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How Energetic Demands and Habitat Utilisation Can Make or Break Giraffes

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ABSTRACT

Understanding how large herbivores balance energy intake and expenditure is critical for effective rangeland management and conservation. Giraffes (*Giraffa camelopardalis*), as selective browsers, depend on high-quality forage resources that vary seasonally, influencing their movement patterns, home range and habitat selection. However, the extent to which nutritional constraints drive giraffe spatial ecology in arid savanna ecosystems remains poorly understood. This study aims to examine the relationship between giraffe movement patterns, habitat selection and the nutritional properties of preferred vegetation communities within the Rooipoort Nature Reserve, South Africa. We fitted seven male and eleven female giraffes with GPS collars to track their spatial movements over 12 months. Habitat selection was analysed using ArcGIS to identify high-use areas and preferred vegetation types. Nutritional analyses of dominant forage species, including *Senegalia erioloba*, *Ziziphus mucronata* and *Vachellia tortilis*, were integrated with movement data. Statistical analyses included *t*-tests for sex-based movement differences, linear regression for home range overlap vs. rainfall, and ANOVA for seasonal habitat use. Males exhibited significantly larger home ranges (utilising ~63% of the study area) and travelled greater distances than females ($p = 0.005$), primarily due to reproductive roaming strategies. Habitat selection varied seasonally, with dry-season nutritional stress leading both sexes to expand their ranging. High-protein browse species (approximately 10%–20% crude protein) were preferentially selected, indicating that nutritional constraints shape spatial distributions. Giraffes rely on specific high-energy forage species and concentrated resource areas, making them vulnerable to habitat degradation and seasonal resource shortages. Conservation management should prioritise the protection of *Senegalia erioloba* woodlands and *Ziziphus mucronata* shrublands—critical dry-season refuges of high-quality forage—to support sustainable giraffe populations.

1 | Introduction

Conservation management requires a comprehensive understanding of both landscape characteristics and animal energy use, particularly in ecosystems where critical habitat resources are limited. Little is known about how large herbivores like giraffes manage their energy balance when key resources (forage, water and shelter) are scarce or patchily distributed. Giraffes (*Giraffa camelopardalis*) live in a fission–fusion social system with herd size and structure varying by season and location (Deacon and Smit 2017). Males are often solitary or roam between groups, while females tend to reside in herds with other females and juveniles (Bercovitch and Berry 2013; Muller 2019). Giraffes are sexually size-dimorphic, yet historically few sex differences in diet composition have been noted; both sexes generally consume similar browse species, adopting foraging strategies aligned with their differing reproductive roles (Bercovitch 2017). Notably, giraffe bulls pursue a roaming reproductive strategy, travelling widely to seek out oestrous females across the landscape (Bercovitch et al. 2006; Dagg 2014). This

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strategy incurs substantial energetic costs for mature bulls, often exceeding those sustained by post-partum lactating cows that remain in smaller home ranges near their calves (Pellew 1984).

Daily forage intake is critical for free-ranging giraffes to maintain a positive energy balance, especially in arid and semi-arid habitats. On average, adult male giraffes consume forage roughly equivalent to 1.6% of their body weight in dry matter per day, while adult females consume approximately 2.1% (Dierenfeld and du Toit 2002; Deacon and Smit 2017). This intake—on the order of ~15–20 kg dry matter daily for an adult—supports essential physiological functions such as basal metabolism and thermoregulation in extreme climates. The field metabolic rate of adult giraffes has been estimated at ~127 MJ per day (Hudson et al. 2013), indicating substantial energetic demands. Giraffes maximise energy gain by selectively foraging on high-quality browse (rich in protein and moderate in fibre) and by relying on a specialised ruminant digestive system that efficiently extracts energy from fibrous plant material. Interestingly, differences in diet quality can affect giraffe health: for example, wild giraffes feeding on diverse fresh foliage have higher intake of omega-3 fatty acids, contributing to improved immune function, compared to those on limited diets (Roggenbuck et al. 2014). These nutritional adaptations allow giraffes to cope with seasonal shortages and maintain body condition, though severe droughts or habitat degradation can still challenge their energy balance.

In addition to natural variability in resources, anthropogenic factors are increasingly recognised as important influences on giraffe ecology. Habitat loss, human disturbance and environmental pollution all have the potential to affect giraffe behaviour and health. The rapid expansion of human activities has encroached on giraffe ranges and introduced new threats (Kühn et al. 2023). For instance, industrial and agricultural pollutants can contaminate soil and vegetation; a recent study detected heavy metal accumulation (notably thallium) in giraffe browse and water sources at a South African reserve (Kühn et al. 2023). Such pollution poses an emerging risk to giraffe nutrition and health, compounding challenges from natural resource fluctuations. Human presence itself can alter giraffe behaviour: giraffes tend to increase movement and vigilance in the presence of tourists or observers and can exhibit elevated stress hormone levels under frequent disturbance (Scheijen et al. 2021). These insights highlight the need to integrate both ecological and human factors when evaluating giraffe energy use and habitat selection.

Given this background, our study provides detailed information about giraffe movement patterns in relation to habitat resources and offers guidelines for conservation management. By tracking giraffe spatial use with GPS technology and analysing habitat attributes (vegetation types and forage quality) across seasons, we assess how giraffes distribute themselves in the landscape and how that reflects their nutritional needs and energy expenditures. We pay particular attention to differences between males and females and to how seasonal resource limitations may differentially affect their space use. Ultimately, understanding these patterns will inform ecology-based management strategies—for example, identifying critical resource areas for protection, setting sustainable giraffe densities in reserves and mitigating potential human impacts—to ensure viable giraffe populations in the face of environmental change. The main objective of this study was to quantify differences in movement, habitat selection and forage quality between male and female giraffes, testing the hypothesis that energetic demands and seasonal resource variation drive distinct space-use patterns.

2 | Study Area

This study was conducted at the Rooipoort Nature Reserve (RNR) in the Northern Cape province of South Africa (Figure 1). RNR is a privately managed semi-arid savanna reserve of approximately 680 km^2 characterised by plains of mixed shrubland and woodland. The vegetation is diverse: a botanical survey identified about 15 distinct plant community types within the reserve (Bezuidenhout 2009), ranging from grasslands to thornveld. Prominent species include camel thorn (*Senegalia erioloba*), umbrella thorn (*Vachellia tortilis*), black thorn (*Senegalia mellifera*), buffalo thorn (*Ziziphus mucronata*) and various savanna grasses. The climate is hot and dry with highly variable rainfall. Mean annual precipitation is on the order of a few hundred millimetres, delivered in sporadic summer thunderstorms. Average daily temperatures range from highs of ~36°C in midsummer to lows near 0°C on winter nights. This erratic rainfall and extreme temperature range impose seasonal constraints on forage quality and distribution, making RNR an ideal natural laboratory to study how giraffes adjust their space use and diet in response to changing resource abundance. Rainfall is highly variable and seasonal, with monthly averages presented in Figure 2 (sourced from WorldClim Global Climate Data, 2023).

3 | Methods

3.1 | Data Collection

3.1.1 | Animal Tracking

We monitored 18 adult giraffes (7 males and 11 females) in RNR, each fitted with a custom-designed GPS tracking unit (Figure 3). The GPS device, developed by Deacon (2015), was mounted on the giraffe's ossicones (horns) using a padded canvas headband, positioned so as not to interfere with the ears or hearing. This unit recorded the animal's location every hour, 24 h a day, and was equipped with a large battery and solar panel to allow long-term operation. The tracking period spanned one full year, covering all four seasons. GPS data were remotely downloaded at regular intervals for analysis. All animal handling and collaring procedures were performed by experienced wildlife veterinarians under ethical approval (University of the Free State Animal Ethics Committee, Reference no. UFS-AED2015/0066).

3.1.2 | Forage Sampling

To link movements with diet quality, we collected representative samples of leaves from predominant browse species in the giraffes' core-use areas (Kühn et al. 2023). Core areas were identified from the GPS data (see analysis below) as hotspots of frequent use. We assumed that giraffes were feeding on the dominant woody plants present in those high-use patches (since direct continuous observation of feeding was impractical over

