University of South Wales

Diet Composition of Large Carnivores in Selati Game Reserve through Faecal Analysis

By Grace Gardner, 2025.

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To my amazing family, especially Mum and Jonny. Thank you for your endless support and words of encouragement. Mum, you are my constant, my best friend and I would not be the person I am today without your unconditional love and support. I will always be externally grateful for everything you have done for me. Jonny, thank you for always believing in me, making me laugh when I need it most, and reminding me to take things one step at a time. James, thank you for always believing in me, even when I do not believe in myself. For being my biggest cheerleader and always wanting the best for me. Your love and patience never go unnoticed. Words will never express how grateful I am to have you all by my side.

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Abstract

The dietary composition of five large carnivores within Selati Game Reserve were examined using scat analysis. A total of 21 scats were collected opportunistically during game drives and field surveys along roads and game trails, 10 from leopards, 6 from wild dogs, 3 from cheetah, 1 from spotted hyena and 1 from lion. From these, 580 hair fragments were extracted from the scat, embedded in glue, cut and analysed using cross sectional techniques to identify prey species. Applying this technique, 9 different species of prey were identified. Leopard scat had 279 hair fragments, with high frequencies of impala, warthog and common duiker. Wild dogs scat contained 161 hair fragments, with high frequencies of impala, steenbok and common duiker. Cheetah scats contained 68 hair fragments, showing a varied diet, including impala, steenbok, greater kudu, and Sharpe's grysbok. Whilst lions and spotted hyenas had smaller sample sizes, with 30 hair fragments containing just impala and 29 hair fragments comprising of greater kudu and impala. Jacob's Index was used to assess prey frequencies, indicating a high frequency of common duiker and steenbok for leopards and wild dogs. Spatial patterns showed leopard scat clustered in the central and southern regions of the reserve near rocky outcrops, while wild dog scat was primarily found near den sites in the west. The different prey frequencies and scat distribution patterns suggests that each carnivore has a specific ecological niche, and strong management strategies should be developed to support prey diversity and preserve areas that hold high ecological value such as den sites and rocky outcrops.

1.0 Introduction

Understanding the diets of large predators such as leopards (*Panthera pardus*), lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta)* is a fundamental aspect of ecological research and effective ecosystem management (Wolf and Ripple, 2016). Diet analysis provides insights into predator feeding behaviour, prey preferences, interspecific interactions, and assesses the ecological roles of predators (Symondson, 2002). As apex predators they help regulate herbivore populations, which, in turn, influences vegetation dynamics and biodiversity across an ecosystem (Estes *et al*., 2011). This is because they exert a top-down control on herbivore populations, meaning predators can help reduce overgrazing, which allows vegetation recovery and regeneration (Frank, 2008). For example, by depredating on species such as impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*), lions and leopards indirectly influence plant community structure and promote species diversity, which contributes to habitat heterogeneity and ecological resilience (Lu *et al*., 2023). However, the effect of predation extends beyond prey abundance, as predators influence the physical condition, genetic adaptability, and behaviour of prey species. When predators are present, prey species become more alert, causing them to alter their space use, group size, and foraging strategies in response to perceived predation risk, which can have a cascading effect throughout an ecosystem (Ripple *et al.,* 2014; Schmitz, 2017).

Whilst most carnivores are reliant on antelope species ranging in body mass from 10 to 1000kg, direct competition is reduced as they exhibit different hunting strategies, social structures, and ecological niches (Hayward and Kerley, 2008; Schmitz, 2017). For instance, lions are cooperative hunters which target prey species such as zebra (*Equus quagga*), kudu, and giraffe (*Giraffa camelopardalis*), which is beyond the capability of solitary predators such as leopards (Schaller, 1972). Leopards, have an opportunistic hunting strategy and often exploit a wider variety of prey, ranging from rodents to medium antelope (Balme *et al*., 2007). Meanwhile, cheetahs hunt medium sized antelope and rely on their speed to capture prey (Durant, 1998). Furthermore, African wild dogs are obligate cooperative hunters, who often target small to medium antelope like impala and steenbok (*Raphicerus campestris*) through strategic pack coordination and high endurance hunts (Hubel *et al*., 2016). Lastly, spotted hyenas are highly adaptable and can be efficient hunters or scavengers. Their diet includes a wide range of prey species and carcasses, enabling them to remain successful when food resources become limited (Smith and Holekamp, 2023). This variation in diet and hunting strategies across species helps reduce interspecific competition and contributes to niche partitioning, which is a key factor enabling the coexistence of these carnivores within ecosystems (Monterroso *et al*., 2018).

