A3).

Using paired t-tests, I investigated whether seasonal home ranges changed from the first year of the study to the second year of the study. The data was normally distributed (Appendix, Table A2). The values in this table represent the mean home range size for each season per year of all the giraffes.

Resource Selection Functions

Resource selection functions were used to model the influence of seven spatial and two temporal variables on giraffe habitat selection. Variables expected to influence giraffe movement were selected and categorized into spatial and temporal variables, as outlined in Fig. 4 and discussed above (Fortin et al. 2005; Valeix et al. 2009a; Périquet et al. 2010; DeMars and Boutin 2018; Holling 1965; Pellew 1984; Burger et al. 2020; Crego et al. 2023). The spatial variables included environmental variables (waterhole proximity, NDVI, elevation, land cover, and landforms; Table 2) and predation risk (lion proximity). The temporal variables considered were time of day and season (Table 2). Initially, random points were generated within the home range, to determine resource availability. Fifteen random points were generated for each "real" point, aligning with similar timestamps throughout the entire study period. Fifteen random points were generated for each real point to give a 1:15 ratio of used to available locations. Spatial variables were extracted at both real and random generated points.

Table 2. List of categorical variables considered for resource selection functions: land cover, landform, season, and time of day

Land Cover	Landform	Season	Time of Day
Grassland	Valley	Wet and Cool	Dawn
Shrubland	Lower slope	Wet and Hot	Day
Woodland	Upper slope	Dry and Cool	Dusk
Transformed		Dry and Hot	Night

The distance from each giraffe GPS location to the closest lion at the nearest point in time was calculated. A two-hour time buffer was made around each giraffe GPS timestamp because lion and giraffe collars were on different time schedules (2 vs 4 hours respectively). The buffer ensured that lion GPS timestamps were within an hour before the giraffe timestamp or within an hour after the giraffe timestamp. Once a buffer was made, the distance to each lion within that time buffer was calculated as well as the difference in time. The closest lion was then selected based on these distances.

Environmental variables, including NDVI (normalized difference vegetation index), elevation, land cover, and landforms, were obtained using the Google Earth Engine using the *rgee* package (Aybar 2023; Appendix VII). NDVI is a measure of vegetation greenness that uses near infrared (NIR) and red (R) values of the Earth's surface to calculate a ratio as (NIR - R) / (NIR + R) which is then scaled to a range between zero and one (U.S. Geological Survey. n.d.). NDVI data was calculated per GPS timestamp from MODIS (Didan 2021). Elevation values were collected from 2000 but are expected to be similar to the elevation in 2012 and 2013 (Farr et al. 2007). Land cover information was extracted from the South African National Land Cover Map of 2018. Land cover types were grouped to minimize the number of categories based on transformed land, bushland, grassland, and woodland. It is important to note that the layer used showed a predominantly grassland landscape, although satellite imagery showed a mixture between grass and tree communities. This is also evident based on Figure 3 in the Methods section, which shows the majority of the landscape as woodland vegetation, as corroborated by Deacon's description of the KKNR study area (Deacon 2015; Deacon and Smit 2017). Landforms were classified by combining the Continuous Heat-Insolation Load Index (SRTM CHILI) and the multi-scale Topographic Position Index (SRTMmTPI) datasets into upper slope, lower slope, and valley as identified by Theobald et al. (2015; Table 2). Landform classifications are based on Theobold et al.'s (2015) classes which are based on hillslope position and physical processes such as soil formation. Although layers used may be outside of the study dates, values are expected to be similar due to minimal change in the variables.

The temporal variables, seasonality, and time of day were based on the timestamp of each point. The month of each data point was used to classify it into one of the four seasons: dry and cool (June to August), dry and hot (September to November), wet and hot (December to February), and wet and cool (March to May). The time of day was classified based on the hour of each data point, categorized as dawn (5 am to 8 am), day (8 am to 6 pm), dusk (6 pm to 9 pm), and night (9 pm to 5 am).

The RSF models were run as no-intercept binomial generalized linear mixed models (GLMMs) with animal ID as the random effect and infinitely weighted available points (Muff et al. 2020). All covariates were centered and scaled to allow comparison between model estimates. The models were run using glmmTMB package (Brooks et al. 2017). All variables were checked for collinearity using the check_collinearity function in the "performance" package (Lüdecke et al. 2021). Landforms and land cover were found to be non-independent ($X^2 = 421.32$, $df = 6$, $p < 0.001$), therefore separate GLMMs were run for landform and land cover (Fig. 4). All other variables were non-collinear. Four models were run (Table 3). The first two models included all variables and either land cover or landform (Table 3). The other two models included an interaction variable and either land cover or landform (Table 3). The four models were run to see whether the interaction was significant and to understand how these two landscape variables affected habitat selection. I was interested in the influence of both variables, but as they were non-independent, the models could not contain both variables. An interaction variable between NDVI and season was included due to considerable variation of NDVI between seasons (Appendix IV). Box plots and maps showing variation between lion proximity, water proximity and season were made to identify other possible interaction variables (Appendix IV). The final models excluded elevation due to low variability. Akaike information criterion corrected for small sample size (AICc) scores were compared across the model with all predictor variable permutations to determine the most parsimonious model. Prediction plots were created for visualization of the models. These plots are marginal response curves that represent the variable of interest across the range of its values and while holding the other variables at their medians or at a designated category for the categorical values. These categories were designated as ‘wet and cool’ for season, ‘day’ for time of day, and ‘grassland’ for land cover. The error bars represent 95% confidence intervals.

Table 3. Full generalized linear mixed models to assess resource selection among giraffes in !Khamab Kalahari Nature Reserve (n = 8). In total, four models were run

Model	NDVI	Waterhole Proximity	Lion Proximity	Season	Time of Day	Land Cover	Landform	NDVI* Season
Land cover	●	●	●	●	●	●		
Landform	●	●	●	●	●		●	
Interaction / Land cover	●	●	●	●	●	●		●
Interaction / Landform	●	●	●	●	●		●	●

Ethics statement

All GPS collar data used here was collected as part of a previous study by F. Deacon representing eight giraffes and four lions collared in the !Khamab Kalahari Nature Reserve in the period 2012 - 2013. Animal capture, handling and collaring methods were approved by the University of the Free State AREC (Animal Research Ethics Committee) - Ethics Approval Protocol Number: ANIMAL EXPERIMENT NR 12/2011, AREC12/2011 and AED2015/0066.

RESULTS

The dataset comprised GPS relocations ranging from 3,458 to 3,938 locations per individual, with simultaneous collaring periods spanning between 601 to 660 days from eight giraffes and three lions (Table 1 and Table 4). Each lion was originally collared for a total of 729 days but the days before giraffes were collared were removed.

Home range estimates for KKNR giraffe and lions

Home ranges for both giraffes and lions generated using t-LoCoH covered much of the reserve, averaging 726.81 (SE = 146.29) km^2 for lions (Table 4 and Fig. 3), and 260.45 (SE = 56.75) km^2 for giraffes (Table 5 and Fig. 4). No giraffe exhibited mutually exclusive seasonal home ranges. In other words, there was high overlap between seasonal home ranges (Fig. 4, Appendix III).

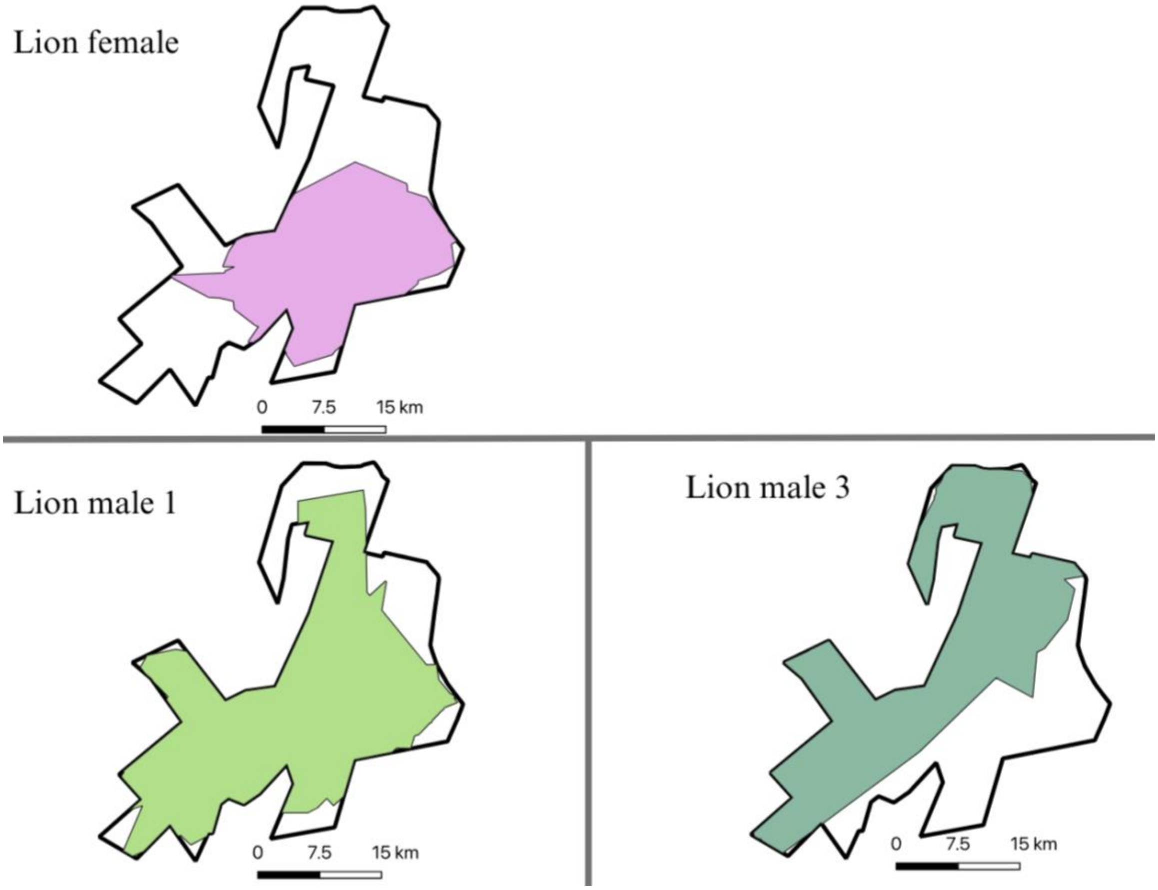


Fig. 3. Home ranges based on 95% t-LoCoH estimates of each collared lion in !Khamab Kalahari Nature Reserve for the period of 4 April, 2012 to 31 December, 2013

Table 4. Description of lions collared in !Khamab Kalahari Nature Reserve for this study (n = 3) with animal ID, collaring information, sex, and home range size.

Animal ID	Time Period Collared dd/mm/yy	Num. Of Data Points	Days Collared	Sex	Home Range Size (km^2)
Lion female	01/01/12-31/12/13	3847	729	F	434.66
Lion male 1	01/01/12-31/12/13	3758	729	M	859.13
Lion male 3	01/01/12-31/12/13	3564	729	M	886.64

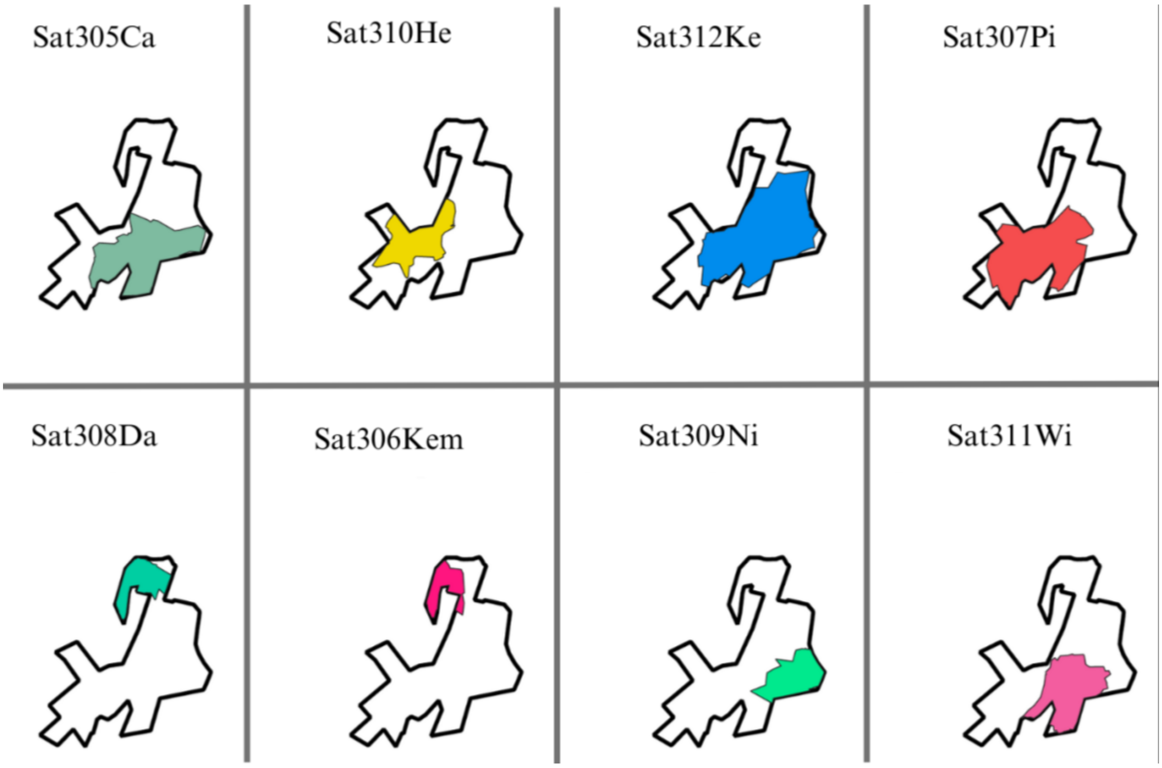


Fig. 4. Overall home ranges based on 95% t-LoCoH estimates of each collared giraffe in !Khamab Kalahari Nature Reserve for the period of collaring

Table 5. Overall giraffe and seasonal home range sizes for each giraffe in km^2 in !Khamab Kalahari Nature Reserve. NA represents seasons where home ranges were not generated due to insufficient data (< 5 days in the season).