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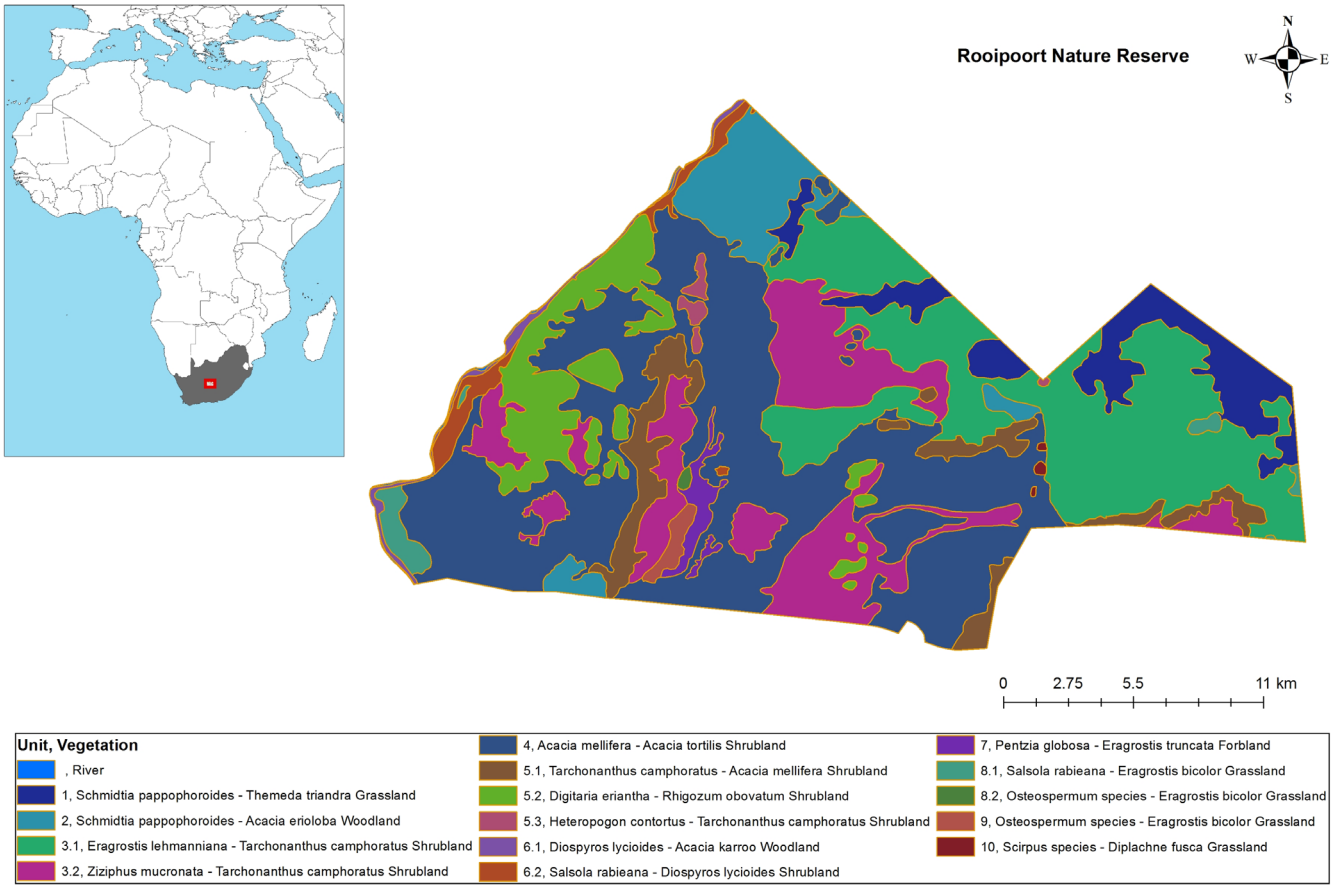


FIGURE 1 | Rooipoort Nature Reserve location, showing the reserve boundary and the vegetation units identified by Bezuidenhout (2009).

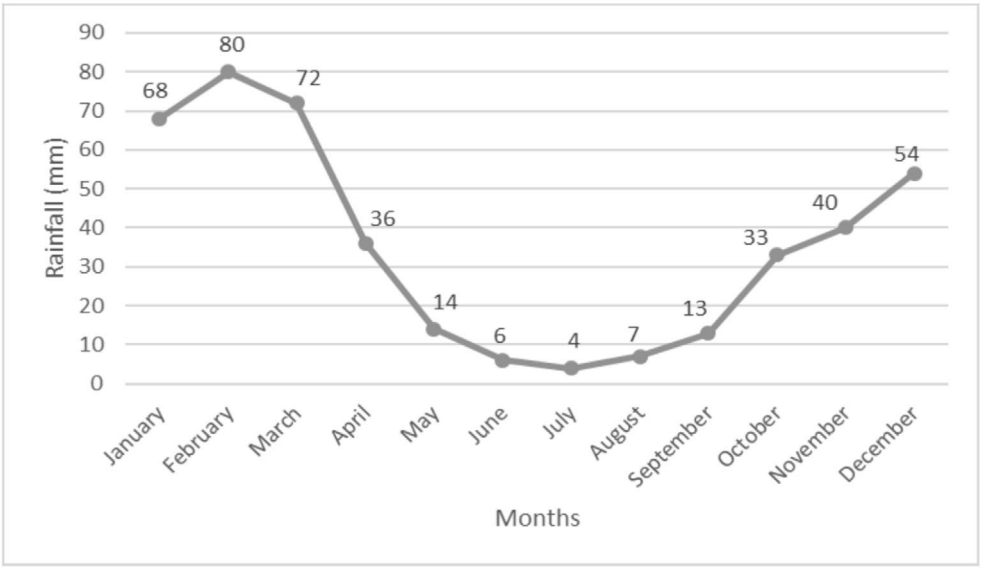


FIGURE 2 | Average monthly rainfall for the Rooipoort Nature Reserve (2014–2015). Rainfall data were obtained from WorldClim—Global Climate Data.

such a large area) and limited diet preferences were indicated by Scheijen et al. (2020). The sampled forage species included *Senegalia erioloba* (camel thorn), *Vachellia tortilis* (umbrella thorn), *Senegalia mellifera* (black thorn), *Ziziphus mucronata* (buffalo thorn), *Tarchonanthus camphoratus* (camphor bush), *Grewia flava* (raisin bush) and other common browse plants at sites frequently visited by the collared giraffes (Kühn et al. 2023). These leaf samples were stored and later analysed in the laboratory for nutritional content. We measured crude protein (via Kjeldahl nitrogen analysis), fibre fractions (neutral detergent fibre and acid detergent fibre using Van Soest methods) and other basic nutritional parameters. Although our focus was on

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FIGURE 3 | Illustration of a GPS tracking device attached to a giraffe's head (ossicone-mounted) to record spatial data continuously.

nutritional energy and protein, we also conducted a mineral screen on these samples (as part of a parallel study) to check for any heavy metal contamination (see Kühn et al. 2023 for details). This dietary sampling approach allowed us to infer the quality of the giraffes' diet based on the vegetation available in their preferred habitats, acknowledging that the diet composition is inferred from habitat use rather than direct feeding observations.

3.2 | Data Analysis

3.2.1 | Spatial Analysis

The collected GPS locations were processed using ArcGIS (ESRI Inc.) and R statistical software. To delineate individual home ranges and core-use areas, we applied a spatial clustering approach. First, we used the ArcGIS 'Aggregate Points' tool with a 1000 m distance threshold to group dense clusters of GPS points into preliminary polygons, thereby identifying areas frequently used by each giraffe. We then calculated both seasonal and annual home ranges for each individual using minimum convex polygons (MCPs) and initially explored options with kernel density estimators (KDE; 95% utilisation distributions). Overlap between male and female ranges was assessed by intersecting these polygons in GIS. We also performed hotspot analysis on the GPS data (ArcGIS Optimised Hot Spot Analysis) to detect statistically significant clusters of intensive use ('hot spots') versus under-use ('cold spots') across the landscape. The hotspot analysis yielded maps highlighting key resource areas for each sex in each season.

3.2.2 | Habitat Selection and Electivity

To evaluate habitat selection, we overlaid each giraffe's GPS coordinates onto the vegetation community map of RNR (Bezuidenhout 2009) and investigated the vegetation type structure, composition and indicator plant species (Table 1). We calculated the proportion of fixes occurring in each of the 15 vegetation types for wet and dry seasons separately. We then compared these use proportions to the availability (areal extent) of each vegetation type in the study area. Selection or avoidance of particular vegetation types was quantified using Ivlev's electivity index:

$$E = (U - A) / (U + A)$$

where U is the proportion of use and A is the proportion available. Ivlev's index values range from −1 to +1 (with positive values indicating selection, negative indicating avoidance). We also performed chi-square goodness-of-fit tests to statistically assess whether habitat use deviated from random expectations based on availability. Vegetation types where giraffes spent disproportionately more time than available were considered preferred, whereas types used less than expected were deemed avoided.

3.2.3 | Movement and Energy Use

From the sequential GPS fixes, we computed movement metrics for each individual. We calculated daily distances travelled by summing the linear distances between successive hourly fixes, then averaged these daily distances by month and by season for each giraffe. This allowed a comparison of movement magnitude between males and females and across seasons. We hypothesised that males would travel farther (due to roaming for mates) and that movements would increase in the dry season when resources are sparse. To estimate the energetic cost associated with movement, we combined our movement data with literature values for giraffe locomotion energy expenditure. Specifically, using reported energy costs of walking for giraffes (from prior studies), we approximated the energy each giraffe expended on locomotion per month. This provided a rough index of energy output from movement to complement our analysis of energy intake from browse. Finally, we conducted statistical comparisons of movement distances and inferred energy expenditure between sexes and across seasons. We used mixed-effects models and ANOVA for these comparisons, with individual giraffe identity as a random factor to account for repeated measures on the same animals.