However, understanding the dietary composition in large carnivores can be complex due to the challenges associated with detecting, and identifying consumed prey items, especially in ecosystems where prey species vary in abundance. Furthermore, factors such as differential digestion rates, scavenging behaviour, and elusive feeding habits can cause abnormalities on what predators are consuming (Ram *et al*., 2024). Despite these challenges, dietary analysis is crucial for informing conservation and management plans. By accurately determining which prey species are most frequently consumed, researchers can monitor predator-prey dynamics, detect shifts in prey selection, and assess the health and sustainability of both predator and prey populations (Symondson, 2002).

1.1 Methods Used to Study Carnivore Diets

Methods that have been used to understand predator diets include direct observations of hunting behaviour or examinations of kill sites (Radcliffe and Du Toit, 2004). Although these methods help to understand predator diets, they can be limited by physical constraints, for example direct observations is challenging in dense habitats or when studying elusive species like leopards (Frohlich *et al*., 2012). Furthermore, kill site analysis, whilst useful, can be sporadic and might not capture the full range of prey species that a predator has consumed and it can be hard to determine what predator killed the prey (Oliverira *et al*., 2022). Moreover, these methods can be invasive, which may alter a species behaviour or prey preference. However, non invasive techniques like scat sampling allow researchers to see undigested remains such as hair and bones within a sample, which can be identified using both traditional morphological methods and modern molecular techniques (Davison *et al*., 2002).

One of the most transformative advances in dietary studies is DNA metabarcoding. This molecular technique involves extracting DNA from scat samples and then amplifying target regions of genetic material using polymerase chain reaction (PCR). The amplified sequences, which include markers specific to different prey species, are then sequenced using sequencing platforms (Davison *et al*., 2002). By comparing these sequences to referenced databases, prey species can be identified with high precision, even when the physical remnants are degraded and are unable to be recognised morphologically (Buzan *et al*., 2024). Furthermore, metabarcoding offers many advantages as it overcomes the limitations of scat analysis by providing species level resolution even when only small traces of DNA remain. This method can detect prey items that leave no observable trace, such as soft bodied organisms, therefore broadening the scope of the dietary investigation (Davison *et al*., 2002; Thuo *et al*., 2019). This is useful in complex ecosystems where multiple prey species are consumed and when differences in digestion rates might lead to an underrepresentation of certain prey in morphological analyses (Brown-Vuillemin *et al*., 2025).

In addition to molecular methods, GPS tracking and remote sensing provide insights into carnivore foraging behaviour and habitat use (Petroelje *et al*., 2020). By having predators fitted with GPS collars, it allows researchers to monitor movements, track habitat preferences, and pinpoint potential kill sites (Odden and Wegge, 2017). Studies using GPS- linked cluster analysis found that kill site identification was 100% successful when a larger prey species had been killed and 40% successful when a small prey species had been killed (Webb *et al*., 2010). Showing, that this technique combined with scat analysis, allows researchers and site managers to determine when and where a kill happened and what has been eaten (Frohlich *et al*., 2012).

Furthermore, remote sensing, including satellite imagery and aerial surveys, offers a broad scale perspective of habitat composition and prey distribution (Jensen *et al*., 2021). A study from 2020 suggests that dietary preferences can be linked to environmental context. For example, changes in vegetation patterns detected through remote sensing can indicate shifts in prey availability, which may be shown in the dietary choices observed through scat analysis (Marston *et al*., 2020). Moreover, the use of camera traps has become an invaluable tool in understanding carnivores and their diets as they capture images and videos of feeding events, predator movements, and interactions at kill sites (Smith *et al*., 2020). This visual evidence allows the identity of the prey species to be confirmed but also provides behavioural context, such as repeated visits to a kill or sharing of a kill within social groups (Caravaggi *et al*., 2017; Cordier *et al*., 2022). Therefore, when these techniques are combined, researchers can clearly see the foraging pattens of predators which further enhances our understanding of the ecological and behavioural contexts underlying dietary choices. Furthermore, these methodological techniques in studying carnivore diets contribute to conservation massively. Precise dietary data enables conservationists to monitor predator health, assess changes in prey dynamics, and design management strategies that ensure sustainability of both predator and prey populations (Wolf and Ripple, 2016; Buzan *et al*., 2024). For example, if dietary analyses show an over dependence on a particular prey species that is experiencing population decline, management strategies can be altered in order to help stabilise the prey population (Wolf and Ripple, 2016).