Animal ID	Home range size (Overall)	Season Year 1				Season Year 2			
		Wet Cool	Dry Cool	Dry Hot	Wet Hot	Wet Cool	Dry Cool	Dry Hot	Wet Hot
Sat305Ca	359.03	68.39	251.56	194.28	145.01	172.86	201.18	53.51	26.01
Sat308Da	117.90	65.91	47.89	59.89	68.17	181.42	33.76	20.92	25.28
Sat310He	193.47	55.43	60.16	47.12	75.65	110.57	134.56	28.66	NA
Sat306Kem	77.51	54.92	28.63	18.32	29.98	76.63	63.83	82.33	19.97
Sat312Ke	534.25	140.28	321.87	297.96	397.16	356.03	235.86	192.47	49.53
Sat309Ni	138.04	52.85	49.47	44.55	55.67	84.86	181.53	103.25	NA
Sat307Pi	410.06	103.89	250.72	142.48	175.55	185.54	325.07	186.89	NA
Sat311Wi	253.34	91.04	165.57	116.92	178.68	105.14	145.68	84.95	22.91

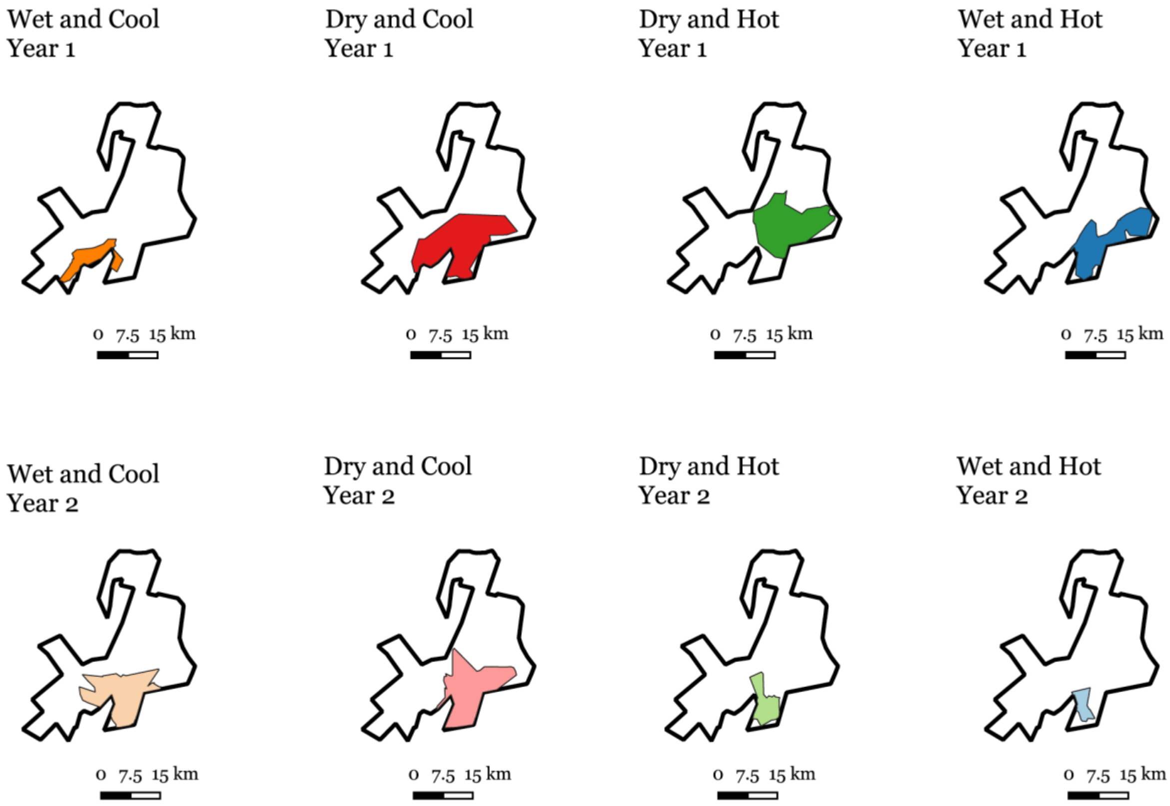


Fig. 5. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat305Ca in !Khamab Kalahari Nature Reserve. Each season over the two years is identified.

Means of each season for giraffes were calculated (Table 6; Fig. 5). The paired t-tests revealed no significant differences in seasonal home ranges between the two years (t = 0.22, df = 3, p-value = 0.843; Table 6; Fig 5). This may be slightly skewed due to lack of data for the wet, hot season of year two in three of the giraffes. The most notable, but non-significant, differences in means between the two years occurred during the wet, hot season (December to February) and the wet, cool season (March to May), while the other seasons exhibited minimal variations in home range sizes between the corresponding seasons over the two years. All seasonal home range maps can be found in Appendix III.

Table 6. Mean giraffe home range per season between years !Khamab Kalahari Nature Reserve. *Note: data collection ended during the wet and hot season of year 2 and therefore minimal data were collected causing smaller home ranges

Season	Year 1 Home Range	Year 2 Home Range	Difference
Wet cool	79.09	159.13	80.04
Wet hot	140.73	28.74*	111.99
Dry Cool	146.98	165.18	18.20
Dry Hot	115.19	94.12	21.07

All giraffes overlapped with all three lions, except two giraffe individuals which overlapped with only two lions (Table 7). Both male lions exhibited overlaps with, if not the majority of, at least one giraffe home range (Fig. 6). The female lion overlapped with all giraffes except two, namely Sat308Da and Sat306Kem, indicating a lower likelihood of encountering a lion for these giraffes. Overlap between giraffes and lions ranged from 3.2% - 92.2%, observed with the same giraffe, Sat309Ni. The largest overlapping area measured 378.39 km^2, representing a 71.9% overlap. The smallest overlap was 4.37 km^2, corresponding to a 3.2% overlap of giraffe Sat309Ni.

Table 7. Total and percentage overlap of giraffe home ranges that overlapped with lions !Khamab Kalahari Nature Reserve

Giraffe	Lion	Overlap Area (sq km)	Percentage Overlap
Sat305Ca	Lion male 1	281.69	80.3
	Lion male 3	87.56	24.9
	Lion female	263.06	74.9
Sat308Da	Lion male 1	40.11	34.8
	Lion male 3	96.97	84.1
	Lion female	0	0.0
Sat310He	Lion male 1	170.8	90.1
	Lion male 3	164.23	86.6
	Lion female	101.56	53.6
Sat306Kem	Lion male 1	29.58	32.0
	Lion male 3	68.33	73.8
	Lion female	0	0.0
Sat312Ke	Lion male 1	452.66	86.1
	Lion male 3	271.33	51.6
	Lion female	378.39	71.9
Sat309Ni	Lion male 1	115.52	85.6
	Lion male 3	4.37	3.2
	Lion female	124.46	92.2
Sat307Pi	Lion male 1	359.35	89.7
	Lion male 3	223.2	55.7
	Lion female	226.93	56.6
Sat311Wi	Lion male 1	205.91	85.5
	Lion male 3	47.34	19.7
	Lion female	204.02	84.8

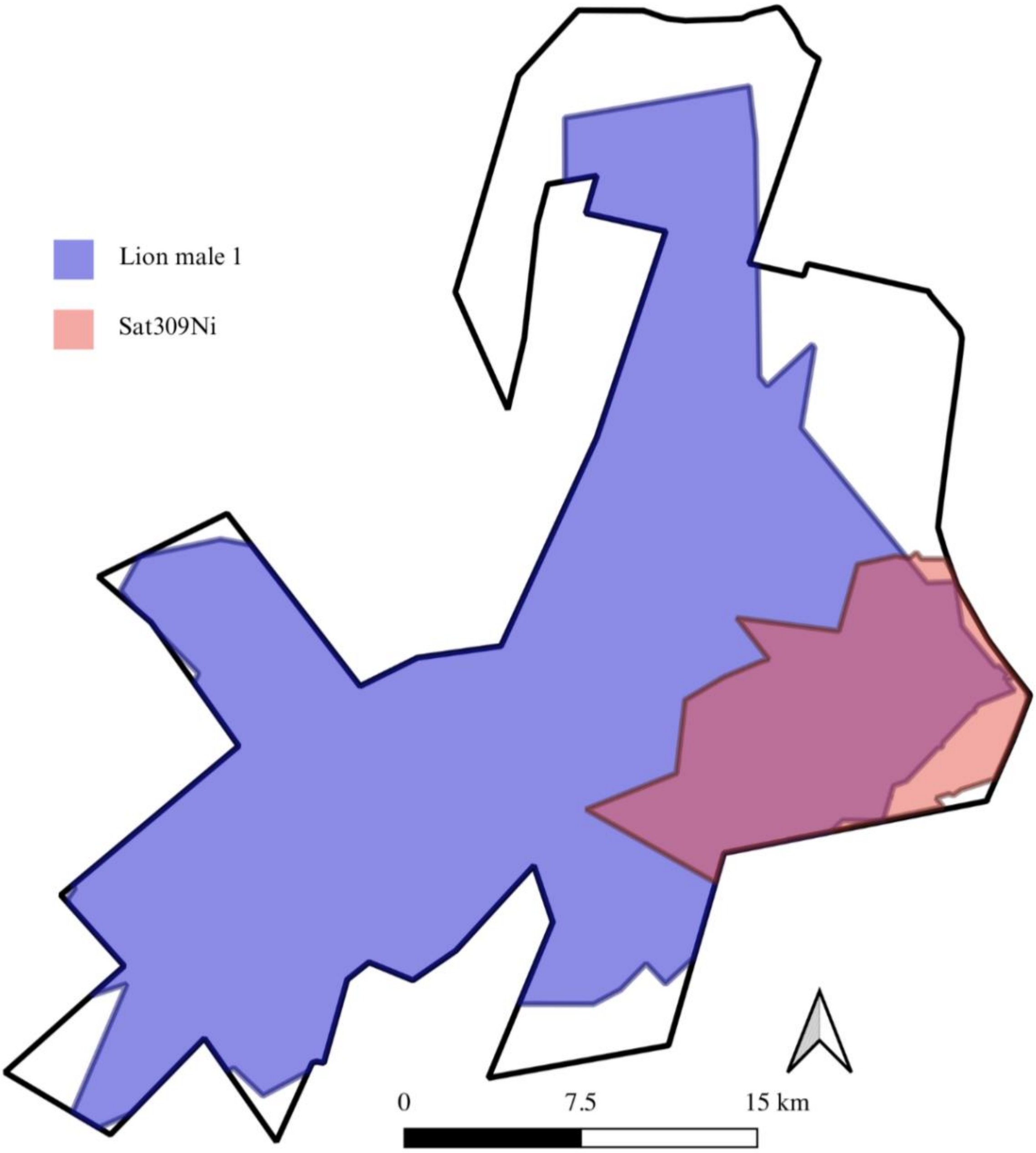


Fig. 6. An example of the home range overlap between lion male 1 and giraffe Sat309Ni in !Khamab Kalahari Nature Reserve

Resource Selection Function Models

Generalized linear mixed models were used to identify resource selection and habitat use in giraffes, with an emphasis on lion proximity as a measure of lion influence on giraffe movement (Table 9). A total of 427,007 GPS data points for giraffes were utilized in the models consisting of both ‘real’ and ‘random’ GPS points. Of these points, 23,364 were real and 397,571 were random points. Table 8 provides a summary of the ranges and means of the continuous variables. Consequently, AICc scores were compared between models incorporating either land cover or landform (Table 9). The model incorporating land cover and the interacting variable of NDVI and season has a lower AICc (642314.3) compared to the model with landform and the interacting variable (642723.1), and thus the land cover GLMM was chosen as the top model (see Table A5 for details). In general, all spatial and temporal features considered had an impact on giraffe movement, except for elevation, which showed little variation across the reserve.

Table 8. Distribution data for continuous variables for giraffe movement in !Khamab Kalahari Nature Reserve

Variable	Mean	Range
Waterhole proximity	2,711.5 m	1.2 - 11255.5 m
Lion proximity	12,315.6 m	11.1 - 51889.1 m
NDVI	0.231	0.128 - 0.489
Elevation	1029 m	1025 – 1045 m

Table 9. Top model results for habitat selection of giraffes in !Khamab Kalahari Nature Reserve showing β estimates and standard error (SE) and *p*-value for the most parsimonious generalized linear mixed model as determined by AICc

Model	**Interaction / Land cover**		**Interaction / Landform**	
Predictors	***β estimate (SE)***	***p-value***	***β estimate (SE)***	***p-value***
Categorical variables				
Land cover: woodland	-10.16 (0.0670)	<0.001		
Land cover: Grassland	-10.60 (0.0421)	<0.001		
Land cover: Shrubland	-11.16 (0.0258)	<0.001		
Landform: Lower slope			-11.11 (0.0266)	<0.001
Landform: Upper slope			-11.14 (0.0265)	<0.001
Landform: Valley			-11.19 (0.0287)	<0.001
Season: Dry and Hot	-11.39 (0.0629)	<0.001	0.20 (0.0252)	<0.001
Season: Wet and Cool	0.21 (0.0252)	<0.001	-0.18 (0.0244)	<0.001
Season: Wet and Hot	-0.17 (0.0244)	<0.001	-0.40 (0.0260)	<0.001
Time of day: Day	-0.40 (0.0260)	<0.001	0.19 (0.0193)	<0.001
Time of day: Dusk	0.19 (0.0193)	<0.001	0.06 (0.0221)	0.008
Time of day: Night	0.06 (0.0221)	0.007	0.05 (0.0196)	0.006
Continuous variables				
NDVI	0.34 (0.0303)	<0.001	0.35 (0.0304)	<0.001
Waterhole distance	-0.22 (0.0067)	<0.001	-0.22 (0.0067)	<0.001
Lion distance	0.04 (0.0068)	<0.001	0.04 (0.0068)	<0.001
Interacting variables				
Season: Dry and Hot * NDVI	0.21 (0.0367)	<0.001	0.21 (0.0367)	<0.001
Season: Wet and Cool * NDVI	-0.35 (0.0348)	<0.001	-0.4 (0.0348)	<0.001
Season: Wet and Hot * NDVI	-0.20 (0.0328)	<0.001	-0.21 (0.0328)	<0.001
Random effects				
σ^2	0.0009925		0.0008986	
N	$8_{\text{giraffe\_id}}$		$8_{\text{giraffe\_id}}$	
Observations	423935		423935	
Marginal R^2 / Conditional R^2	0.028 / 0.028		0.025 / 0.025	
AIC_c	642314.3		642723.1	
BIC_c	642500.6		642898.4	
Deviance	642280.3		642691.1	

GLMMs indicated that giraffes select greener vegetation (i.e., areas with higher NDVI; *β* = 0.34, *z* = 11.2, *p* = <0.001; Fig. 6). Giraffes also select areas closer to waterholes (*β* = -0.22, *z* = -32.4, *p* = <0.001) and further from lions (*β* = 0.04, *z* = 6.3, *p* = <0.001). The top models included an interaction variable between season and NDVI (Table 9).