4 | Results

4.1 | Home Range and Movement Patterns

Both male and female giraffes utilised large areas of the reserve, but as expected, males ranged over substantially broader areas than females. The total combined area explored by the seven GPS-tracked males (union of their MCP home ranges) encompassed roughly 63% of the entire reserve (~42,700 ha). In contrast, the 11 collared females collectively used about 39% of the reserve area, mostly concentrated in central regions of RNR (Figure 4). Individual adult bulls often travelled long distances, periodically venturing to the farthest corners of the reserve, whereas cows tended to remain in more localised home ranges near consistent resource patches. Over the year, males travelled significantly greater distances than

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TABLE 1 | Summary of vegetation types in the Rooipoort Nature Reserve modified from Bezuidenhout (2009).

Number	Classification	Description
1	*Schmidtia pappophoroides*—*Themeda triandra* Grassland	• Primarily Grassland
2	*Schmidtia pappophoroides*—*Senegalia erioloba* Woodland	• This section represents around 2388 ha in size. Characterised by the tree *Vachellia erioloba* and sparsely distributed *Vachellia tortilis*, grasses *Aristida stipitata* and *Eragrostis pallens*, and forbs *Indigofera daleoides* and *Pollichia campestris*. • *Senegalia erioloba*: Also known as camel thorn, this tree species produces pods rich in proteins and carbohydrates. The crude protein content of the pods can range from 12% to 18%, serving as a crucial nutrient source for wildlife and livestock in arid regions.
3	*Tarchonanthus camphoratus* Shrubland	• Shrubland is found throughout the reserve, the largest at 15088 ha. *Tarchonanthus camphoratus*: Known as camphor bush, it has aromatic leaves with moderate nutritional value, primarily serving as browse for certain herbivores. Specific protein values are not well-documented, but similar browse species in arid regions typically have crude protein contents ranging from 8% to 12%. *Eragrostis lehmanniana*: This drought-tolerant grass species provides moderate forage quality, with crude protein levels typically between 5% and 9%, contributing essential fibres to the diet of grazing animals. *Ziziphus mucronata*: Commonly known as buffalo thorn, its leaves and fruits are rich in nutrients, offering crude protein content ranging from 10% to 15%, making it a valuable food source in arid landscapes.
3.1	*Eragrostis lehmanniana*—*Tarchonanthus camphoratus* Shrubland	
3.2	*Ziziphus mucronata*—*Tarchonanthus camphoratus* Shrubland	
4	*Senegalia mellifera*—*Senegalia tortilis* Shrubland	• Plains and footslopes. Shrubland is 14,947 ha. Poorly developed tree stratum is 5.3 m tall with a canopy cover of 2.3%. Two tree species are prominent, namely *Boscia albitrunca* and *Vachellia tortilis*. • *Senegalia mellifera*: Also known as black thorn, it provides browse with moderate protein content, typically between 10% and 14%, essential for herbivores in dry areas. • *Senegalia tortilis*: Known as umbrella thorn, its pods and leaves are nutritious, offering crude protein content ranging from 12% to 18%, vital for livestock nutrition.
5	*Senegalia mellifera* Shrubland	• Shrubland strongly correlated with mountainous areas, size 5292 ha, distributed throughout the study area. Rocks and stones cover more than 80% of the soil surface, while the soil is shallow and well-drained with three sub-classifications. Dominated by *Senegalia mellifera*, this shrubland offers moderate-quality browse, supplying essential nutrients with crude protein levels typically between 10% and 14% to herbivores in arid regions. A combination of *Tarchonanthus camphoratus and Senegalia mellifera* provides a mix of browse options with varying nutrient profiles suitable for different herbivores. *Digitaria eriantha*: Known as finger grass, it offers high-quality forage with significant protein content, typically between 8% and 12%, beneficial for grazing animals. • *Rhigozum obovatum*: This shrub provides browse with moderate nutritional value, contributing to the diet diversity of herbivores. Specific protein values are not well-documented, but similar shrubs in arid regions typically have crude protein contents ranging from 8% to 12%. • *Heteropogon contortus*: Also known as spear grass, it provides moderate-quality forage, offering essential fibres and proteins, with crude protein content typically between 6% and 10%.
5.1	*Tarchonanthus camphoratus*—*Senegalia mellifera* Shrubland	
5.2	*Digitaria eriantha*—*Rhigozum obovatum* Shrubland	
5.3	*Heteropogon contortus*—*Tarchonanthus camphoratus* Shrubland	

(Continues)

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TABLE 1 | (Continued)

Number	Classification	Description
6	*Diospyros lycioides* Woodland	• Woodland is closely associated with the Vaal River and floodplains. • *Diospyros lycioides*: Commonly referred to as bluebush, its fruits and leaves are consumed by wildlife, offering vitamins and minerals essential for their diet. Specific protein values are not well-documented, but similar species in arid regions typically have crude protein contents ranging from 8% to 12%. • *Senegalia karroo*: Also known as sweet thorn, it enhances soil nitrogen content through nitrogen-fixing bacteria in its root nodules, improving soil fertility and providing nutritious browse with high protein content, typically between 12% and 18%. • *Salsola rabieana*: This saltbush species is adapted to saline soils and offer forage with moderate nutritional value, including salts and minerals beneficial for certain herbivores. Specific protein values are not well-documented, but similar saltbush species typically have crude protein contents ranging from 8% to 14%.
6.1	*Diospyros lycioides—Senegalia karroo* Woodland	
6.2	*Salsola rabieana—Diospyros lycioides* Shrubland	
7	*Pentzia globosa—Eragrostis truncata* Forbland	• Primarily Karoo bushes
8	*Eragrostis bicolor* Grassland	• Primarily Grassland
8.1	*Salsola rabieana—Eragrostis bicolor* Grassland	
8.2	*Osteospermum species—Eragrostis bicolor* Grassland	
9	*Cynodon dactylon—Sporobolus ioclados* Grassland	• Grassland
10	*Scirpus species—Diplachne fusca* Grassland	• Grassland

females. On average, a male giraffe covered about 8–12 km per day, roughly double the daily distance of an average female (approximately 4–6 km per day) (*t*-test, $p < 0.01$; Table 2). This sex difference in movement was most pronounced in the dry season (Figure 5), when several bulls undertook wide-ranging forays and female movements were more restricted. During the driest months, overlap between male and female range areas was minimal compared to the total available area (Figure 6). In late winter (peak dry season), only about 10%–15% of each sex's range overlapped with the other, compared to ~30% overlap in the wet season (Table 3). Females in dry months often constrained their movements to small core areas containing the last green foliage or remaining water sources, presumably to conserve energy. By contrast, males continued to roam extensively in search of any remaining forage and receptive females. Despite these differences, both sexes showed some flexibility: when resource distribution shifted after the first rains, females expanded their range use slightly, and males correspondingly shifted to overlap more with female group areas (Table 3).

Seasonal changes in movement were evident for both sexes (Figure 5). Giraffes of both sexes had larger home ranges in the dry season than in the wet season. On average, seasonal home range area (MCP) was about 1.5–2 times larger in the dry season, reflecting the need to travel farther to find adequate forage and water as resources became scarce (see also Deacon 2015; Deacon and Smit 2017). Home range estimates based on 95% kernel utilisation distributions showed a similar expansion in the dry season for both sexes. Total distance travelled per month peaked in late winter (August–September) for most individuals (Table 4), then declined when spring green-up provided abundant food in a smaller area (Figure 7). Our GPS data also revealed individual variability in movement behaviour (Table 2). For example, one younger adult male (M3) remained near a specific valley year-round and travelled relatively little, while an older bull (M6) ranged almost the entire reserve and had the highest recorded daily distance (~18 km on 1 day). Among females, those with young calves had the smallest range sizes and lowest daily movement, which is consistent with calf-rearing behaviour limiting how far mothers travel. These findings collectively demonstrate that both sexes and season strongly influence giraffe movement patterns (Figure 8).

4.2 | Habitat Use and Vegetation Selection

Analysis of habitat preferences revealed that giraffes did not use all vegetation types in proportion to their availability. Instead, they showed clear selection for certain key resource areas rich in browse. Both sexes heavily utilised habitats