One of the most widely used methods to achieve an understanding on what a predator is consuming is through the morphological analysis of prey hairs found in scat samples (Mumma *et al*., 2016). This method provides direct evidence of what predators have consumed without requiring capture or direct observation of a species (Steenweg *et al*., 2015). This technique has shown to detect 85-95% of consumed prey species in studies using comparative kill-site data, offering a reliable approach that minimises disturbances to species and ensures that natural feeding patterns remain the same (Klare *et al*., 2011).

1.2 Hair Morphology Differences

During the analysis of scat, identifying prey species and knowing the difference between adults and juveniles is crucial in understanding what a predator typically depredates upon. This process is carried out with a microscope and allows researchers to examine undigested hair fragments (Chaka, 2004). Each species has hair with distinct morphological characteristics such as cuticle scale patterns, medulla structure, cross-sectional shape and pigmentation, which allows researchers to distinguish between prey species and in some cases, infer the age of the individual consumed (Keogh, 1975).

Hair can be separated into two main groups, the first being guard hair, which is the outer coat and is thick and long. The second group is the underfur, which is short, soft and fine. Guard hairs are distributed all over the body and come in many forms including spines and bristles which includes the mane (Keogh, 1979; 1983). Furthermore, the underfur can be divided into vellus, which are the shortest hairs, fur, which is thick, and relatively short and wool, which is longer, soft, and sometimes curly (Keogh, 1975;1983). Many antelope species have distinct hair structures that vary depending on their evolutionary adaptations to habitat, thermoregulation needs, and camouflage (Blank and Yaoming, 2022). For example, the medulla, which is the central core of a hair can be fragmented, continuous or absent, whilst the cuticle scales can be smooth and tightly packed, or they can be wavy and serrated (Chaka, 2004). Additionally, within the same species, hair morphology can differ between adult and juvenile individuals. Adult hair can be coarser and denser compared to that of a juvenile and adults often have a more defined cuticle pattern, which can include uniform scales and a well-developed medulla (De Marinis, 2006). In contrast, juvenile antelopes often display softer, finer hair with less pronounced scale structures, which could be due to differences in their growth stage, thermal insulation needs, or habitat use (De Marinis, 2006; Taru *and* Blackwell, 2014). These developmental differences can influence the resistance of hair to digestive processes, and consequently, affect the quality and quantity of hair fragments recovered in scat samples (Tintner *et al*., 2020). Overall, studying these morphological distinctions helps to understand predator prey dynamics. For instance, a higher proportion of juvenile antelope hair in predator scat might indicate selective predation or suggest that juvenile individuals are more vulnerable to predation as they are inexperienced and have lower physical defences. Alternatively, a predominance of adult hair could suggest that predators are depredating on larger, more energetically rewarding prey (Barber-Meyer and Mech, 2008).

1.3 Prey Species

The availability and diversity of prey is a key driver that influences predator distribution, behaviour, and prey preference (Comley *et al*., 2020). Prey species range in size, habitat preference, social

structure, and anti predator strategies, all of which affect their vulnerability to different predators (Brashares *et al*., 2002). Southern African savanna ecosystems are dominated by medium to large antelope species, including impala, kudu, zebra, giraffe, and wildebeest (*Connochaetes taurinus*). Among these species, impala is the most abundant and widely distributed, which means they are often depredated by a range of predators' (Furstenburg, 2016). Kudu and wildebeest are depredated on by lions and occasionally hunted by spotted hyenas and wild dogs, while zebras and giraffe are primarily pursed by lions due to their size and defensive capabilities (Sinclair *et al*., 2003). Moreover, smaller prey species such as duiker (*Sylvicapra grimmia*), steenbok, and scrub hare (*Lepus saxatilis*) contribute to the diets of more opportunistic predators such as leopards and cheetahs, particularly when larger prey species are scarce (Hayward *et al*., 2006). However, these smaller prey species are not exclusively targeted by solitary or small predators as generalist carnivores like lions and spotted hyena exhibit dietary flexibility and are capable of depredating on a wide range of species including small antelopes and lagomorphs (Forbes *et al*., 2024).