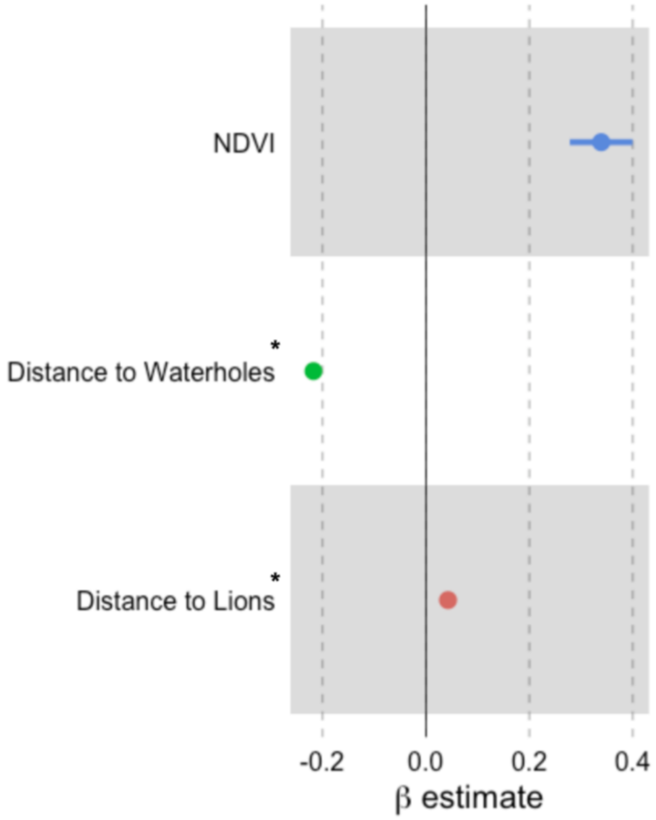


Fig. 6. Continuous variable selection estimates and 95% confidence intervals based on standard error for the RSF. Estimates are shown for those parameters included in the top model (as determined by AICc). *Note that negative values indicate selection for habitat closer to the feature. 95% confidence intervals are too small for distance variables to appear on the diagram for ‘distance to waterholes’ and ‘distance to lions’

Selection varied by land cover and landform (Table 9; Appendix VI). Transformed land (*β* = -10.16, *z* = -151.6, *p* = <0.001) and woodland (*β* = -10.60, *z* = -251.9, *p* = <0.001) were the most selected land cover types. In contrast, grassland had a comparatively lower probability of selection (*β* = -11.16, *z* = -433.4, *p* = <0.001). Shrubland (*β* = -11.39, *z* = -181.1, *p* = <0.001) had the lowest probability of selection. In terms of landform, lower slopes have a higher selection probability (β = -11.11, z = -417.8, p = <0.001), followed by higher slopes (β = -11.14, z = -420.7, p = <0.001) and valleys (β = -11.19, z = -389.5, p = <0.001).

Habitat utilization

Grassland was the primary land cover type in KKNR (Fig. 7). Woodland was also a prominent vegetation type in KKNR (Fig. 7). While grassland constituted a high proportion of the land cover, it appeared to be less selected in comparison to woodland and transformed land (Fig. 7).

Transformed areas had the highest proportion of used land (Table 10; Fig. 7). However, its proportion relative to other land cover types was relatively minimal (Fig. 7). On the other hand, water bodies and shrubland were comparatively less abundant in KKNR (Fig. 7).

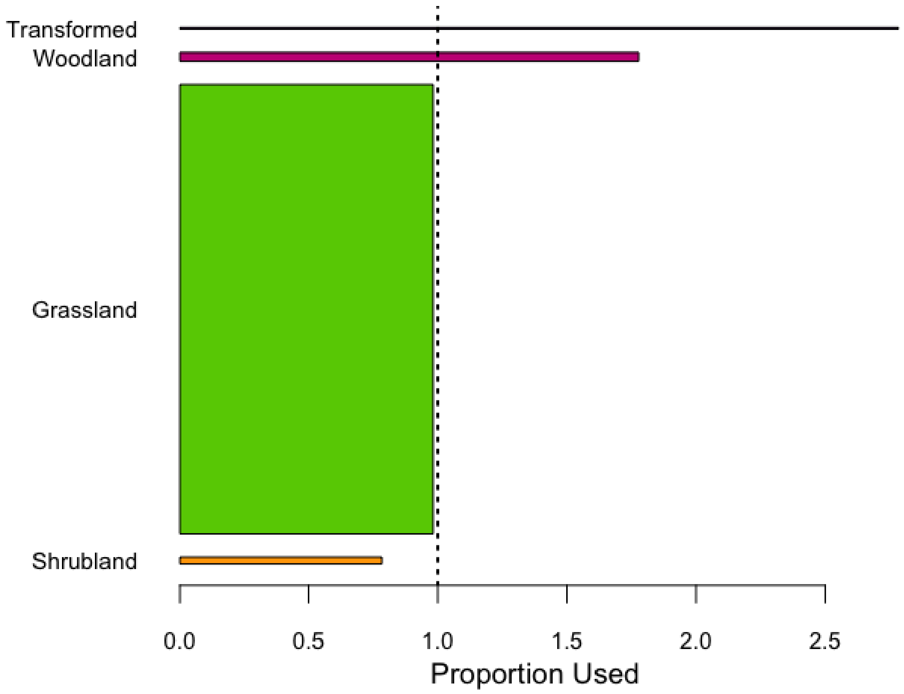


Fig. 7. Relative use plot identifying the greatest land cover used. The width identifies the proportion of availability within the landscape and the length determines the use. The dotted line shows where the expected use is equal to the availability in the landscape.

Prediction plots of categorical variables revealing selection preferences of giraffes

Trends in the categorical variables season and time of day show that the patterns of selection for the continuous model variables to be stronger during the day and the dry seasons, particularly the dry and hot season. Patterns of selection are less strong at dawn and in the wet seasons, particularly the wet and hot season. Trends in land cover type also show that the patterns of selection for the continuous variables are stronger on transformed land and woodland, followed by grassland and shrubland. These land cover selection trends are evident in Fig. 8a, 9a, and 10a.

Prediction plots of continuous variables revealing selection preferences of giraffes

In general, there was a consistent increase in the probability of selection as lion distance increased, indicating giraffe avoidance of lions ($\beta = 0.04$, $z = 6.3$, $p = <0.001$; Fig. 8a). Fig. 9 reveals that giraffes exhibited selection for areas in proximity to waterholes ($\beta = -0.22$, $z = -32.4$, $p = <0.001$). The likelihood of selection diminished as the distance from a waterhole increased. The likelihood of selecting for greenness, as measured by NDVI, increased as NDVI values rose ($\beta = 0.34$, $z = 11.2$, $p = <0.001$; Fig. 10).

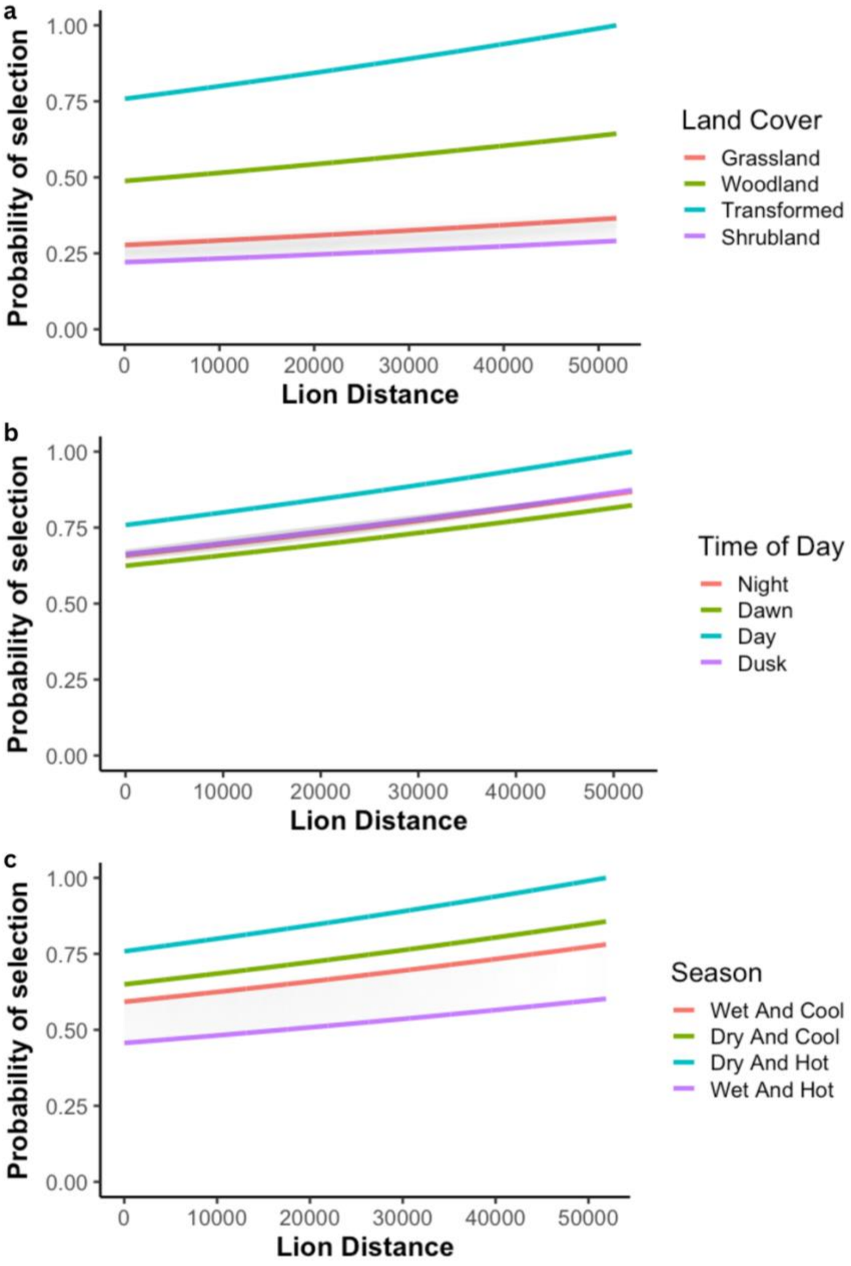


Fig. 8. Prediction plots identifying the probability of selection of a site by giraffes based on lion distance and a) land cover, b) time of day, and c) season in !Khamab Kalahari Nature Reserve

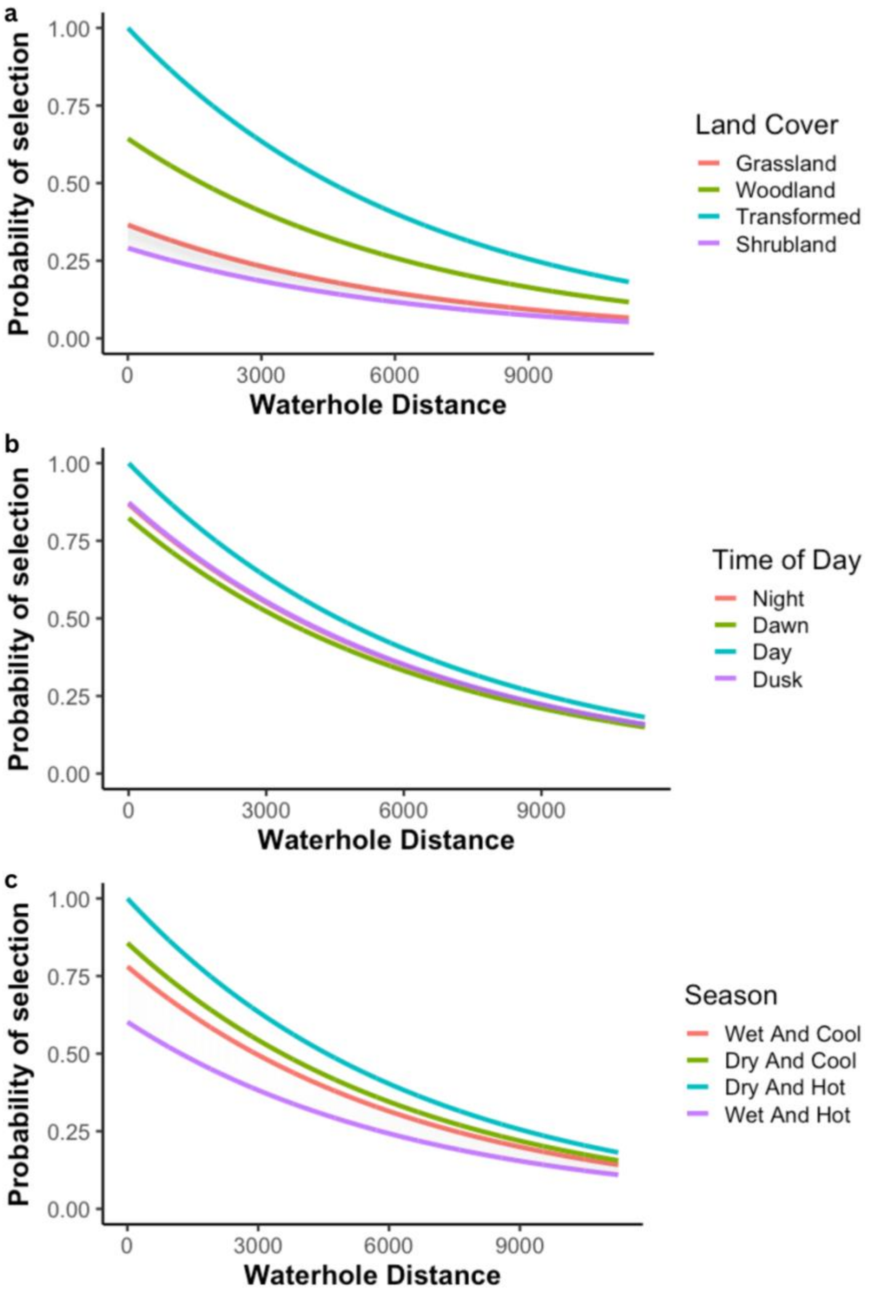


Fig. 9. Probability of a giraffe selecting for proximity to a waterhole based on a) land cover, b) time of day, and c) season in !Khamab Kalahari Nature Reserve