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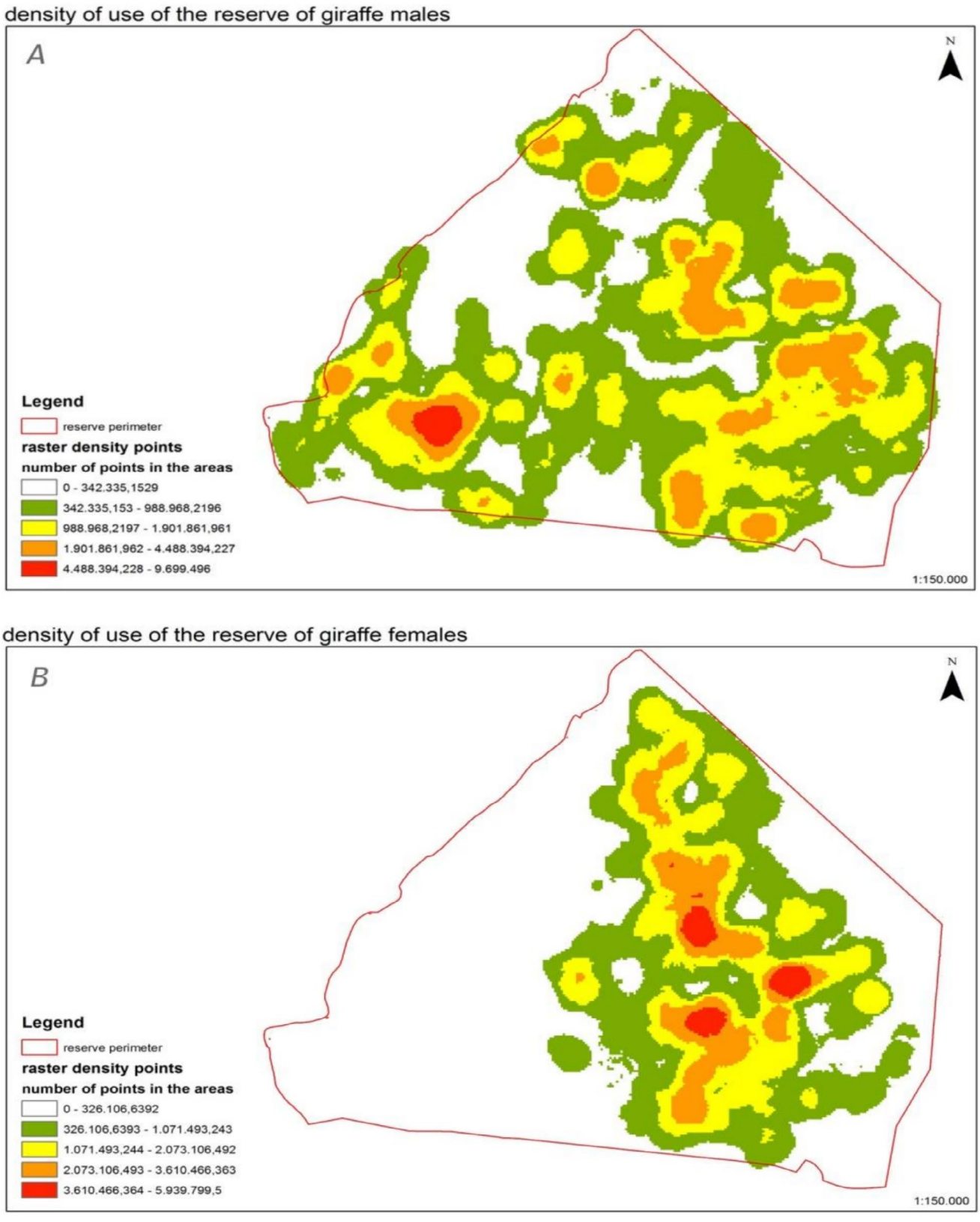


FIGURE 4 | Point-density distribution map of giraffe GPS locations. The figure shows a heatmap of space use generated from Minimum Convex Polygon (MCP) density estimation of GPS collar data. Darker shading indicates areas with higher concentrations of giraffe locations (more intensive use), while lighter shading represents lower use. This density map allows visual comparison of core-use areas across the reserve.

characterised by highly nutritious browse species, especially during the dry season (Table 5). Statistical analysis confirmed that habitat use was non-random (χ^2 tests, $p < 0.01$ overall): giraffes spent disproportionately high time in a subset of vegetation communities while largely avoiding others. The results showed that giraffes concentrated the bulk of their foraging in

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TABLE 2 | Data of each individual giraffe used for comparison analyses.

	Collar	Total metres	Date	Months	Average km per month	Amount of points transmitted by the GPS	Analyses				
							Vegetation	Home range	Overlap	Rainfall	Distances
Male	2289	4,495,056,05	02/10/2017–05/10/2018	12	374.59	5235	■	■	■	■	■
	2291	4,862,244,76	02/10/2017–05/10/2018	12	405.19	6508	■	■	■	■	■
	2295	3,970,702,65	02/10/2017–03/09/2018	11	360.97	5712	■	■	■	■	■
	2296	4,435,891,60	02/10/2017–05/10/2018	12	369.66	7454	■	■	■	■	■
	2293	203,998,76	02/10/2017–21/10/2017	0.66	309.09	472		■			
	2292	1,097,385,48	02/10/2017–16/08/2017	9.5	115.51	357		■			■
	2290	143,056,61	02/10/2017–12/10/2017	0.33	433.50	279		■			
Female	2277	1,824,343,12	02/10/2017–04/10/2018	12	152.03	4592	■	■	■	■	■
	2283	1,388,999,08	02/10/2017–28/03/2018	6	231.50	3490	■	■	■	■	■
	2285	2,692,892,25	02/10/2017–05/10/2018	12	224.41	7168	■	■	■	■	■
	2280	682,712,01	02/10/2017–24/04/2018	7	97.53	1452		■			■
	2279	875,663,61	02/10/2017–18/12/2017	2.5	350.27	1707		■			■
	2286	633,092,11	02/10/2017–18/12/2017	2.5	253.24	253					■
	2284	749,638,82	02/10/2017–11/12/2017	2.33	321.73	1390					
	2282	659,435,67	02/10/2017–16/12/2017	2.5	263.77	2254					■
	2278	989,830,28	02/10/2017–18/12/2017	2.5	395.93	1948					■
	2281	818,522,05	02/10/2017–16-02/2018	4.5	181.89	1932		■			■

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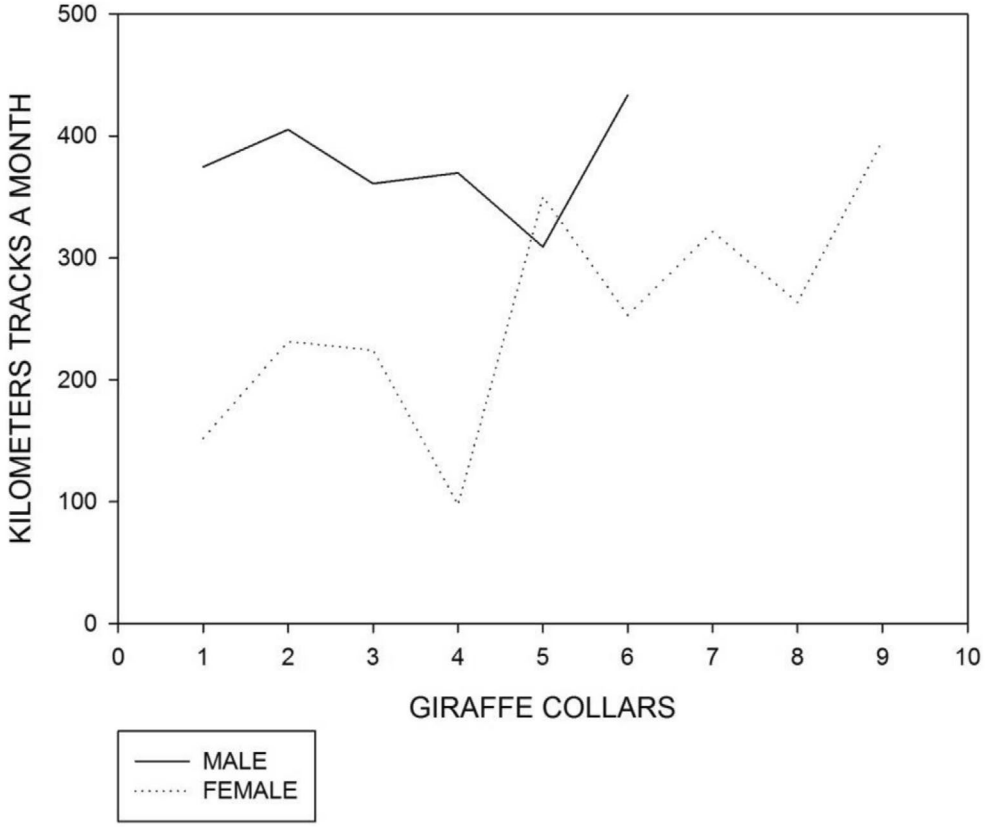


FIGURE 5 | Comparison of average monthly movement distances (km) between male and female giraffes.