Furthermore, prey availability can fluctuate in response to seasonal shifts and habitat heterogeneity (Gorini *et al*., 2012). During the dry season, water dependant species like wildebeest and zebra tend to congregate around permanent water sources, increasing their vulnerability as predators will exploit these areas to increase their hunting success (Davidson *et al*., 2013). In contrast, the wet season brings greater vegetation cover and prey dispersal, meaning predator-prey encounters become less frequent, and predators must alter their spatial movements in response to shifting resource distributions (Vettorazzi *et al*., 2022). These changes not only influence encounter rates but also impact predator energy expenditure, and foraging efficiency, predators must learn to utilise their time and energy more strategically to locate and capture different prey species (Gil *et al*., 2025). Additionally, predators have a range morphological and behavioural adaptations such as endurance, speed and social coordination which influences their hunting success (Schmitz, 2017). These functional traits interact dynamically with those of prey, which exhibit their own anti-predation strategies. Impalas demonstrate herd vigilance and alarm calls, while smaller antelope like duiker and steenbok rely on crypsis and quick movements to avoid detection (Schmitz, 2017; Palmer and Packer, 2021). These factors show the functional complexity and adaptability of predator-prey relationships.

However, prey preference is not only determined by availability. It also depends on the predator’s hunting strategies, energetic trade-offs, risk of injury, and the presence of other competing carnivores (Owen-Smith and Mills, 2008). Each predator has evolved distinct adaptations in order to hunt efficiently, whether physical, behavioural, or social. For example, lions, can afford to pursue larger prey species such as giraffe as they can use group tactics to minimise individual risk while minimising energy expenditure (Owen-Smith, 2019). In contrast, solitary predators like leopards must weigh the energetic cost of a hunt against the risk of injury and the potential of

loosing their kill to scavengers. As a result, they often hunt medium sized prey that can be subdued alone and dragged into trees to reduce kleptoparasitism (Stein *et al*., 2015). Furthermore, interspecific competition influences hunting success as many predators will spatially avoid more dominant competitors. For example, cheetahs and wild dogs many shift their hunting times or areas to reduce encounters with lions and spotted hyenas, which can outcompete them or cause direct threat (Durant, 2002; Periquet and Revilla, 2014). These ecological and behavioural trade-offs are key to understanding prey choice in multi-species predator systems.

Hypothesis:

It is expected that there will be observable differences in the frequency of prey hair fragments detected in the scat samples of different carnivore species. Cheetah scats are expected to contain a high frequency of impala hairs. Lions and leopards will have a broader prey frequency, including larger species such as kudu. In contrast, spotted hyenas and African wild dogs are predicted to have a higher frequency of smaller prey species, such as duiker.