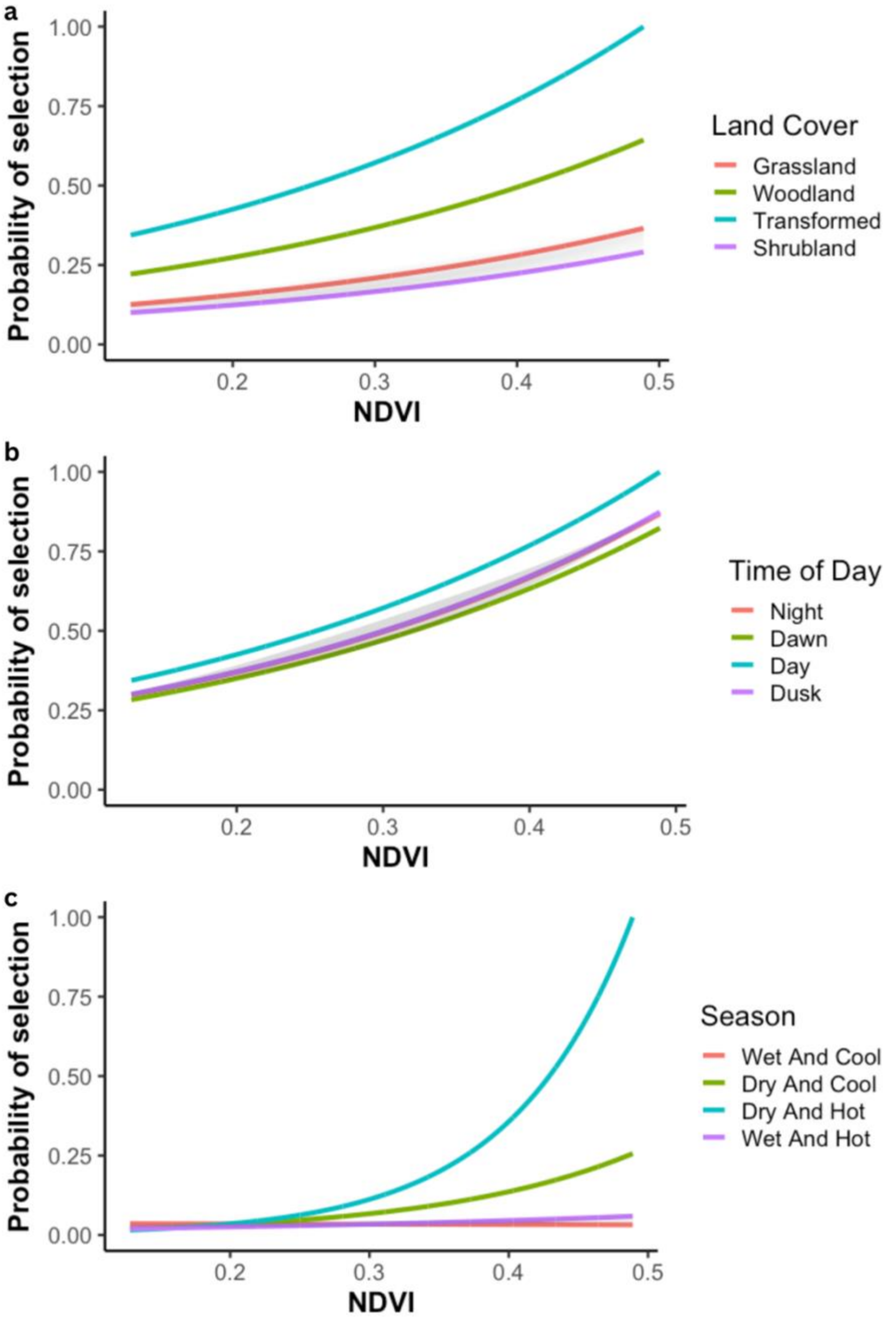


Fig. 10. Probability of a giraffe selecting for greenness based on a) land cover, b) time of day, and c) season in !Khamab Kalahari Nature Reserve

The interaction term revealed that the effect of NDVI depended on season, where selection for greener areas is stronger in the dry season (Table 9). Specifically, the dry and hot season has a positive relationship (($\beta = 0.21$, $z = 5.7$, $p = <0.001$) with NDVI and the probability of selection for higher NDVI (i.e., greener vegetation) is higher than in the wet, cool season (($\beta = -0.36$, $z = -10.4$, $p = <0.001$) and wet, hot season (($\beta = -0.21$, $z = -6.3$, $p = <0.001$) (Table 9; Fig. 10).

DISCUSSION

This study explored resource use by giraffes in !Khamab Kalahari Nature Reserve and demonstrates evidence for both selection of environmental variables and avoidance of lions, their main predator. Though the study area appears relatively homogeneous, fine-scale differences in land cover, landform, NDVI values, and reserve design influence resource distribution and thus giraffe selection. Although these differences are possibly less pronounced than in other reserves, they still influence variance in the availability of key resources and giraffe preference for specific areas. The avoidance of lions suggests the possibility of a landscape of fear and antipredator behavior strategies in how giraffes utilize the resources within KKNR. The approach used in this study can provide a better understanding of how species use landscapes in areas like KKNR and the results can be used to inform evidence-based adaptive management approaches that ensure ecological integrity and general welfare of wildlife within them.

How do giraffe home ranges vary on KKNR and do they overlap with lions?

Giraffe home ranges in this study vary in size and in location in KKNR with the six of the giraffes having centrally located home ranges and two located in the top section of KKNR (Appendix III). Due to the variation in size and location, there is high overlap with lions in KKNR. The size of the giraffe home ranges in this study compare with those reported by previous studies (McQualter 2018; Knüsel et al. 2019; Brown et al. 2023). However, a relatively large variability of home range sizes has been reported (McQualter 2018; Knüsel et al. 2019; Brown et al. 2023). This variation may be influenced by reserve size and home range estimation methods, which lack a time component or restriction of movement due to fencing. Compared to the less arid area of northern Tanzania, giraffes in this study had 110% larger mean home ranges which may be attributed to lower landscape productivity and limited access to essential resources in KKNR (Knüsel et al. 2019). However, Knüsel et al. (2019) did not find any correlation between home range size and vegetation type in northern Tanzania which consists of open grassland, dense deciduous bushlands, and thickets. In another study identifying home range sizes over the four species of giraffe, the home range for the southern giraffe was found to be 392.1 km^2 (Brown et al. 2023), larger than the mean giraffe home ranges in this study.

In reserves with spatially heterogeneous habitat resources such as the northern Namib desert which is extremely arid and has uneven resource distribution and northeast Uganda, which is seasonally variable, overall giraffe home ranges are generally larger to meet resource requirements due to the patchiness of the landscape and movement between suitable patches (Fennessy 2009; Brown et al. 2023). KKNR does have other megaherbivores, including rhinoceros, as well as other smaller herbivores including zebra, and buffalo which may influence habitat patchiness of the landscape at the smaller scale through foraging. However, based on satellite imagery, the fairly homogeneous landscape in KKNR of woodland and grassland represents minimal patchiness which may be greater on other reserves due to higher herbivory effects. Patchiness and resource availability may be important to consider for reserve management as resources become depleted and patchiness occurs in KKNR and in other reserves. Furthermore, some studies have suggested that males have larger home ranges than females which could increase the overlap in spatial activity between lions and giraffes (Fennessy et al. 2009). The giraffes in this study were all female of which most were lactating or pregnant and therefore may have different responses to males. Female giraffes have an interbirth period of 19 to 22 months of which 15 months may be spent pregnant (Jirik 2023). Therefore, incorporating pregnancy and lactation as variables may also influence resource use patterns in RSF models. Going forward, including reproductive status and male giraffes into the models might indicate differences between sexes as grouping behaviors and energy requirements may be different (Young and Isbell 1991; Ginnett and Demment 1997).

Do giraffe home ranges change seasonally?

Seasonal home range estimates of giraffes in this study revealed a wide range of sizes across the reserve and time period of sampling. Mean seasonal home ranges were relatively similar from one season to the next. However, there were relatively smaller home ranges for the second year wet, hot season which may be attributed to the lower number of data points available. Despite this, seasonal home ranges were comparable to the literature with a previous study reporting home ranges between 219.2 km^2 in the dry season and 140.7 km^2 for the wet season (McQualter 2018). The seasonal home ranges in this study were 126 km^2 and 130 km^2 in the wet and dry seasons respectively. However, these findings identify similarities between seasons which were not evident in McQualter's study which showed large differences between seasons (2018). Other studies also found no obvious patterns between dry, wet, cool, or hot seasonal home ranges as seen in KKNR (Le Pendu and Ciofolo 1999; Fennessy 2009). McQualter's (2018) findings are more comparable to other studies indicating larger dry season home ranges due to scarce resources like water in arid desert regions such as in Niger (Le Pendu and Ciofolo 1999), and Northwest Namibia (Fennessy 2009; Brown et al. 2023). Artificial water sources are a management intervention required in a fenced reserve such as in KKNR as fencing prevents movement outside of the reserve to find water sources. In the above studies, fencing is not an issue and therefore home range sizes may be larger. Season has been shown to be linked with accessibility to seasonal browsing and to water availability in herbivores and may impact home range sizes (Hall-Martin 1974). Seasonal variations in temperature can also act as an additional stressor that may alter an individual's activity patterns also altering home range size (Belovsky & Slade 1986).

Lion home ranges span the majority of the reserve indicating possible influence on giraffes

The collective lion home ranges covered the majority of the KKNR. Every giraffe overlapped with at least two of the three collared lions indicating the use of shared areas. The lion home ranges in this study were larger or comparable to those in other studies, despite being in a smaller reserve (Loveridge 2009; Funston 2011). Loveridge (2009) used kernel density and LoCoH to estimate home ranges in Hwange National Park whereas Funston (2011) used MCP to estimate home ranges in the Kgalagadi Transfrontier Park. These home range estimation methods are different and may lead to differences in home range sizes. This study used t-LoCoH to incorporate a time aspect into the home ranges which MCP and kernel density lack. Furthermore, LoCoH takes into consideration hard boundaries such as fencing which in this study is pertinent but may not be so in Hwange National Park and Kgalagadi Transfrontier Park. Hwange National Park is approximately 15 times the size of KKNR but lion home ranges are comparable (Loveridge 2009). Kgalagadi Transfrontier Park on the other hand is about 38 times larger than KKNR and lion home ranges were estimated to be around five to six times larger (Funston 2011). This may have more to do with lower lion density than the size of the reserve as higher density increases competition between lions and shrinks home ranges (Funston 2011). Therefore, in KKNR, the low density of lions may allow greater movement and territory size, increasing home range size. The male home range sizes were bigger than the females in this study, a pattern consistent with findings in other studies (Loveridge 2009). Lion home ranges in large reserves have been found to be associated with biomass of prey, density of prides, distribution of surface water, and distribution of herbivores (Loveridge 2009; Valeix et al. 2009a; Funston 2011).

Resource selection reveals the importance of environmental variables and predation risk on giraffes in KKNR

This study found influencing environmental variables in KKNR on giraffe habitat selection with positive selection of sites that are closer to waterholes, further from lions and predation risk, in land categorized as transformed or woodland, and higher NDVI and foraging availability. Giraffe habitat selection is influenced by many environmental variables, including water availability, vegetation type, predation pressures, and seasonal and daily timing but other variables may also be influential (Hall-Martin 1974; Valeix et al. 2009a; Périquet et al. 2010; Hart et al. 2019). Furthermore, giraffes showed stronger habitat selection during specific seasons and times of day. These variables also showed connectedness throughout the literature and were not independent of each other (Schaller 1976; McQualter 2018; Crego et al. 2023). For example, predation happens throughout the landscape, in giraffes foraging areas, by waterholes, and at all times of day. This was evident in my findings with season, time of day, and land cover influencing patterns of selection in foraging behavior, movement to waterholes, and movement away from predators. Going forward, there are most likely many more which also influence giraffe movement that might be worth considering in a resource selection framework, including giraffe behavioral variables, such as social displays and grouping behavior (Valeix et al. 2009a). Further, it could be beneficial to include other variables that may affect predator detection, such as wind direction and speed especially in relation to predation.

Giraffes significantly selected for areas closer to water points on the reserve. This result is consistent with giraffes being water dependent and drinking approximately once a day depending on water availability (Hayward & Kerley 2005; Valeix et al. 2009a). Nevertheless, research on water-dependence by Angolan giraffes in the Northern Namib Desert of Namibia revealed that surface water was not a variable influencing giraffe movement (Fennessy 2009), likely influenced by the low availability of man-made waterholes unlike in KKNR. In other studies, comparing artificial water source use and natural sources, giraffes were indifferent to the waterholes and preferred rivers (Smit et al. 2007). Additionally, Fennessy et al. (2009) found giraffes to move toward river areas where vegetation remained during the dry seasons. In KKNR, where artificial waterholes are the main source of water and fences restrict movement, giraffes are positively associated with them. Provisioning of clean water is another issue for reserve management. In the Central Kalahari Reserve, heavy metals in water lead to survival and reproductive issues (Selebatso et al. 2018). Because of giraffes' water dependence and positive trends towards waterholes in a system that is fenced, ensuring clean water is also important.

In this study, NDVI has a consistently positive influence on giraffe habitat selection. NDVI relates to the greenness of vegetation in an area, which is essential for browsing animals such as giraffes. This may suggest that in drier conditions, NDVI is more strongly linked to habitat selection of giraffes, whereas in the wet season, other environmental factors are driving selection. This study included an interaction variable between season and NDVI which showed selection preference for higher NDVI in the dry seasons. A study on Angolan giraffes in the northern Namib Desert, Namibia, report similar findings, where giraffe herds would relocate to areas of higher NDVI immediately available to them (Hart et al. 2019). This is also supported in other ungulate species within the Naboisho Conservancy, Kenya, such as eland, impala, Plains zebra, and wildebeest, highlighting the importance of high-quality foraging habitat (Crego et al. 2023). Crego et al. (2023) found higher NDVI values to be associated with woodlands and intermediate values to be associated with grasslands in dry seasons, whereas high NDVI values in the wet seasons were associated with grasslands in the Conservancy. This study included an interaction variable between season and NDVI with higher NDVI in the wet seasons and lower NDVI in the dry season, similar to Crego et al.'s findings (2023). This finding is likely due to the deciduous nature of the trees in KKNR which shed their leaves in the dry season (e.g., *Acacia erioloba*, *Acacia luederitzii, Acacia mellifera, Grewia flava, Terminalia sericea, and Ziziphus mucronata*; Deacon 205). Of these species, all are browsed on by giraffes in KKNR but *A. erioloba* and *A. mellifera* are preferred forage.

Findings reported in this study indicate that while a large proportion of the reserve has grassland cover, woodland was more selected when considering the availability of land cover, which is expected due to giraffes' browsing nature (Pellew 1984). This is consistent with previous work, which shows that while giraffes are browsers, they also depend on open areas with high visibility (Pellew 1984; Burger et al. 2020; Crego et al. 2023). It is important to note that when looking at satellite imagery of the reserve, grassland looked similar to woodland but was denoted as grassland by the GIS layer used (SANLC 2018). Using NDVI in the study, which was based on satellite imagery, may indicate more impactful results. More detailed vegetation and land cover maps might improve what is indicated as grassland or woodland. The area was historically extensively farmed for cattle with its impacts not showing on the layer used in this study. Finer scale data on tree locations or specific tree and vegetation species could give more insight to habitat use of giraffes in KKNR and selection for specific species or vegetation types.