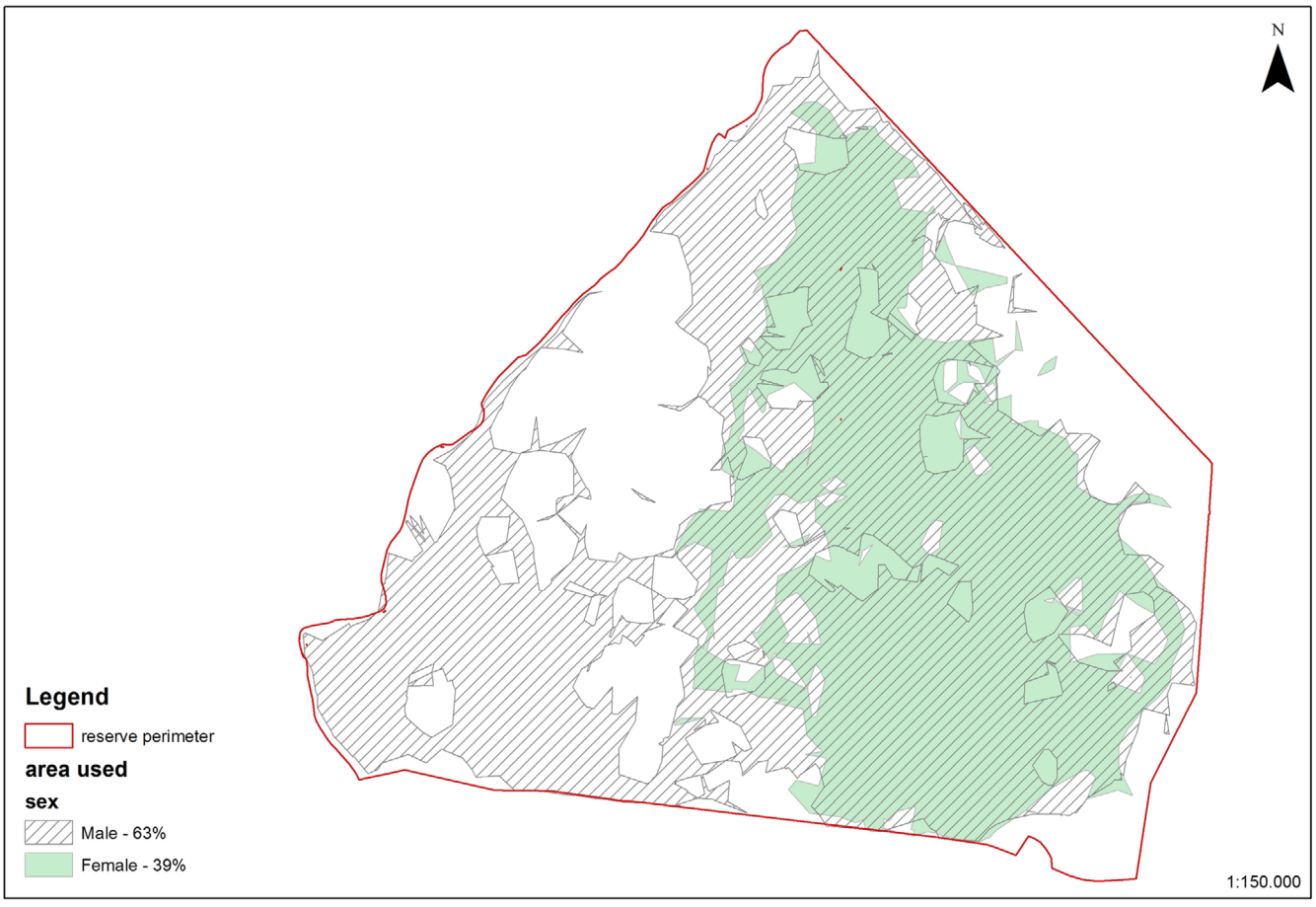


FIGURE 6 | Percentage of the reserve area explored by males and females compared to total available area.

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TABLE 3 | Comparison between home range overlap and average monthly rainfall (linear regression).

		4 males	3 females	
		Hectares of overlap	Hectares of overlap	Average monthly rainfall (mm)
Months	January	423.7	192.9	68
	February	207.9	247.1	80
	March	698.2	138.8	72
	April	476.5	No data	36
	May	2.2		14
	June	104.1		6
	July	143.7		4
	August	37.3		7
	September	40.3		13
	October	186.9	0.0	33
	November	0.0	0.0	40
	December	333.7	0.0	54
Linear regression	*F*	8.095	18.425	
	p	*0.017	*0.013	

TABLE 4 | Comparison of the kilometres travelled per month between males and females.

Collar	Metre	Date	Month	Averages per month	km
Male					
2289M	4495,056	02/10–05/10/2018	12	374,588	374.59
2291M	4862,245	02/10–05/10/2018	12	405,187	405.19
2295M	3970,703	02/10–03/09–2018	11	360,973	360.97
2296M	4435,892	02/10–05/10/2018	12	369,658	369.66
2293M	203,999	02/10–21/10/2017	0.66	309,089	309.09
2290M	143,057	02/10–12/10/2017	0.33	433,505	433.5
Female					
2277F	1824,343	02/10–04/10/2018	12	152,029	152.03
2283F	1388,999	02/10–28/03/2018	6	231,500	231.5
2285F	2692,892	02/10–05/10/2018	12	224,408	224.41
2280F	682,712	02/10–24/04/2018	7	97,530	97.53
2279F	875,664	02/10–18/12/2017	2.5	350,265	350.27
2286F	633,092	02/10–18/12/2017	2.5	253,237	253.24
2284F	749,639	02/10–11/12/2017	2.33	321,733	321.73
2282F	659,436	02/10–16/12/2017	2.5	263,774	263.77
2278F	989,830	02/10–18/12/2017	2.5	395,932	395.93

four vegetation community types (out of the 15 mapped in the reserve) described in Table 1. These four preferred community types, with their dominant plant species (see Table 5), were as follows. The distribution of time spent in different vegetation types is shown in Figure 9, highlighting the proportional use of each mapped habitat community based on GPS location data.

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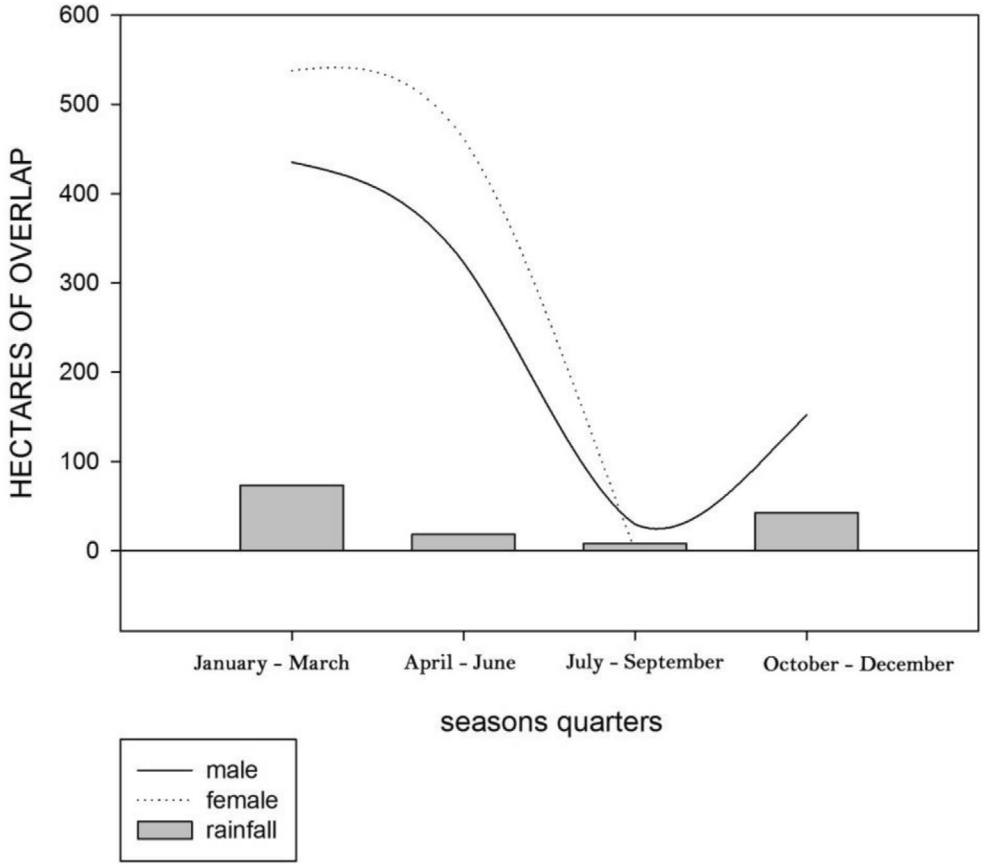


FIGURE 7 | Seasonal rainfall and spatial overlap of male and female giraffe home ranges. The bar graph represents average rainfall (mm) per calendar quarter, while the line graph shows the percentage overlap in home range areas between males and females during corresponding periods. This figure illustrates how home range overlap varies with rainfall seasonality, allowing direct comparison of environmental conditions and giraffe spatial behaviour.

4.2.1 | *Schmidtia Pappophoroides—Senegalia Erioloba* Woodland

An open woodland where camel thorn (*S. erioloba* or camelthorn acacia) is the dominant tree and *Schmidtia* grass carpets the understory. Giraffes frequented this community year-round. *Senegalia erioloba* is known to be a vital nutrient source for herbivores in arid environments; its seed pods and leaves are rich in protein and soluble carbohydrates, with crude protein content ranging ~12%–18% on a dry matter basis (Bezuidenhout 2009). These high-protein pods become especially important in the late dry season, providing a crucial food resource when most other vegetation is nutritionally poor. In our study, giraffes intensively browsed camel thorn trees, often congregating in these woodlands during late dry-season months when camel thorn pods were abundant on the ground.