2.0 Materials and Methods:

2.1 Study Area

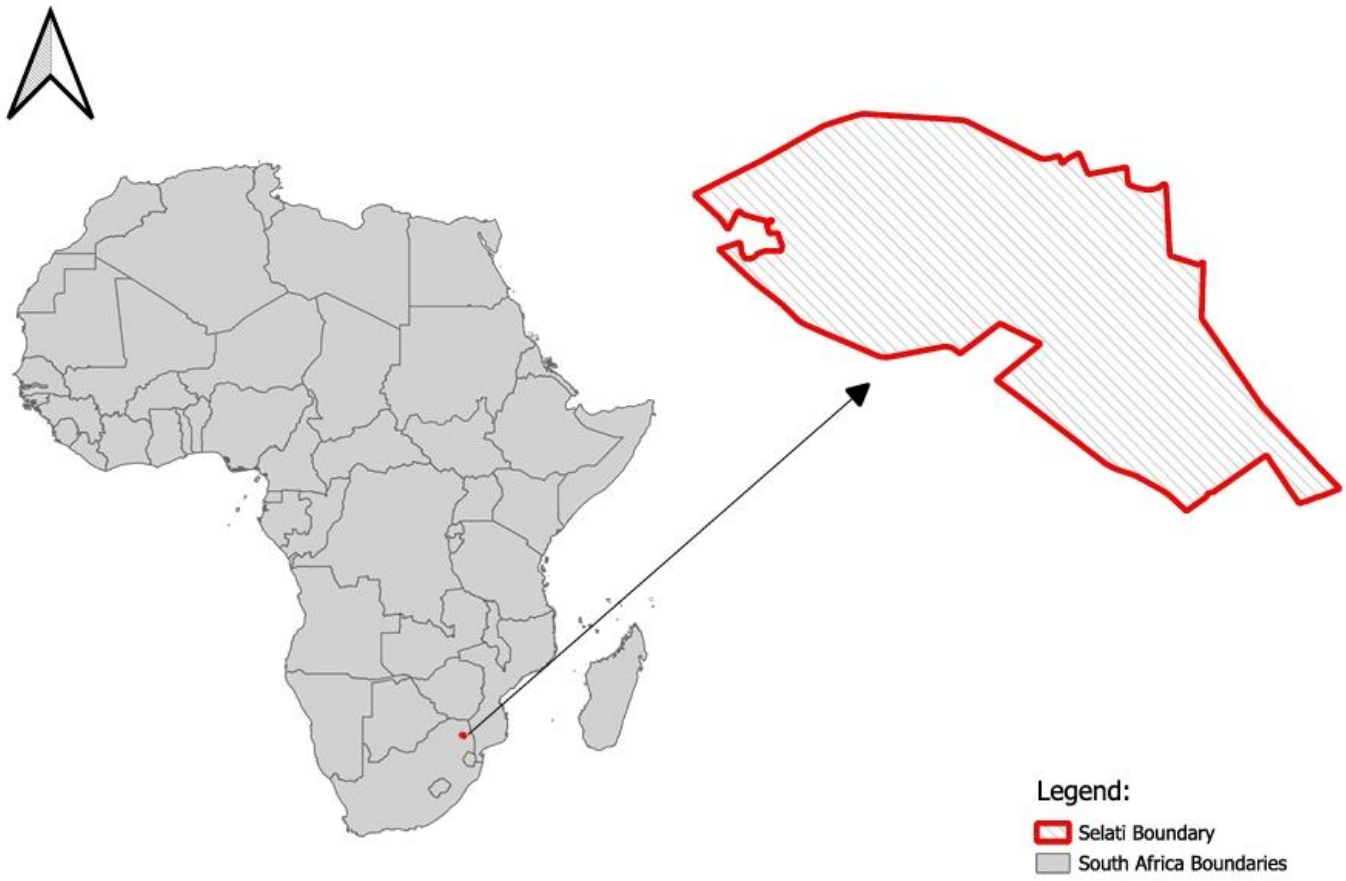

Figure 1: Map of South Africa showing the location of Selati Game Reserve. The red outline highlights the boundaries of Selati Game Reserve.

The study was conducted in Selati Game Reserve, which is located in the lowveld region of the Limpopo province, South Africa. It is situated between longitudes 30° 38’ 42” E and 30° 54’ 26” E and latitudes 23° 54’ 25” S and 24° 05’ 09” S and covers a total of 27,000 hectares. Selati consists of a mixture of savanna woodland, open grassland, rocky outcrops, riverine and disturbed areas which provides a variety of habitats for the wildlife. The reserve supports a range of large carnivores including leopards, lions, cheetahs and spotted hyenas. These predators rely on a diverse prey base, made up of mostly antelope species such as impala, kudu, steenbok, and duiker, as well as larger species like zebra and giraffe, which are all found within Selati. The reserve is fenced and managed primarily for conservation and research purposes, with limited human activity apart from regulated ecotourism.

2.2 Data Collection

2.2.1 Scat Sampling

Prior to data collection, a full ethics form was completed and approved on 28/05/2024 (Appendix 1). A risk assessment was conducted to ensure safety and minimal disturbance to wildlife (Appendix 2). All faecal samples were collected non- invasively and reference hair samples were obtained only from animals that had died naturally or undergone veterinary procedures.

Scat samples from leopards, lions, cheetahs, wild dogs and spotted hyena were collected opportunistically during game drives and field surveys along roads, and game trails. Scat samples were collected by Selati staff and volunteers over 5 years from 2019 to 2024. Each sample was placed in a labelled zip lock bag with GPS coordinates, date, time and the suspected species the scat was from. Samples were stored in a cold, dark room to preserve the hair prior to analysis.

2.2.2 Reference List Collection

Reference hair fragments were collected from prey species within the reserve from known carcasses or from species that had undergone a vet procedure. These hair fragments were used to create a reference library for microscopic comparison during species identification. Each scat sample was labelled with species name, hair type, age (when known), and stored in a paper envelope in a dry, cool environment following the protocol by Lasisi (2020).

2.2.3 Hair Storage and Extraction

Scat samples that did not easily disaggregate were washed through in a fine sieve using warm water to extract undigested remains. Hair fragments with longer, easily separable hairs were taken directly from the scat without washing. Hair fragments were collected from the scat using tweezers before being transferred to small envelops that were labelled with the scat sample number, which predator the scat was from, date, and GPS coordinates. From each scat, 30 individual hairs were randomly selected for microscopic analysis to ensure a representative sub sample of prey remains and ensure that multiple prey species would be identified if present.

2.2.4 Hair Cross Sections

Hair fragments were embedded and prepared for cross sectional analysis following the methodology outlined by Lasisi (2020). Instead of polycaprolactone, a hot glue gun was used as the embedding medium to secure the hair fibres.