Transformed land was more selected for than other land cover types. Another study on giraffes in a relatively dense human populated area of Niger has shown a lack of avoidance of villages and transformed land (Le Pendu and Ciofolo 1999). Roads, which are included in the transformed land category may also be preferential to giraffes, much like game trails are used as they are easier to move through which may account for this preference (Hill et al. 2020). In future studies it may be of interest to look at the proportion of land cover used seasonally to see if they are consistent with the above findings. This would give us insight into the importance of different land cover types during seasons. For example, roads may be more heavily used when bush is denser and harder to move through. A “human shield effect” is evident in some prey species which use transformed areas to evade predators (Berger 2007; Moll et al. 2018; Rodrigues et al. 2023). In coffee forests of southeastern Ethiopia, bushbuck and bush duiker positively co-occurred with humans whereas predatory leopard and spotted hyena neither positively or negatively co-occurred with humans indicating a possible human shield effect where humans are present and where transformed land occurs (Rodrigues et al. 2023). Similarly, in the moose breeding season in Yellowstone National Park, births were observed closer to paved roads which bears avoid showing evidence for positive association with transformed land (Berger 2007). Finally, although not evident in the literature, transformed land in the form of lodging in protected areas may increase resources such as water from pools or waterholes placed for tourist viewing near lodges. Additionally, a more heterogeneous environment to study lion and giraffe interactions may provide insight into the variables influencing giraffe movement. Additionally, repeating this study in a savanna or forest landscape that is less arid would be of interest, especially where natural water bodies and open systems are available.

The risk of predation by lions increases as lion proximity to its prey increases (Mönkkönen et al. 2007; Møller et al. 2017). In KKNR, giraffes consistently showed preferences for sites which are further from lions with a mean distance of 12 km. Lion activity peaks between 17:00 and 8:00 and thus lions are more active at night but may encounter prey species less at this time due to the inactivity described in my study (Schaller 1976; Yiu et al. 2022). This may have to do with asynchronous timing which has been shown in moose and wolves as an antipredator behavior in which one species is active while the other is less active and vice versa (Eriksen et al. 2011; Kasiringua et al. 2017).

Lions themselves show increased activity nearer to surface water or waterholes in reserves, most likely due to the importance of water sources for herbivores, which make it easier for the ambush predators to hunt (Hopcraft et al. 2005; de Boer et al. 2010). Our findings suggest more giraffe movement away from these waterholes at night compared to dawn which may be a predator avoidance behavior. In a similar study with Plains zebras in Hwange National Park, daytime encounters with lions were more probable at waterholes but were less risky and did not lead to large-scale spatial responses such as long-distance movement away from these areas (Courbin et al. 2015). Long-scale displacements were considered to have high associated energetic costs but their significance for individual and group fitness is unknown (Courbin et al. 2015). Therefore, selection of waterholes may be less influenced by the presence of lions if the energetic costs of antipredator behaviors are insignificant, and rather are selected based on the necessity of the resource. Valeix et al. (2009a) showed that site selection near waterholes by giraffe, kudu, and buffalo in Hwange National Park, Zimbabwe, was influenced by both the distance to water and the long-term predation risk, with all three species avoiding risky waterholes. Interestingly, the authors also found browsers avoided risky foraging areas less when they were closer to water, suggesting a tradeoff between resource use and the risk of predation. In a study analyzing vigilance behavior of giraffes at waterholes in Hwange National Park, Zimbabwe, group vigilance increased around waterholes most likely due to the risk of attack when in the splay-legged position (Périquet et al. 2010; Ferry et al. 2016).

In KKNR, there was a greater probability of selection during the day, including selection of areas closer to waterholes and with greater NDVI. Weaker patterns of selection during the night may indicate lower probability of selecting areas closer to waterholes and with greater NDVI than daytime. The stronger selection patterns during the day aligns with predator avoidance and using open areas with fewer trees. For effective comparison, further research in less arid areas may provide a more informative framework for understanding the significance of lion proximity as an influence on giraffe movement when water availability and NDVI are higher or less limiting resources. Future research identifying differences between reserves with artificial waterholes versus open areas with more seasonal rain sources may be of interest to identify their importance on habitat selection by resident giraffes. With changing climates, man-made waterholes and water management by reserves may be important for survival of animals on reserves and to maintain these predator-prey relationships (Epaphras et al. 2008). Furthermore, using observational studies in partnership with GPS data may work better to also identify real life instances where giraffes leave waterholes due to lions' presence for example.

To run the RSF models in this study, overlap of home ranges between giraffes and lions was used to infer interaction events between lions and giraffes in KKNR as well as GPS data points which were spatially and temporally buffered. These direct interactions were inferred due to long intervals between GPS data points and mismatch in timing of lion GPS and giraffe GPS data. Simultaneously spaced and timed GPS collar data would have ensured identification of specific interaction events rather than inferring them. Even with this, GPS data has pitfalls including satellite errors, pauses in data, and overall failure of the GPS system. Future analysis of finer GPS data could provide insight to direct interaction events and the response by giraffes. Using continuous time movement modeling (CTMM) which identifies interaction events, interaction specific RSF models could be compared to overall RSF models (Yang et al. 2023). These model differences could illustrate how habitat selection changes when predation risk is elevated. Step selection function models and more fine-scaled GPS data could then be used to provide more insight to real-time interactions with lions and the post-interaction behavior. Previous predator-prey relationship studies with zebra and lions (Courbin et al. 2015), and between wolves and elk (Fortin et al. 2005) show its effective use in understanding resource use after interaction events. Other issues that dealt with my data collection and study site included the lack of data from the other female lion which was collared and may have provided more accurate data about proximity to giraffes and possible encounters with lions. However, the two females were part of the same pride and during preliminary analysis looking at the GPS points which were available, they were almost identical to the female lion included in the study (data not shown). Therefore, throughout the entire study they likely would have moved in close proximity to one another (Packer et al. 2001; Mosser and Packer 2009).

Wildlife management in the age of GPS technology

There are challenges associated with ensuring successful management of wildlife while ensuring ecological integrity and animal welfare needs of wildlife in small, fenced reserves. This study demonstrates the value and utility of high precision GPS collar data to inform evidence-based decisions and allows the findings to be embedded in the highly applied field of wildlife management and demonstrate the utility of highly tech-oriented approaches for studying the ecology and behavior of species and the insight we gain from this. Not only can scientists look at movement of a species, but they can analyze resource use and interactions with other species, as demonstrated in this study. By identifying resource use in giraffes via GPS collar data, reserve managers are better able to understand the effects of the specific reserve landscape on their animals and how management interventions may influence this. This is critical in reserves that are highly managed to provide food and water to animals such as through artificial waterholes. Combining this with evidence of interactions with other species and testing for changes in resource use provides us with valuable insight into the ecological patterns of a landscape and the behavioral ecology of the animals within it.

Conclusions

Resource selection function models suggest that giraffe habitat selection in KKNR is influenced by access to food and water, but also the avoidance of lions. This study focused on several important spatiotemporal variables which have significant influences on giraffe habitat use. Home range estimates based on t-LoCoH and resource selection function models revealed the significance of predatory avoidance, selecting sites in proximity with waterholes, and using habitat in green areas. These variables were also influenced by season, time of day, and land cover types. Although these are evident and important in the KKNR, other reserves or protected areas may have additional or different variables which influence movement such as elevation or topography. Giraffes exhibit behavioral and evolutionary plasticity which creates differences in the variables which influence their habitat selection. Identifying how the risk of lion predation influences resource selection provides further insight into predator-prey relationships and mimicking them on a small reserve. From this study, NDVI and the presence of browse is strongly seasonal and influences giraffe habitat selection, which may influence the risk of predation. Furthermore, it is evident that management of waterholes can alter these interactions and potentially influence the likelihood of survival in giraffes. The methods used in this study can help identify the relative importance of both habitat and landscape variables. Together with species-specific interactions that need to be considered, small reserves can ensure and maintain the ecological integrity of giraffes, while also facilitating the broader ecological functioning of predator-prey relationships as the size and number of protected areas grow.

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APPENDICES

Appendix I

Excerpt from Deacon and Smit (2017) explaining giraffe immobilization and collaring methods from the original study; 10.1016/j.baae.2017.04.003

“A total of eight adult female giraffes within eight different herds—one from each herd at the time of collaring were selected and fitted with a custom made head harness equipped with a satellite GPS tracking device (manufactured by Africa Wildlife Tracking in South Africa). The focal animal selection was based on examination and evaluation of the physical condition of all the animals by a team of experts, including two wildlife veterinarians. The selected animal had to be a healthy, fully grown female without any deformities of the ossicones and the skull in order to ensure that the GPS head harness fit properly. The capture of the eight giraffes and placement of harnesses were from 4 to 8 April 2012. At the time of capture and placement of collars, the various herds were widely dispersed over the study area. All selected female giraffes were immobilized with the aid of a dart gun from either a helicopter or a ground vehicle. Drugs were delivered using a Pneudart® dart gun to propel a 2 ml Pneudart® projectile syringe with a 1.5″ 13GA barbed side-pointed needle. The darts contained 10 mg etorphine hydrochloride (Activon® , 9.8 mg/ml; Wildlife Pharmaceuticals, South Africa) as the narcotic agonist in combination with 100 mg hyaluronidase (Kyron Laboratories, South Africa) to increase absorption time. After the onset of significant ataxia, a helicopter was used to maneuver the giraffe away from the herd and a trained ground team slowed the animal until it fell to a prone position with the aid of a long belt held firmly in front of the animal. A veterinarian immediately injected 24 mg diprenorphine (Activin® 12 mg/ml; Wildlife Pharmaceuticals, South Africa) as an opioid antagonist to reverse the severe respiratory depressant effect of etorphine.”

Excerpt from Donaldson et al. (2023) explaining lion immobilization methods similar to this study, 10.36303/JSAVA.544

“A 3 ml dart (Dan-Inject International, Pietermaritzburg, South Africa) was prepared with either TZM – 0.6 mg/kg tiletamine-zolazepam (500 mg powder reconstituted in the supplied diluent to 100 mg/ml, Zoletil 100, Virbac RSA Pty Ltd, Halfway House, South Africa) plus 0.036 mg/kg medetomidine (Metonil 40 mg/ml, Wildlife Pharmaceuticals, White River, South Africa), KM – 3.0 mg/kg ketamine (Ketamine 1 g reconstituted with sterile water to 200 mg/ml, Kyron Laboratories, Johannesburg, South Africa) plus 0.036 mg/kg medetomidine, or KBM –

1.2 mg/kg ketamine plus 0.24 mg/kg butorphanol (Butonil 50 mg/ml, Wildlife Pharmaceuticals South Africa Pty Ltd., South Africa) plus 0.036 mg/kg medetomidine. The dart was fired using a carbon dioxide pressurised dart gun (Dan-Inject, International S.A., South Africa) and the drugs administered intramuscularly into the shoulder or upper hind leg. At the end of the data collection, butorphanol and medetomidine effects were antagonised with naltrexone (2 mg/mg butorphanol) (40 mg/ml, Kyron Laboratories, South Africa) and atipamezole (5 mg/mg medetomidine) (50 mg/ml, Vet Tech (Pty) Ltd), respectively, administered intramuscularly. Recovery times to sternal recumbency, standing and walking, following antagonist administration, were recorded. Quality of recovery was assessed using a descriptive score ranging from 1 (excellent) to 4 (poor) (Table I) (Wenger et al. 2010). All lions were monitored and protected from potential attack by other lions or hyaenas until they were fully recovered and able to rejoin the pride."

Appendix II

Table A1. Example of raw GPS collar data provided for giraffes in !Khamab Kalahari Nature Reserve

Animal	Date & Time	Lat	Lon	Temp (deg C)	True Speed (km/h)	Dir	Alt. (m)	Cov	HDOP	Dist. (m)	Count
Cas	4/8/12 2:39	-25.603233	23.204217	22	0	0	1021	5	0	1148	124
Cas	4/8/12 6:39	-25.60425	23.20415	18.5	0	0	1023	2	1	113	125
Cas	4/8/12 10:39	-25.598783	23.213533	32	0	0	1025	5	0	1121	126
Cas	4/8/12 14:39	-25.594517	23.232333	32	0	0	1022	5	0	1946	127

Appendix III - Seasonal home ranges

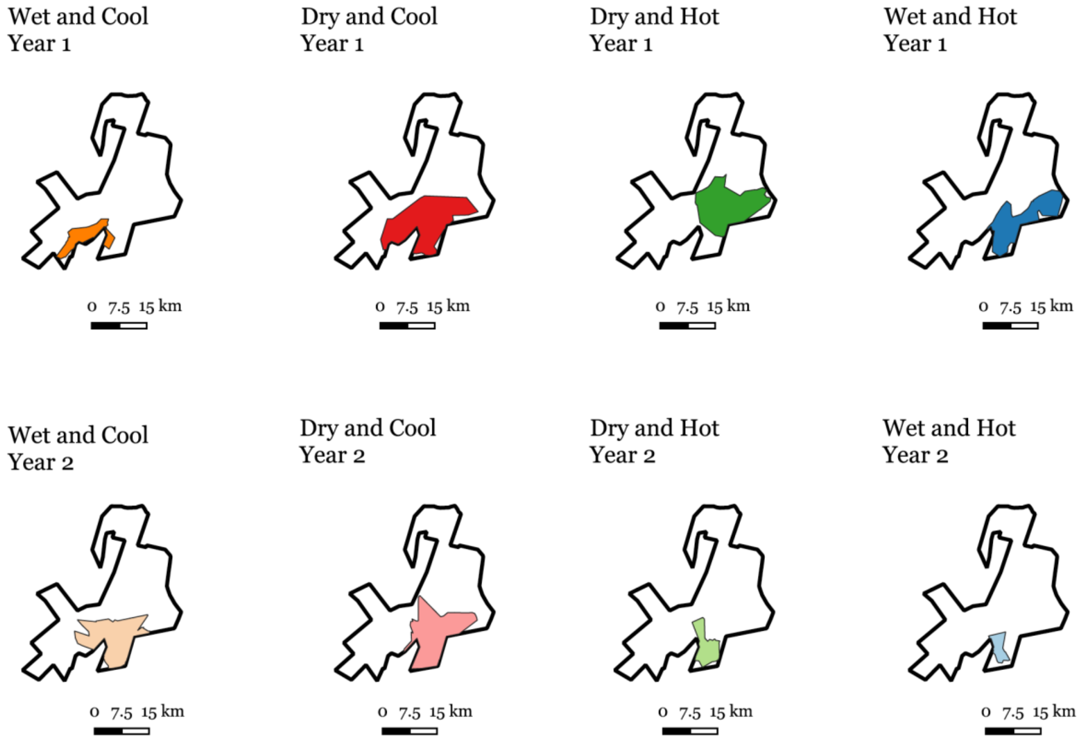

Fig. A1. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat305Ca in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