4.2.2 | *Tarchonanthus Camphoratus* Shrubland

Thickets dominated by camphor bush (*T. camphoratus*) were another habitat type used frequently, particularly by giraffes in the dry season. This vegetation type (sometimes mapped as 'shrubland on rocky soils') provides moderate-quality browse. While specific protein values for camphor bush leaves are not well documented, similar evergreen shrubs in semi-arid regions typically contain roughly 8%–12% crude protein in their foliage (Mudau et al. 2021). We observed that giraffes browsed camphor bush only to a limited extent—usually targeting it after preferred acacia species (e.g., camel thorn) had shed their leaves. Thus, *Tarchonanthus* served as a fallback food, contributing dietary fibre and some micronutrients during critical periods of forage scarcity. Its widespread availability in the reserve makes it a reliable resource in drought times, even if it is not a preferred food when more palatable species are available.

4.2.3 | *Eragrostis lehmanniana—Tarchonanthus Camphoratus* Mixed Shrubland/Grassland

This is a mixed grass–shrub community, where Lehmann lovegrass (*E. lehmanniana*, a drought-tolerant grass) grows alongside patches of camphor bush and other shrubs. Giraffes showed interest in this community mainly for its woody components rather than the grass itself. Notably, *Ziziphus mucronata* (buffalo thorn) often occurs in these areas as a sub-dominant tree. Buffalo thorn is a highly important browse species for giraffes; its leaves (and occasionally fruits) contain roughly 10%–15% crude protein, making it a valuable food source in arid landscapes (Hassen et al. 2009). In our observations, giraffes actively sought out buffalo thorn thickets within this community. The grass *Eragrostis* was not directly eaten by giraffes (being a

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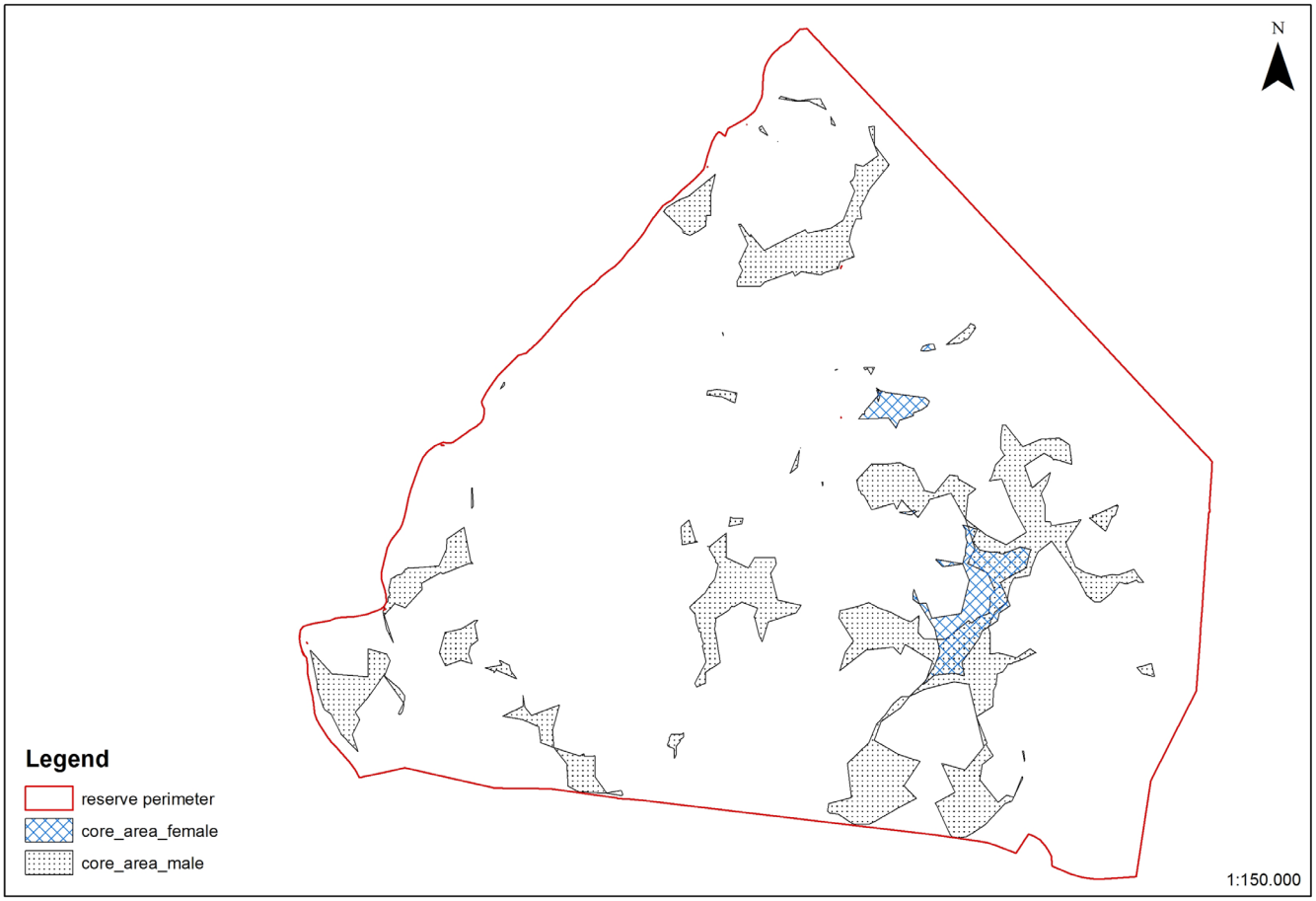


FIGURE 8 | Areas of annual overlap between male and female giraffes. An intersect analysis was used to quantify the overlap of their home ranges.

grazer resource), but its presence indicates certain soil and moisture conditions that also support browseable shrubs. Overall, this community provided a mix of medium-quality forage that giraffes used opportunistically—especially younger individuals and females that stayed near more open areas offering both browse and good visibility for predator awareness.

4.2.4 | *Senegalia mellifera—Vachellia tortilis* Shrubland

In this community, black thorn (*S. mellifera*) and umbrella thorn (*V. tortilis*) form a dense thorny shrubland or low woodland. Giraffes frequently visited these areas, particularly in the late dry season and early wet season. *Senegalia mellifera* offers moderate-quality forage; its leaves contain roughly 10%–14% crude protein, and this species often retains some green leaves later into the dry season than many other deciduous plants (Schmidt et al. 2007). *Vachellia tortilis* (umbrella thorn) is an even more nutritious species: its foliage and seed pods are rich in protein (approximately 12%–18% CP) and minerals, making it a crucial resource for giraffes and other browsers in this ecosystem (Hassen et al. 2009). We observed giraffes stripping leaves from live umbrella thorn branches and foraging on fallen pods beneath these trees. This vegetation type consistently provided essential nutrients, and giraffes showed a strong preference for it whenever it was available. Even during the peak dry months, black thorn and umbrella thorn shrubs retained enough edible material (including dry pods) to attract giraffe browsing. These acacia-dominated shrublands appear to act as nutritional refuges that help sustain giraffes through periods of scarcity.

Across all these favoured vegetation types, the common thread is that they offer relatively high crude protein and digestible carbohydrates, helping giraffes meet their nutritional requirements. In contrast, plant communities dominated by less palatable species (e.g., pure grasslands or woodlands without high-protein browse) were under-utilised by giraffes, especially in the dry season. We found that open grassy areas and woodlands lacking nutritious foliage were largely avoided. Ivlev's electivity indices reflected these patterns: for instance, the camel thorn woodland had a strongly positive electivity value ($E \approx +0.5$ in the dry season), indicating selection, whereas the open grassland community showed a negative index ($E < 0$, roughly -0.8), indicating consistent avoidance. The chi-square tests for habitat use versus availability were highly significant ($p < 0.001$), confirming that giraffe habitat use was non-random. In summary, giraffes of both sexes concentrated their foraging in a few key vegetation communities that provided the highest quality browse, and they largely avoided habitat types that offered little nutritional value. Notably, there was no evidence of major differences between males and females in the types of vegetation preferred; both sexes converged on the same critical resource zones within the landscape.

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TABLE 5 | Dominant woody browse species in the four most frequently used vegetation communities by giraffes.