A small amount of hot glue was dispensed in a line around 3cm onto a clean, flat surface covered with parchment paper. For each sample, 5-6 hair fibres were selected randomly and stretched taut, and placed parallel to each other across the surface of the partially cooled glue, using fine tweezers. This was done until all 30 hairs from each sample had been embedded. Once positioned, an additional layer of hot glue was applied to fully embed the hairs and a weight, approximately 1kg was placed on top to flatten and fuse the layers. Each layer of glue was 1 cm thick, and care was taken to ensure uniform layer thickness.

After 5 minutes, the glue had solidified at room temperature and the embedded samples were cut into rectangular chips approximately 20 x 10 mm in size using a sharp scalpel (Fig 2).

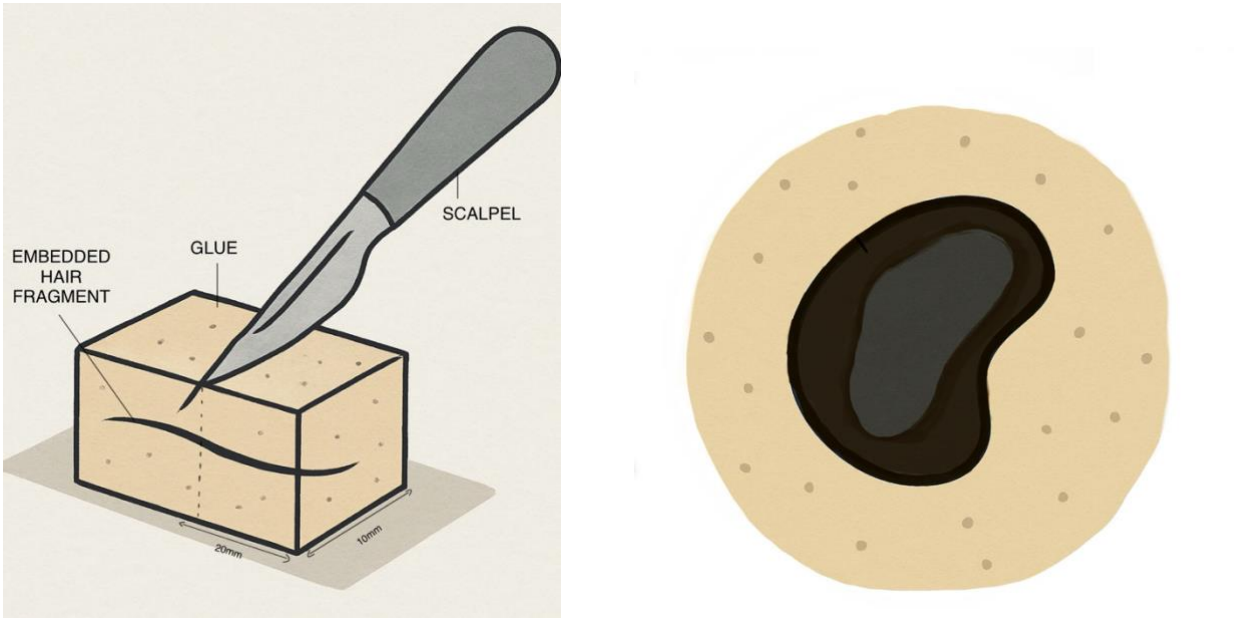

Figure 2: An example of how each of the embedded samples were cut into rectangular chips and how the cross section of the cut hair fragment looked under a microscope.

2.3 Data Analysis

2.3.1 Hair Identification

Hair fragments were placed vertically using double sided tape onto a microscope slide and were analysed under a light microscope at 10x magnification. Identification was based on characteristics such as cross-sectional shape, colour, medulla structure and size of the cross section (Fig 3). These features were compared with the referenced library to decide the prey species.