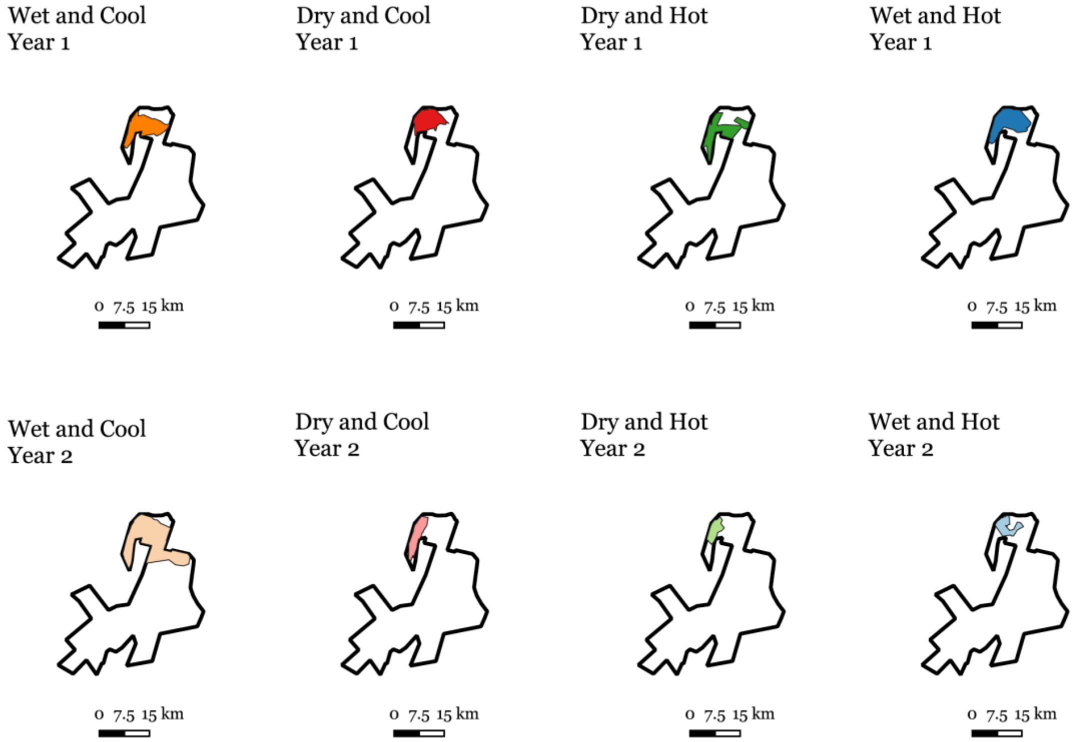

Fig. A2. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat308Da in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

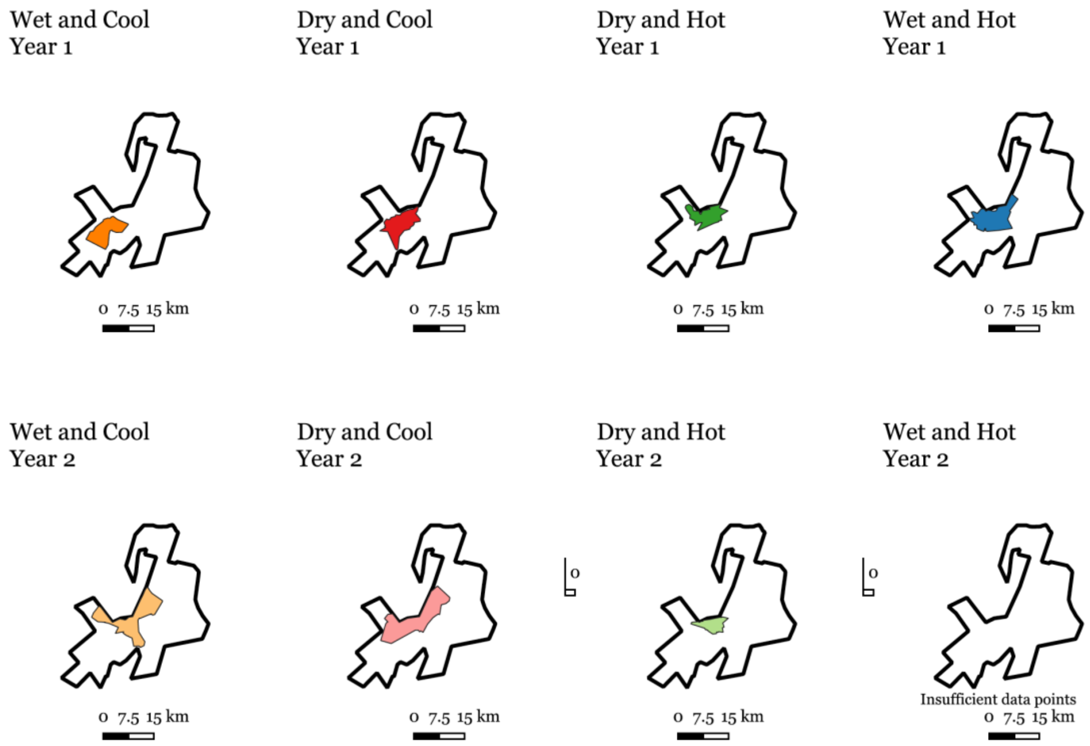

Fig. A3. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat310He in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

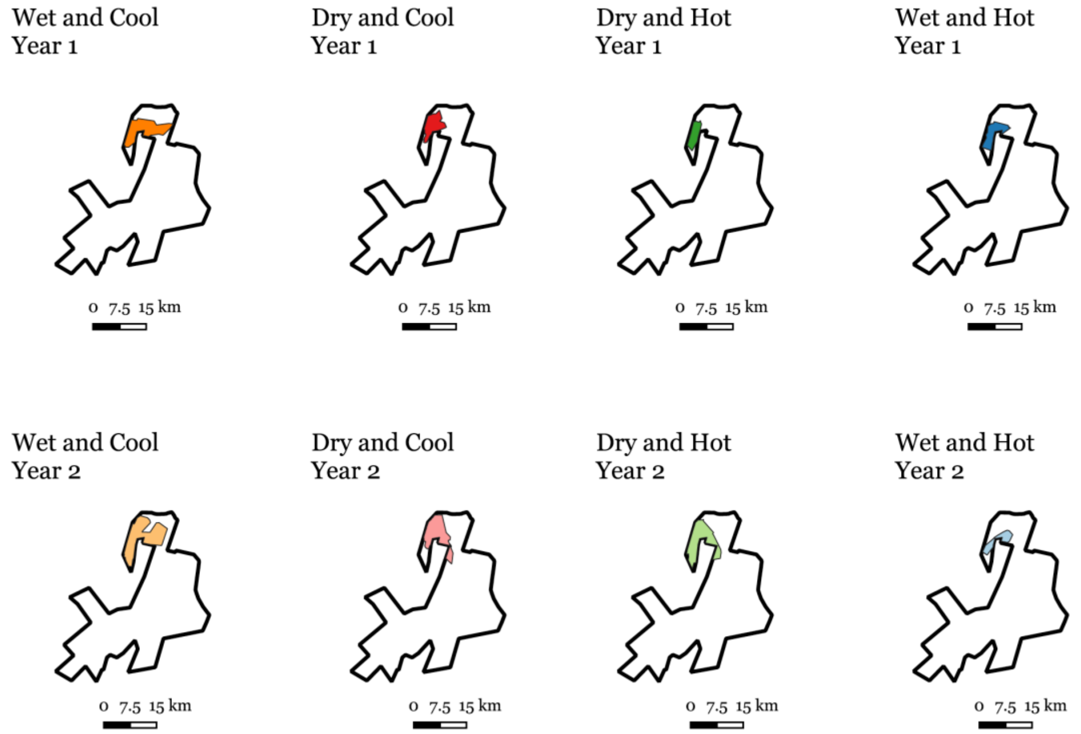

Fig. A4. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat306Kem in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

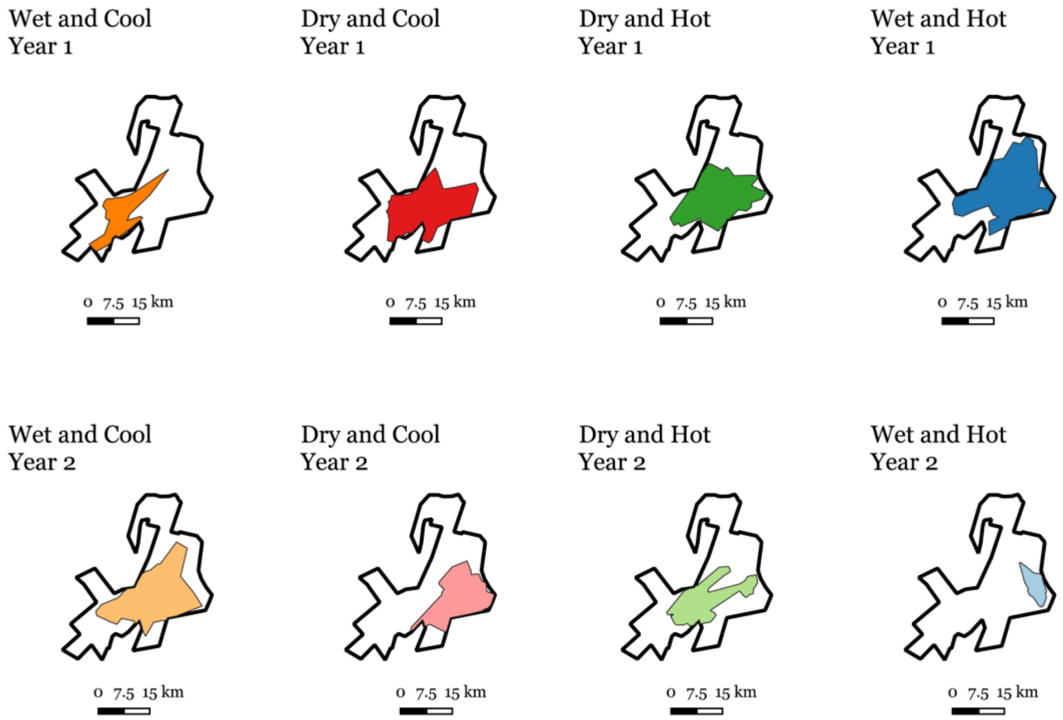

Fig. A5. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat312Ke in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

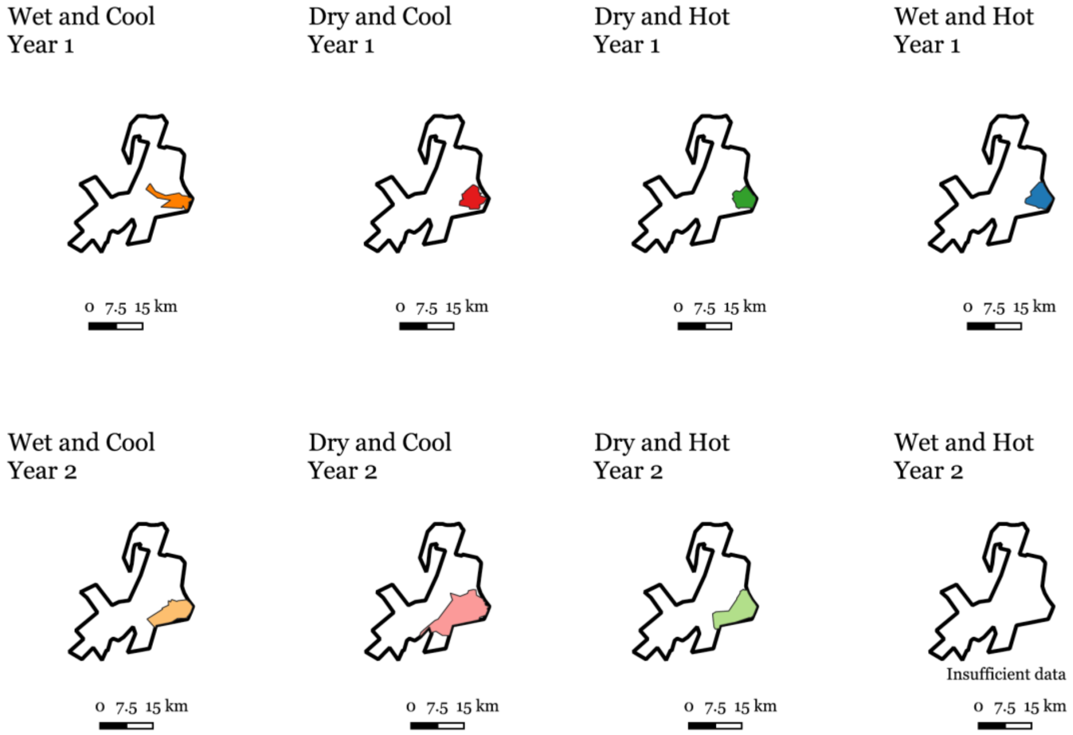

Fig. A6. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat309Ni in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