	Vegetation code[b]	Quarter[a]					Season	
		1°	2°	3°	4°		Wet	Dry
Male	1	22.5	0.3	9.3	10.0		16.3	4.8
	2	152.3	0.0	26.3	108.5		130.4	13.1
	3.1	102.3	16.3	129.8	88.5		95.4	73.0
	3.2	376.5	160.3	209.0	585.3		480.9	184.6
	4	452.8	257.3	363.5	703.0		577.9	310.4
	5.1	23.3	12.5	38.3	59.5		41.4	25.4
	5.2	10.0	27.5	43.8	56.0		33.0	35.6
	5.3	4.3	9.0	8.0	14.8		9.5	8.5
	6.1	16.3	1.3	12.3	21.0		18.6	6.8
	6.2	32.3	3.0	17.0	99.0		65.6	10.0
	7	4.5	3.3	6.0	15.0		9.8	4.6
	8.1	40.0	5.5	0.0	2.0		21.0	2.8
	8.2	0.5	0.3	0.0	1.5		1.0	0.1
	9	1.8	1.5	0.0	2.5		2.1	0.8
Female	1	4.7	0.0	0.0	9.0		6.8	0.0
	2	54.3	0.0	169.7	235.3		144.8	84.8
	3.1	137.3	10.3	119.7	141.7		139.5	65.0
	3.2	483.3	88.0	12.7	715.3		599.3	50.3
	4	562.0	43.0	41.0	768.3		665.2	42.0
	5.1	3.3	0.0	0.0	36.0		19.7	0.0
	5.2	2.3	0.0	0.0	9.0		5.7	0.0
	5.3	0.0	0.0	0.0	1.0		0.5	0.0
	6.1	0.0	0.0	0.0	0.0		0.0	0.0
	6.2	1.3	0.0	0.0	3.0		2.2	0.0
	7	6.7	0.0	0.0	4.7		5.7	0.0
	8.1	0.0	0.0	0.0	0.0		0.0	0.0
	8.2	0.0	0.0	0.0	0.0		0.0	0.0
	9	0.0	0.0	0.0	0.7		0.3	0.0
One-way analysis of variance		$H = 10.882$	$H = 11.587$	$H = 10.395$	$H = 9633$	*t*-test	$t = 235$	$t = 256$
		$p = 0.092$	$p = 0.072$	$p = 0.109$	$p = 0.141$		$p = 0.148$	$p =$ ***0.014**

Note: The table lists plant species composition and dominant forage trees and shrubs across the most utilised vegetation types. These communities were identified from spatial data analysis and are now linked to electivity index results, as described in the Results text. This association helps explain dietary preferences in relation to habitat use.

[a]Quarters comprise 1 (January to March), 2 (April to June), 3 (July to September) and 4 (October to December).

[b]Vegetation code represents vegetation type described in study area.

5 | Discussion

Our results underscore how energetic demands and habitat utilisation are tightly linked in giraffe ecology. Giraffes exhibited distinct space-use patterns driven by the pursuit of nutritional resources and mating opportunities, and these patterns have important implications for their health and for habitat management. One key finding is the pronounced difference in ranging behaviour between males and females. Adult bulls roam widely, effectively covering most of the reserve over time, whereas adult cows operate in smaller core areas centred on dependable resources. Quantitatively, our home range analyses confirmed this disparity: the seven tracked bulls' combined MCP home range encompassed ~63% of RNR (vs. ~39% for the

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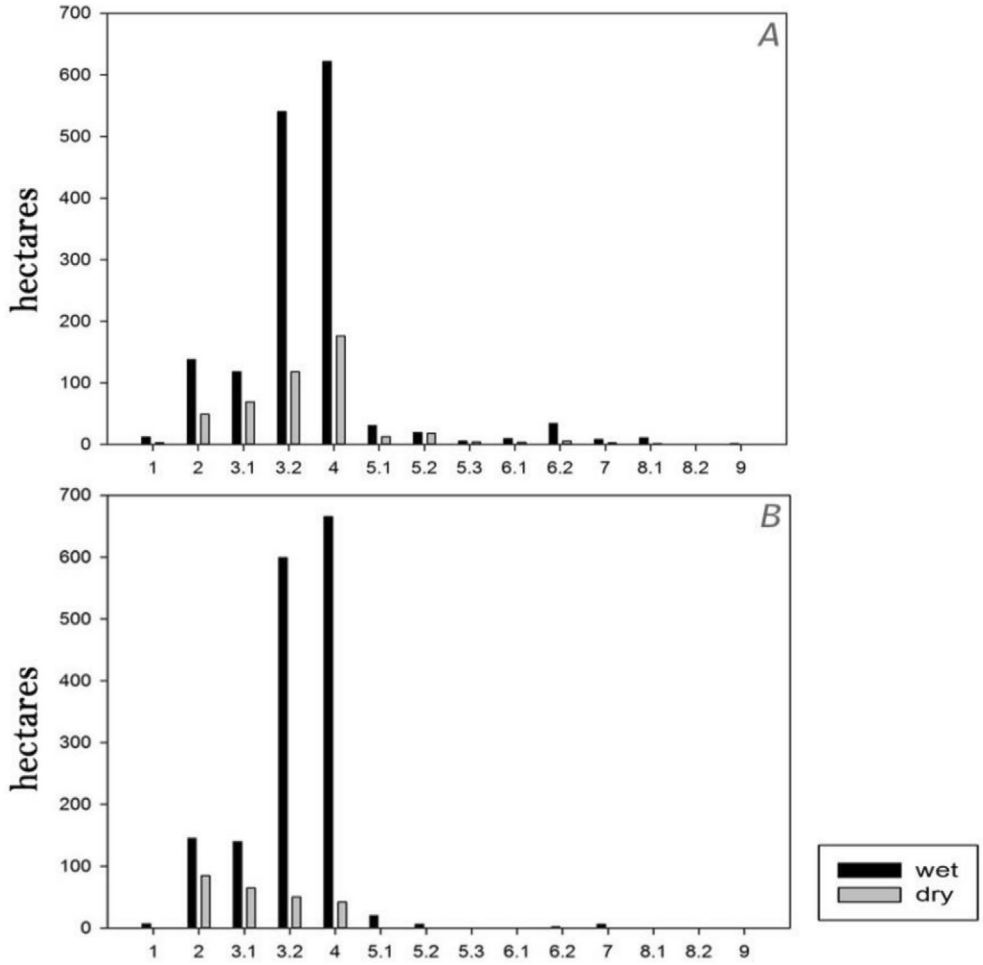


FIGURE 9 | Proportional use of vegetation community types by giraffes across the study area. Bars represent the relative time spent in each mapped vegetation community based on GPS tracking data. Although area availability was factored in, selection or avoidance patterns (electivity) are described in the text, with key examples such as high use of camel thorn woodland ($E \approx +0.5$) and strong avoidance of open grassland ($E \approx -0.8$).

11 cows), and similarly, their 95% kernel utilisation distributions were substantially larger than those of females. This divergence reflects the classic life-history trade-off: male giraffes prioritise reproductive opportunities over energy conservation, leading them to forage less efficiently and travel more in search of females, while females (especially those with calves) prioritise energy intake and predator avoidance within safe, resource-rich zones. The consequence is that female groups tend to exert heavy browsing pressure on relatively small 'core' habitat patches, whereas males have a more diffuse impact across the landscape. From a conservation standpoint, this means that protecting the high-quality forage patches that female giraffes depend on—particularly during calving and nursing periods—is crucial. Those patches sustain not only adult females but also their growing calves, which cannot travel far in their early months. Lactating females often remain near their calves and thus concentrate feeding in nearby high-quality forage patches (Bercovitch and Berry 2017), a behaviour we observed as smaller range sizes for females with young calves. Ensuring that these critical nursery areas remain intact and productive will directly support recruitment and population growth. At the same time, the wide-ranging movements of males suggest that maintaining connectivity across large areas can facilitate natural mating behaviour and gene flow. Our data showed that males can traverse the entire reserve; if adjacent reserves or suitable habitats are available, adult bulls could potentially link otherwise isolated subpopulations. Wildlife managers should consider establishing or preserving corridors between protected areas, as a roaming bull might travel through a network of conservancies if given the chance, mimicking the natural metapopulation dynamics that are lost when habitats are fragmented.

Another major finding is the giraffes' strong selection for specific vegetation communities within a heterogeneous landscape. Out of many available habitat types, giraffes consistently focused their foraging on four community types dominated by thorny acacias and other nutritious browse plants. These preferred habitats provided higher protein content and sustained edible biomass, particularly through the dry season. For example, camel thorn (*Senegalia erioloba*) woodlands and umbrella thorn (*Vachellia tortilis*) shrublands retained protein-rich pods and foliage well into the late dry season, buffering the giraffes' diet quality at a time when most other vegetation had deteriorated. This selective habitat use aligns with the known ecology of giraffes as concentrate browsers: they seek out the most nutritious plant parts and plant communities (Pellew 1984; Parker and Bernard 2005). It also highlights the nutritional constraints giraffes face—they require a diet with

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fairly high-protein content (on the order of 12% crude protein or more) to maintain their large body mass and support functions like gestation or, in males, the high-energy expenditure of rut. In our study area, only certain plant communities could consistently meet those nutritional requirements year-round; hence the giraffes' disproportionate reliance on those communities. These findings have direct conservation implications: to conserve giraffe populations, it is not sufficient to provide ample space alone—one must also ensure the availability of key nutrient-rich foraging habitats. If these high-quality patches are lost or degraded (through over-browsing, bush clearing, invasive plant spread or climate change effects), giraffes would struggle to meet their dietary needs even if lesser quality vegetation remains abundant. Managers should prioritise the conservation and, if necessary, restoration of such critical forage patches. This could include protecting important feeding trees, preventing over-utilisation of preferred areas and possibly habitat enrichment planting of high-nutrition browse species in depleted zones.