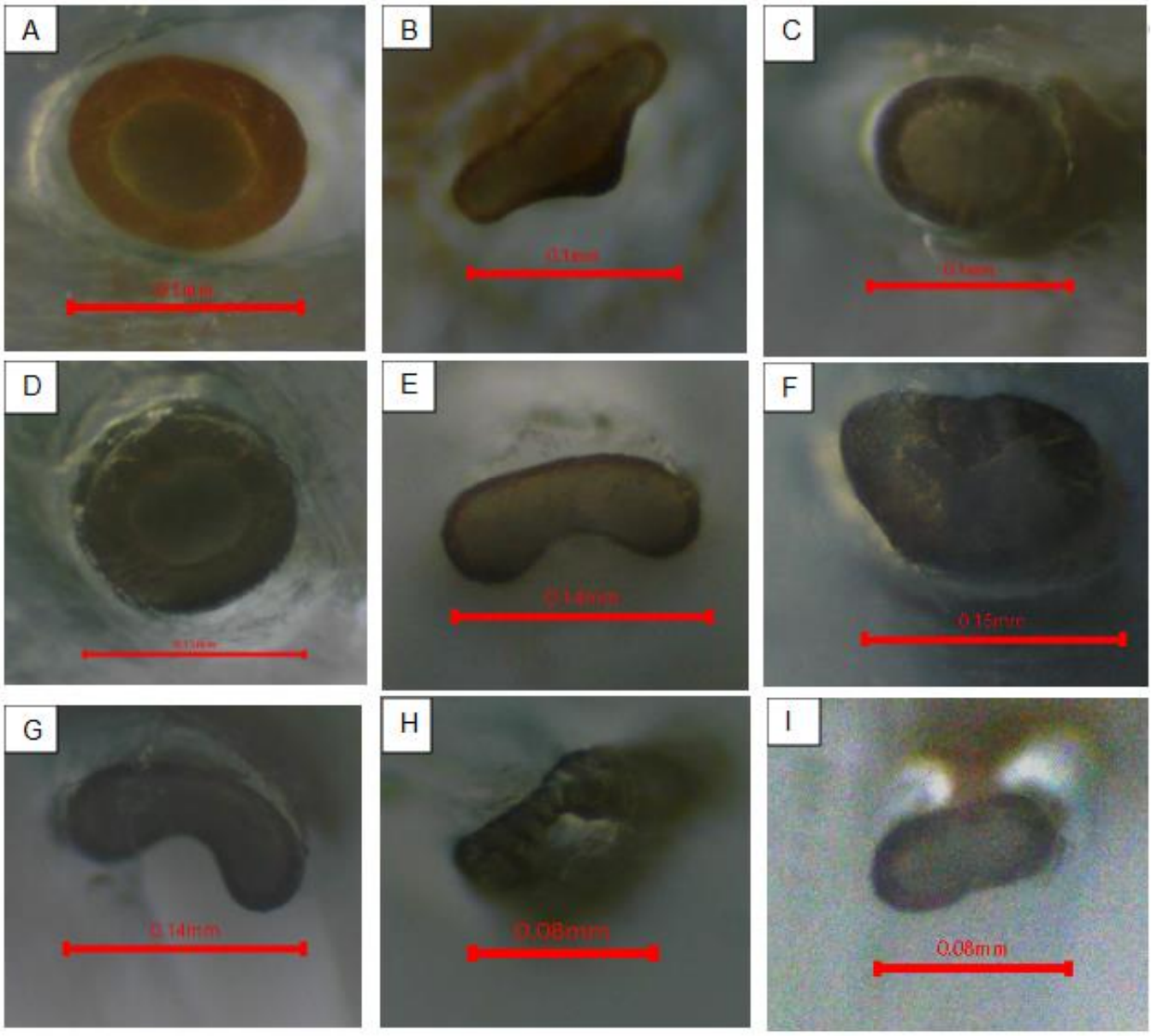

Figure 3: Cross section of different hair fragments from identified species, showing the variation in medulla structure. The medulla is the central core of a hair, and it can look different depending on each prey species. For example, it can be fragmented, continuous or absent (Chaka, 2004). Giraffe (A), Greater Kudu (D), and Warthog (F) exhibit thick, continuous medullas which encompasses a large portion of the hair cross section. Impala (B), Common Duiker (C), and Nyala (I), show irregular medullas that are less centralised or slightly compressed. Steenbok (E) and Sharpe's Grysbok (G) have a dense, dark medulla with a kidney-shaped profile. Scrub Hare (H) has a narrow, fragmented medulla.

2.3.2 Jacobs' Index

Jacobs' Index was used to quantify prey preference by comparing the proportion of prey species found in scat to the estimated availability of each species in the reserve. Prey availability data was derived from annual aerial counts provided by Selati Game Reserve (Appendix 4.1). The index produces values between -1 and +1, where +1 suggest more frequent depredation, 0 indicates neutral depredation, and values near -1 suggests a scarce amount of depredation (Fig 9 and Fig 10). Jacobs' index = (r-p) / (r+p – 2rp) (r = proportion of prey species found in the predator's diet and p = prey species available in the reserve) (Jacobs, 1974). Due to the limited sample size, the results do not allow strong conclusions about true preference or avoidance. Therefore, terms such as frequent, neutral, and scarce depredation have been used to more accurately reflect observed trends.