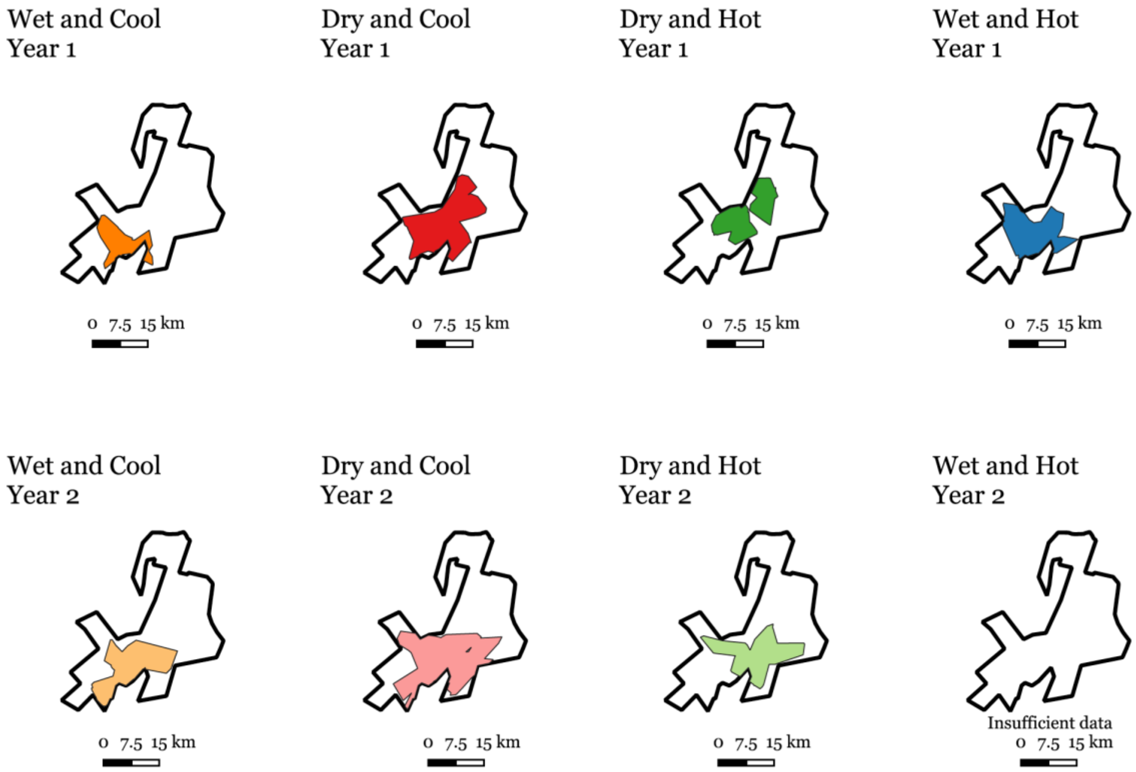

Fig. A7. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat307Pi in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

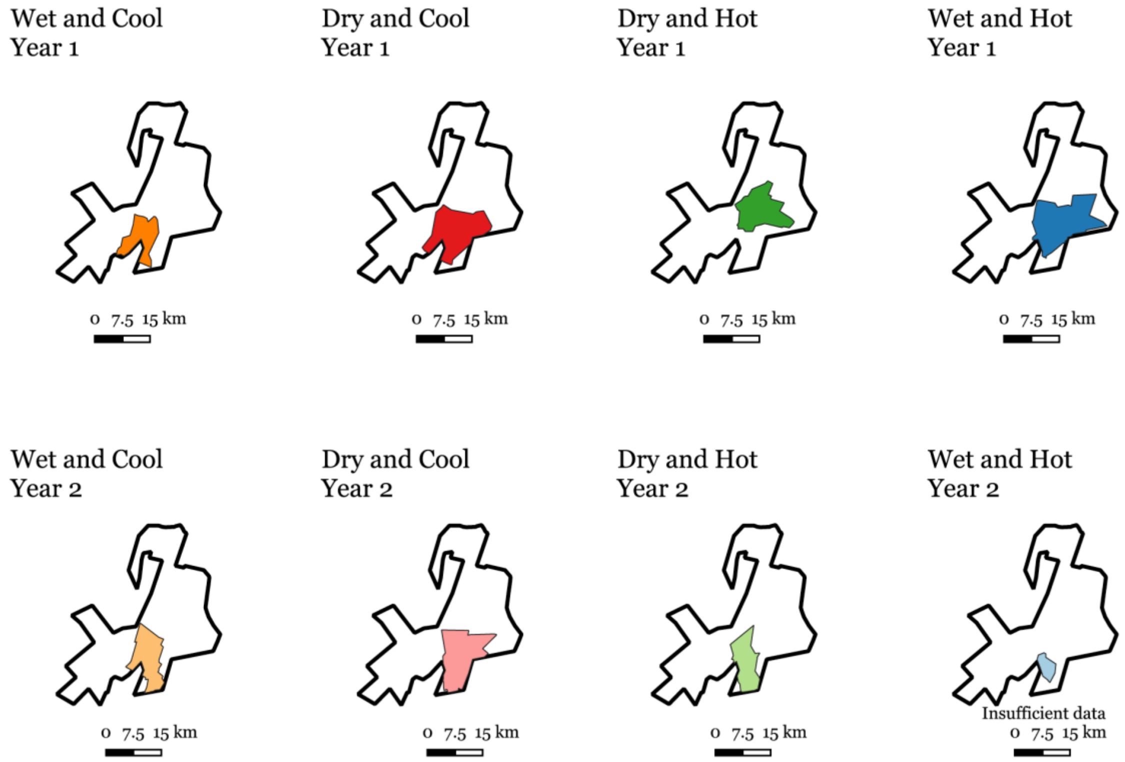

Fig. A8. Seasonal home ranges based on 95% t-LoCoH estimates of collared giraffe Sat311Wi in !Khamab Kalahari Nature Reserve. Each season over the two years is identified

Table A2. Mean giraffe home ranges per season in !Khamab Kalahari Nature Reserve

Season	Year 1	Year 2
Wet cool	79.08875	159.13125
Wet hot	140.73375	28.74
Dry Cool	146.98375	165.18375
Dry Hot	115.19	94.1225

Table A3. Number of GPS points for each giraffe in each season of year 2.

Giraffe ID	**Season**			
	Dry & Cool	Wet & Cool	Dry & Hot	Wet & Hot
Sat305Ca	554	555	552	186
Sat308Da	553	552	547	193
Sat310He	553	554	547	21
Sat306Kem	552	558	554	100
Sat312Ke	552	555	551	191
Sat309Ni	551	554	377	0
Sat307Pi	552	553	366	0
Sat311Wi	563	561	378	75

Appendix IV - Seasonal variation in spatial variables

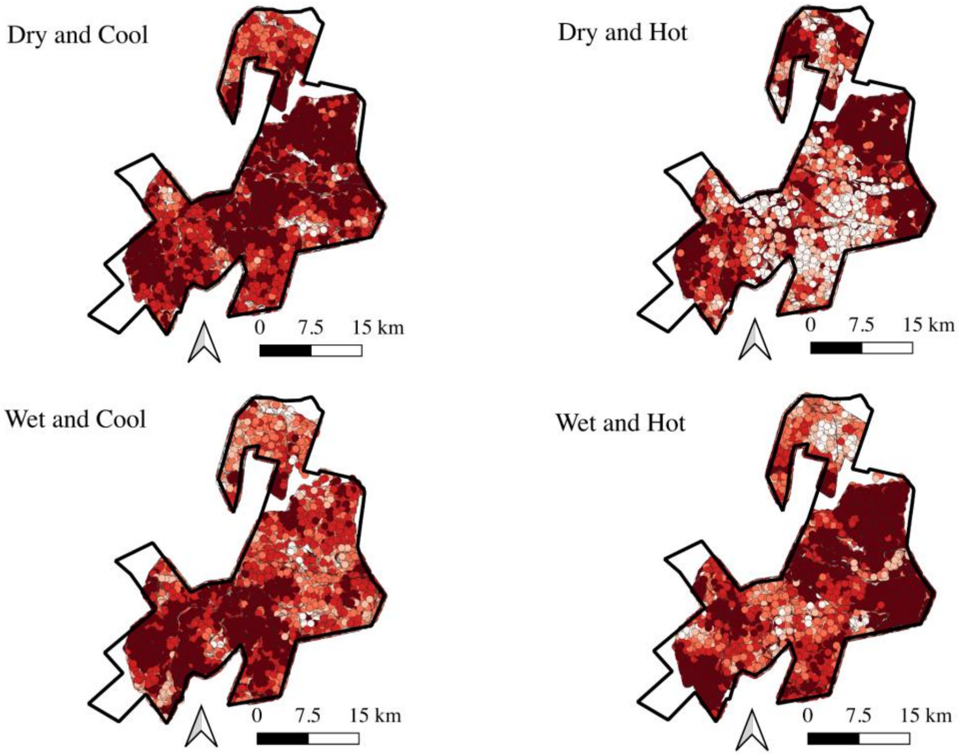

Fig. A9. Seasonal variation in NDVI with lighter coloring representing more giraffe use in !Khamab Kalahari Nature Reserve

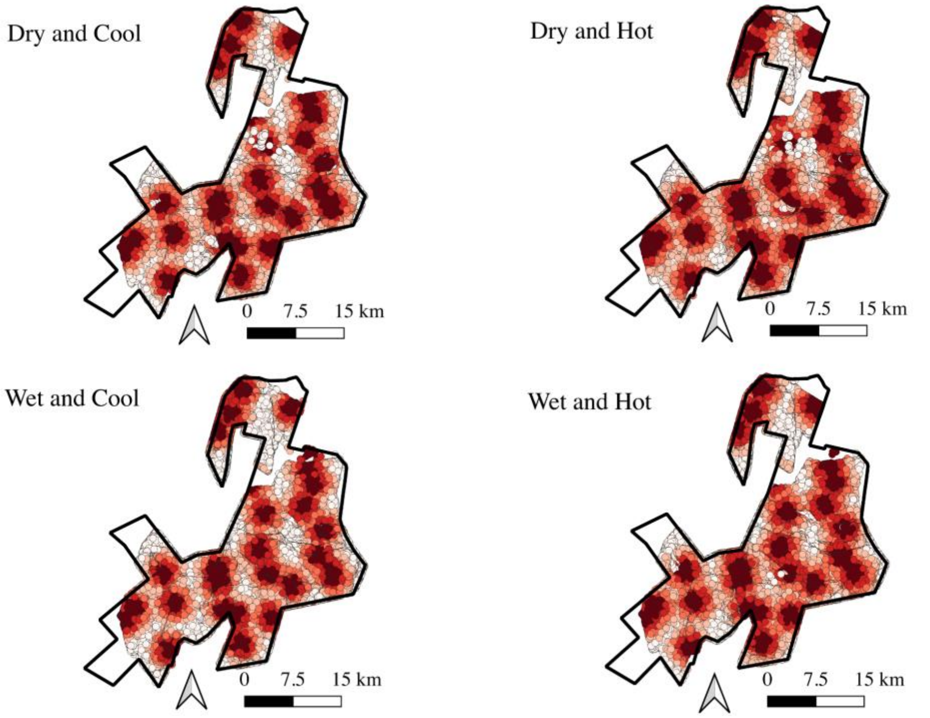

Fig. A10. Seasonal variation in waterhole placement with darker coloring representing more giraffe use in !Khamab Kalahari Nature Reserve

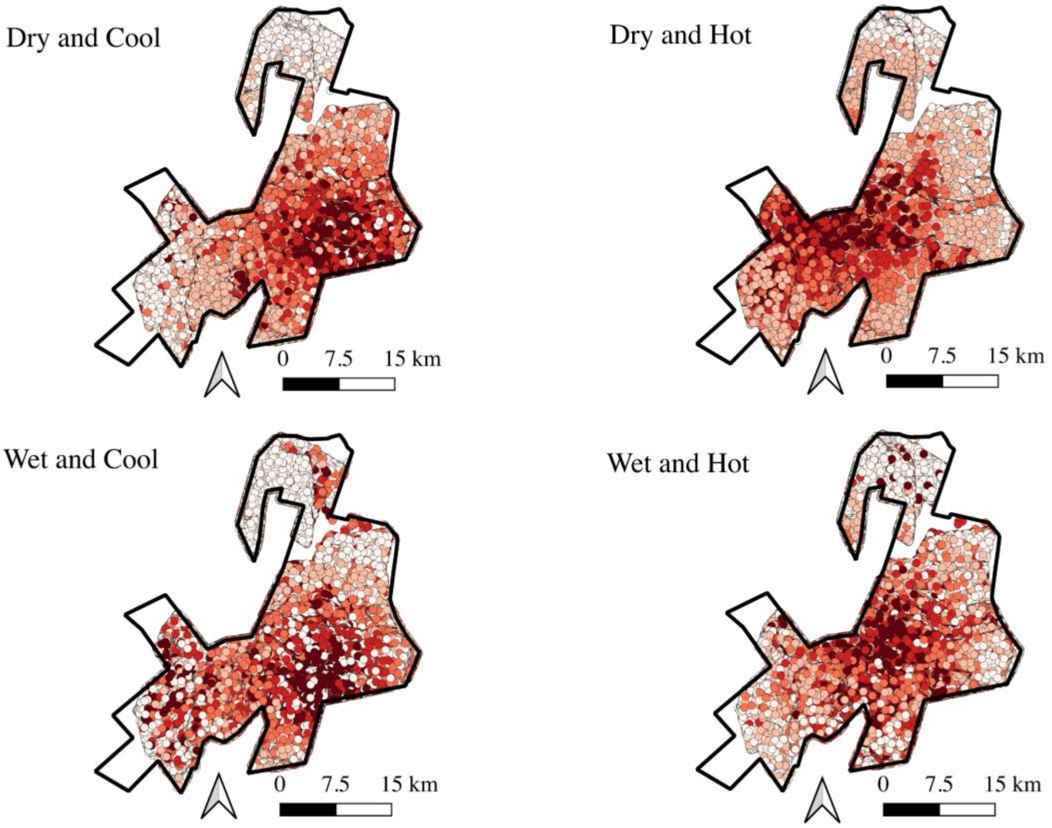

Fig. A11. Seasonal variation in lion distance to giraffes with darker coloring representing a lesser distance from lion to giraffe in !Khamab Kalahari Nature Reserve

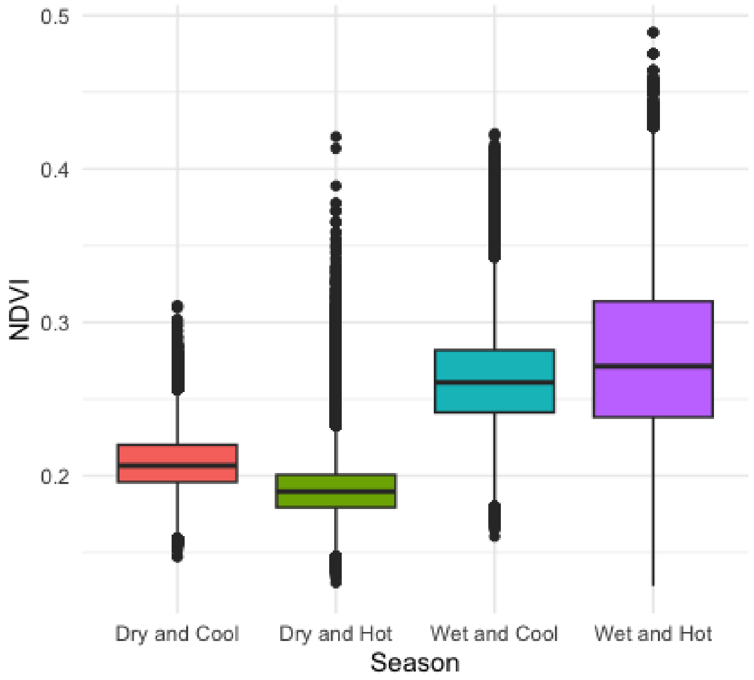

Fig. A12. Box plot showing seasonal variation of NDVI in !Khamab Kalahari Nature Reserve