Giraffes employ several strategies to cope with seasonal nutritional bottlenecks in this semi-arid ecosystem. During the late dry season, when crude protein and moisture levels in most forage drop to annual lows, we documented behavioural and physiological adjustments: (1) a diet shift to protein-rich resources like acacia pods and evergreen leaves; (2) reduced movement by females to conserve energy; and (3) likely reliance on stored body reserves by males to subsidise their high activity levels. By using these strategies, giraffes appear to avoid the severe negative energy balance that might otherwise lead to rapid loss of body condition. It should be noted that we did not directly measure the giraffes' energy expenditure or balance in this study; our discussion of energetic constraints is based on inferences from literature rather than on direct measurements. We measured only dietary energy content (forage quality), while metrics such as actual energy expended or changes in body condition were derived from published data on giraffe physiology and nutrition (Dierenfeld and du Toit 2002; Hudson et al. 2013; Deacon and Smit 2017). This contrasts with sympatric grazing ungulates in the region, which often experience pronounced weight loss in dry seasons when grass quality and quantity plummet. The relatively stable diet quality that giraffes can maintain across seasons—thanks to their access to browse that retains nutrients longer—likely gives them an advantage in drought resilience. However, this strategy has limits: extreme, prolonged droughts or chronic over-browsing could erode even the giraffes' advantage. Indeed, if too many giraffes (or other browsers) concentrate on the same key plant populations, those food resources can decline over time. There is evidence that confined giraffe populations can over-browse preferred trees, leading to local declines in those species (Strauss 2019). In our study area, we noted that the central part of RNR, heavily used by female herds, contained the highest densities of favoured browse and showed signs of intensive use. Wildlife managers should be vigilant for signs of over-browsing in such core areas. Proper management may require balancing giraffe densities with the regenerative capacity of crucial browse species. Interventions such as controlled burning to stimulate new growth in under-used areas or strategic water placements could encourage more even distribution of foraging pressure if certain zones are under-utilised.

While natural factors predominantly shape giraffe foraging and ranging, human-induced factors are emerging as significant modifiers of these patterns. A surprising insight from a parallel study in our region (Kühn et al. 2023) was the discovery of high levels of heavy metals in the giraffes' diet and water sources. Leaf samples from the very sites our GPS-tracked giraffes frequented contained multiple heavy metals, with thallium (Tl) in particular exceeding acceptable levels (Kühn et al. 2023). Water from local rivers and waterholes also showed elevated concentrations of elements like aluminium and chromium. The source of this contamination is likely anthropogenic—mining and industrial activities in the broader region have introduced pollutants that leach into soil and groundwater. Alarmingly, the giraffes in RNR cannot easily avoid these contaminated areas because they coincide with the 'hotspots' of preferred forage. In essence, the giraffes are constrained to an environment where their diet is laced with toxins they have no way of detecting or evading (Kühn et al. 2023). This finding carries serious conservation implications. It highlights that protecting habitat for giraffes is not only about ensuring quantity of forage and space but also about maintaining the quality of that habitat in terms of freedom from pollutants. Conservation plans for giraffes (and other wildlife) should incorporate environmental monitoring for pollution. In regions with known mining or industrial activities nearby, regular testing of soil, foliage, and water is advisable. If harmful levels of contaminants are found, mitigation measures should be pursued—these could include remediation of polluted soils (e.g., phytoremediation), provision of alternative clean water sources for wildlife, or even supplemental feeding in extreme cases to avoid toxic exposure. Ultimately, controlling pollution at its source is the most effective solution: wildlife managers may need to collaborate with environmental regulators and local industries to prevent heavy metals and other toxins from entering the food web and threatening biodiversity.

Considering climate change, the interplay of these stressors becomes even more critical. Climate projections for southern Africa suggest increased frequency and intensity of droughts. Giraffes may face longer or more severe dry seasons in the future, which will put their adaptive strategies to an even greater test. If at the same time human pressures (such as land-use change or pollution) intensify, the resilience of giraffe populations could be severely challenged. Our study reinforces that identifying and protecting dry-season refugia—those pockets of habitat that provide food and water through the lean times—is vital for climate change adaptation. These refugia act as buffers that allow giraffes (and other wildlife) to survive drought spells. However, if anthropogenic impacts reduce the carrying capacity or safety of those refuge areas (e.g., by contaminating the forage or by excessive human disturbance), the outcome could be detrimental for giraffes. Climate change mitigation and adaptation strategies in conservation should thus include securing the integrity of key giraffe habitats under future conditions, and reducing additional stressors like pollution and disturbance that could exacerbate the effects of drought.

Our research also sheds light on giraffe energy budgeting and potential trade-offs in energy allocation. By estimating the energetic costs of giraffe movements and considering their forage intake, we infer that adult giraffes generally manage to meet their daily energy requirements in the wet season when food is

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plentiful. In the dry season, particularly for active adult males, there may be periods of energy shortfall. Male giraffes in rut will reduce feeding time and increase roaming, effectively trading off food intake for mating effort (Scheijen et al. 2021). This can lead to depletion of fat reserves and a decline in body condition for bulls during extended rutting periods or prolonged resource scarcity. Although we did not directly measure body condition in our study, it is likely that males incur some condition loss as a consequence of their high movement and reduced feeding during the dry season and peak rut. Such a trade-off between breeding opportunities and body condition is well-documented in other large herbivores and appears to hold for giraffes as well (Scheijen et al. 2021). Giraffes, like other mammals, must balance energy among various needs (maintenance, growth, reproduction and immunity). Thus, any conservation interventions that improve nutritional intake during critical periods could have cascading benefits, improving not only body condition but also disease resistance and reproductive success.

Finally, our study contributes valuable data for practical conservation management. By using high-resolution GPS tracking and GIS habitat analysis, we have demonstrated how modern technology can map the spatial needs of giraffes in fine detail. Wildlife managers can use such information to inform decisions on reserve design and population management. For example, our estimates of home range size and habitat use can help determine appropriate stocking densities for giraffes—essentially, how many giraffes a given reserve can sustain without overbrowsing its vegetation. In RNR, we observed that females primarily used the central ~40% of the reserve. If too many giraffes (or other large browsers) are confined to that area due to social structure or habitat preferences, they could over-exploit those vegetation types. Managers might consider strategies to encourage a more even use of the landscape. This could include siting waterholes or mineral licks in under-utilised areas, managing vegetation (e.g., controlled burns or bush thinning) to stimulate fresh browse in less-used zones, or even spatially rotating supplementary feed if ever provided—all aimed at drawing animals away from over-taxed core areas and preventing local habitat degradation. Conversely, knowing that males roam widely and can cover an entire large reserve suggests that maintaining connectivity between protected areas is beneficial for gene flow and demographic rescue among giraffe subpopulations. A bull giraffe could potentially travel through a mosaic of properties if dispersal corridors exist, which would mimic the natural movement dynamics otherwise curtailed by fences and fragmentation.

In summary, our study highlights the importance of an energy- and habitat-centric approach to giraffe conservation. Giraffes require not just vast spaces, but the right kinds of spaces—areas rich in the browse species that fulfil their nutritional needs during both wet and dry seasons. Conservation strategies for giraffes should recognise the differing behaviours and requirements of males and females, the seasonal shifts in habitat use, and the overlay of human-induced challenges such as disturbance and pollution. By integrating detailed ecological data (like we have provided on habitat use, movement patterns and diet quality) with broader conservation measures (anti-poaching, land-use planning and pollution control), we can formulate more effective management plans to ensure giraffes continue to thrive in their natural habitats. The insights gained from the Rooipoort population are likely applicable to similar savanna ecosystems across Africa, with adjustments for local conditions. Safeguarding the spatial and nutritional resources that giraffes depend on, while mitigating adverse human impacts, will improve the long-term prospects for giraffe populations in Southern Africa and beyond. Ultimately, conserving giraffes in the wild will benefit not only this iconic species but also the savanna landscapes they help shape and the myriad other species that share these ecosystems.

6 | Conclusion

Giraffes in the Rooipoort Nature Reserve demonstrate how balancing energy constraints with habitat utilisation is essential for their survival. They adjust their movements, habitat preferences and even physiology in response to the availability of high-quality forage. Males traverse great distances and incur energy costs in pursuit of mates, while females concentrate in resource-rich areas to efficiently raise young—yet both sexes converge on the same key habitats that offer critical nutrition. Seasonal droughts push giraffes to the limits of their energetic strategies, but they exploit particular vegetation communities as refuges to avoid malnutrition. When those natural challenges combine with human pressures like habitat fragmentation or pollution, the stakes become even higher. Our research provides a clear mandate for conservation: protect the crucial foraging habitats (such as acacia woodlands and thornveld) and maintain sufficient space and connectivity for giraffes to roam, especially for wide-ranging bulls. At the same time, minimise anthropogenic threats—ensure their food and water are not silently poisoned by human activities, and reduce disturbance so that giraffes can feed and move efficiently without chronic stress. By following these science-based guidelines, reserve managers can support the energy needs and ecological behaviours of giraffes. This will help sustain healthy giraffe populations, which in turn will continue to play their role in shaping and maintaining the biodiversity of African savannas.

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Ethics Statement

All procedures were approved by the University of the Free State Animal Ethics Committee (Reference no. UFS-AED2015/0066).

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Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

The GPS tracking and habitat use datasets generated during the current study are not publicly available due to ongoing analyses in related projects, but they are available from the corresponding author upon reasonable request.

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