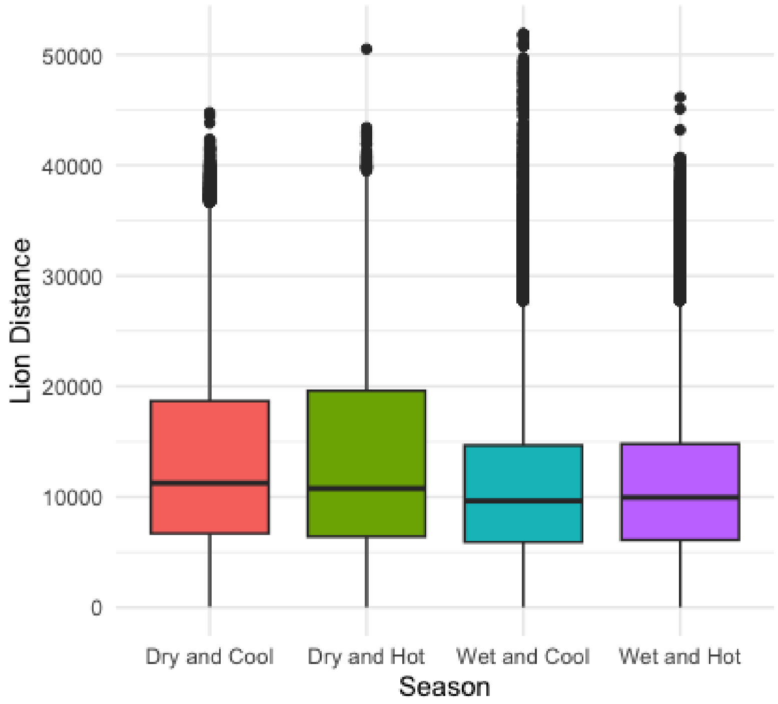

Fig. A13. Box plot showing seasonal variation of lion proximity in !Khamab Kalahari Nature Reserve

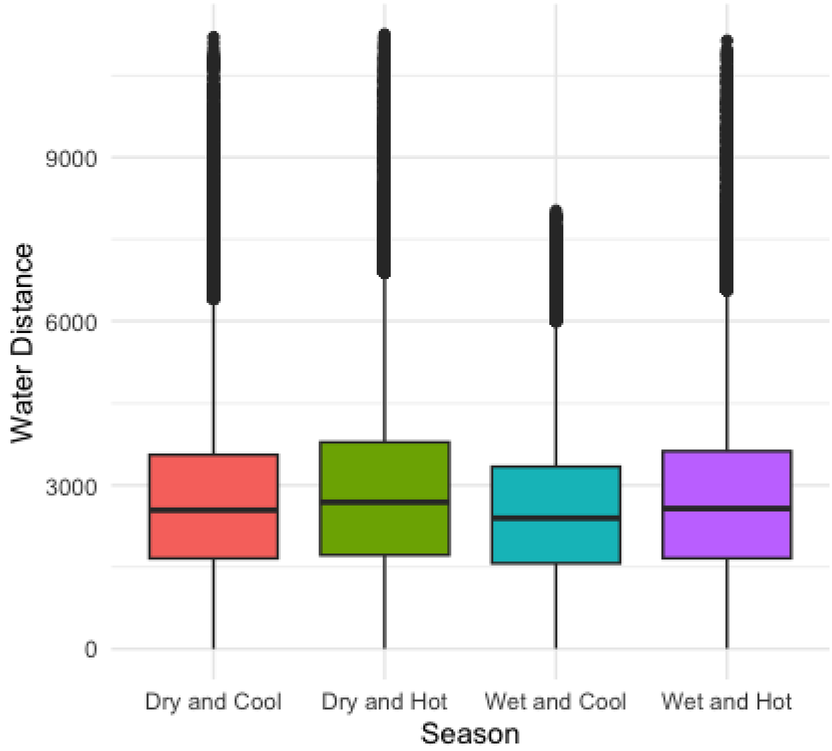

Fig. A14. Box plot showing seasonal variation of waterhole proximity in !Khamab Kalahari Nature Reserve

Appendix V - Overall Home Ranges

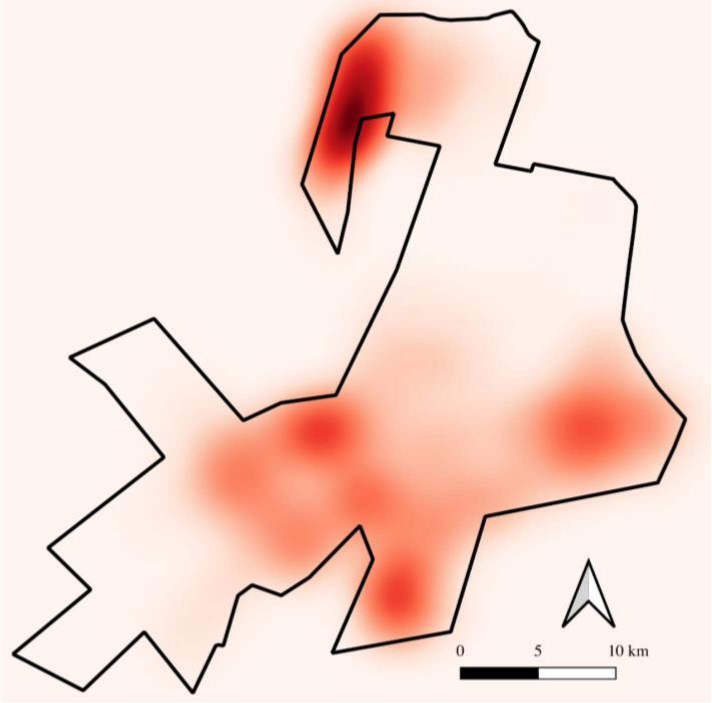

Fig. A15. Heat map showing areas of giraffe density in !Khamab Kalahari Nature Reserve. Darker coloring shows higher density of giraffe points.

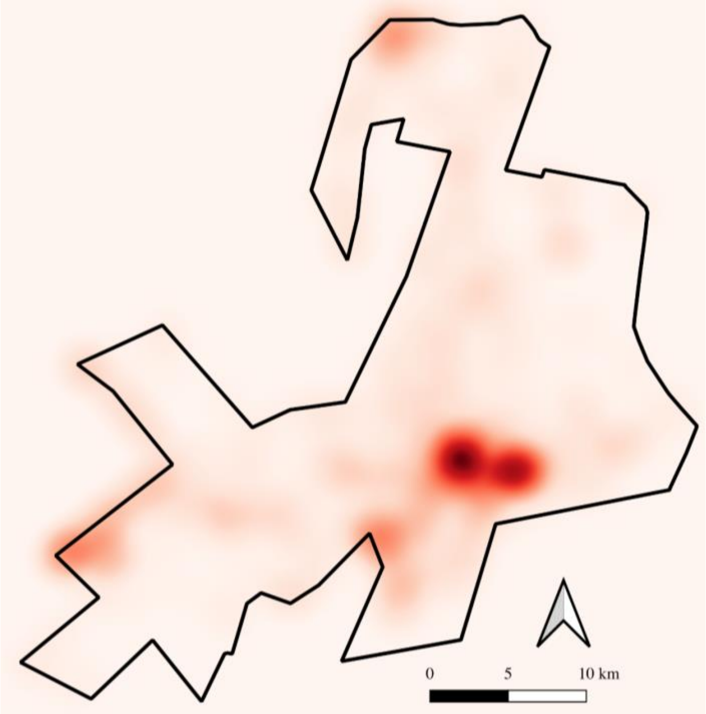

Fig. A16. Heat map showing areas of lion density in !Khamab Kalahari Nature Reserve. Darker coloring shows higher density of lion points.

Appendix VI - Beta estimate plots

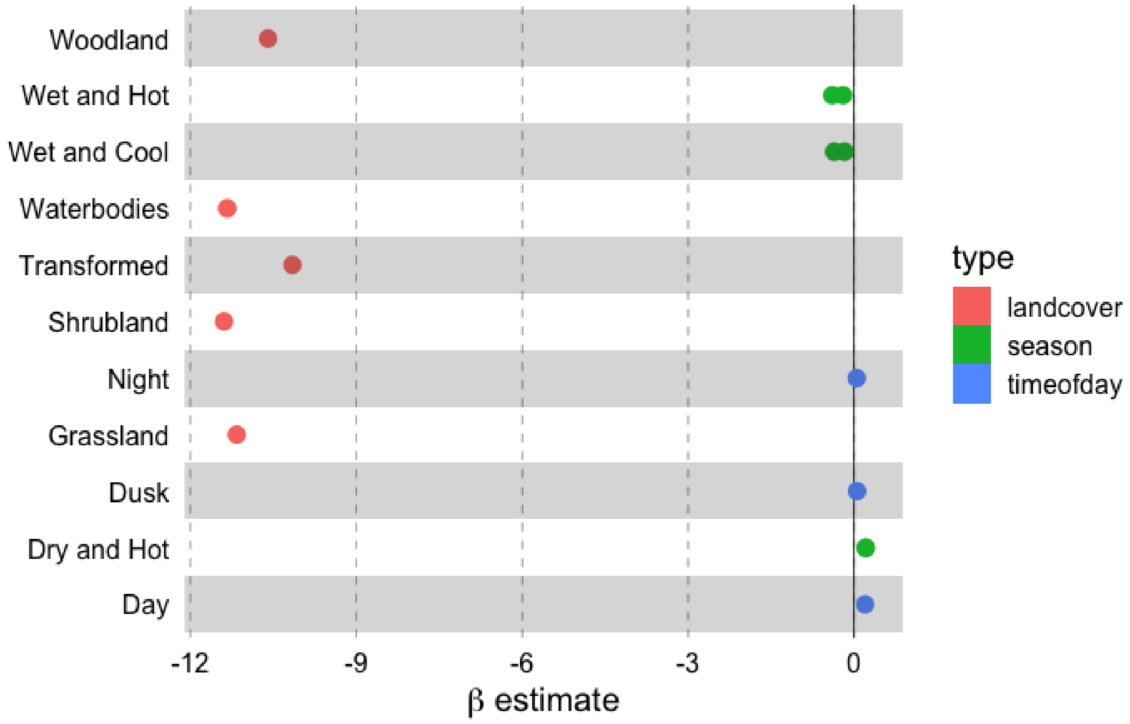

Fig. A17. Categorical variable selection estimates and 95% confidence intervals based on standard error for the RSF. Estimates are shown for those parameters included in the top model (as determined by AICc).

Appendix VII - Spatial variables extraction information

Table A4. Spatial variables extraction information considered in the resource selection analysis

Variable	Type	Range	Source	Description
Elevation	Continuous	1025 – 1045 m	NASA SRTM Digital Elevation 30m accessed through Google Earth Engine (https://developers.google.com/earth-engine/datasets/catalog/USGS_SRTMGL1_003).	30m resolution
NDVI	Continuous	0.128 - 0.489	Normalized Difference Vegetation Index from MOD13Q1.061 Terra Vegetation Indices 16-Day Global 250m (MOD12Q1.061) accessed through Google Earth Engine (https://developers.google.com/earth-engine/datasets/catalog/MODIS_061_MOD13Q1).	16 day, 250m resolution
Landform	Categorical	0-15	SRTM Landform dataset provides landform classes created by combining the Continuous Heat-Insolation Load Index (SRTM CHILI) and the multi-scale Topographic Position Index (SRTM mTPI) datasets (https://developers.google.com/earth-engine/datasets/catalog/CSP_ERGo_1_0_Global_SRTM_landforms#:~:text=The%20SRTM%20Landform%20dataset%20provides,EE%20as%20USGS%2FSRTMGL1_003).	90m resolution. 15 categories simplified to 3 (Upper slope, Lower slop, Valley).
Land Cover	Categorical	0-73	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (https://egis.environment.gov.za/gis_data_downloads)	20m resolution. 73 categories simplified to 4 (Woodland, Shrubland, Transformed land, Grassland)

Appendix VIII – Model Outputs

Table A5. Full generalized linear mixed models used to identify resource selection in giraffes. Akaike Information Criterion (AICc), Bayesian Information Criterion (BICc), and deviance. Giraffe ID is a random effect. The best model is in bold.

Candidate models	AICc	BICc	Deviance
NDVI + season + time of day + waterhole distance + lion distance + landform	643186.8	643329.3	643160.8
NDVI + season + time of day + waterhole distance + lion distance + land cover	642767.1	642920.5	642739.1
NDVI + season + time of day + waterhole distance + lion distance + NDVI*season + landform	642723.1	642898.4	642691.1
NDVI + season + time of day + waterhole distance + lion distance + NDVI*season + land cover	642314.3	642500.6	642280.3

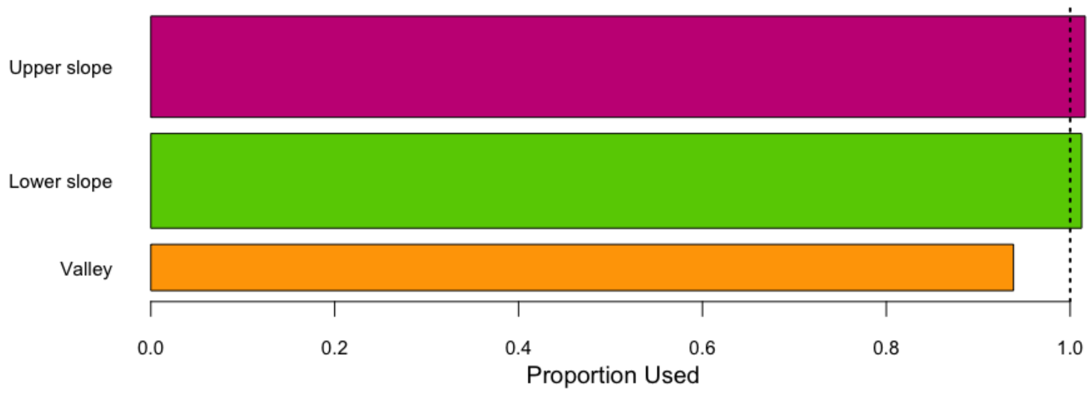

Fig. A18. Relative use plot identifying the greatest landform used. The width identifies the proportion of availability within the landscape and the length determines the use. The dotted line shows where the expected use is equal to the availability in the landscape.