2.3.3 Chi Squared Test

Chi squared tests were conducted to determine whether differences in prey selection among the different carnivore species were statistically significant. Observed prey frequencies were compared to expected frequencies based on prey availability.

3.0 Results

A total of 21 scats samples were collected and 580 hair fragments were analysed using a cross-sectioning methodology.

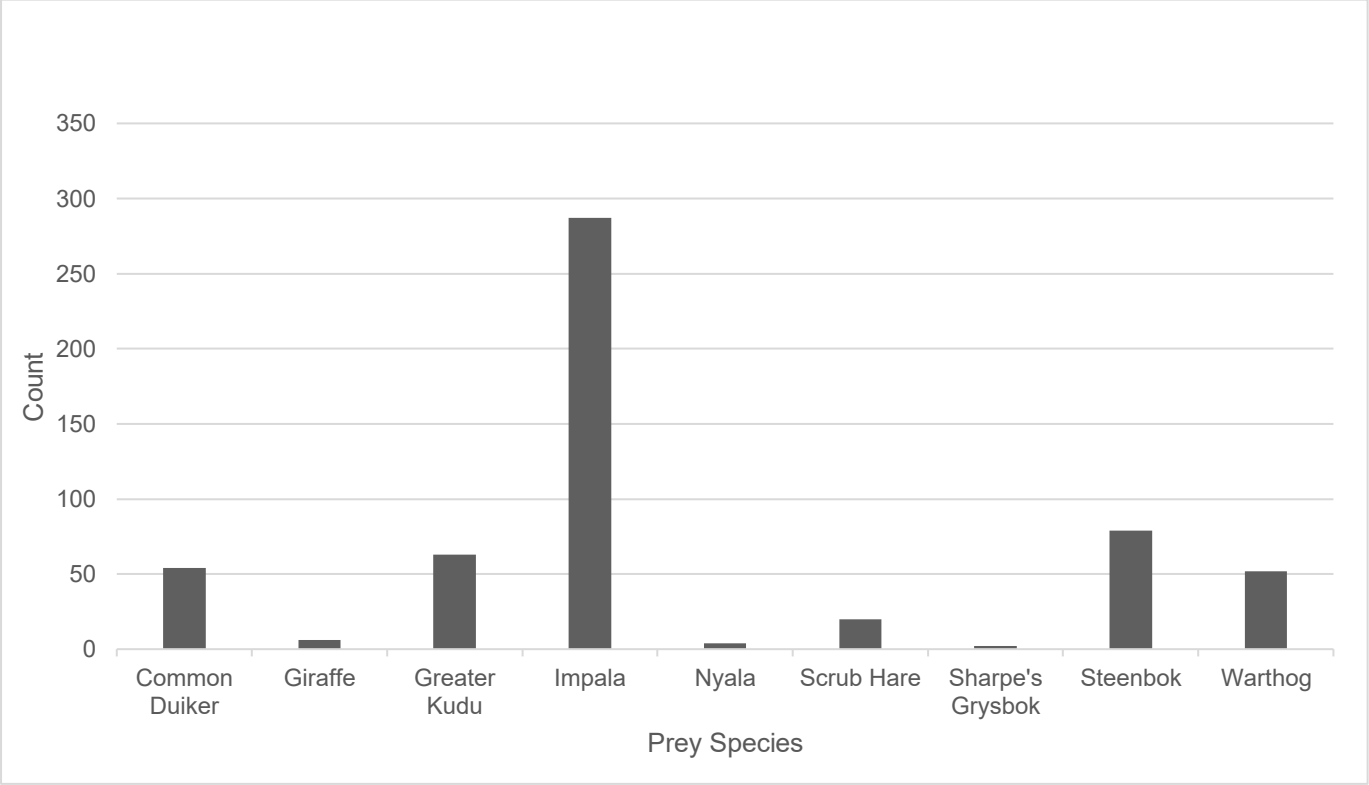

Figure 4: Frequency of prey species identified in large carnivore scat samples collected across Selati Game Reserve.

Impala hair fragments were the most frequently occurring in the scat samples (284 hairs; 50.1%). Then steenbok and greater kudu (78; 13.8%) and (63; 11.1%). These were followed by common duiker (54; 9,5%), warthog (52; 9.2%) and scrub hare (*Lepus saxatilis*) (20; 3.5%). Less frequently detected hair fragments were from giraffe (6; 1.1%), nyala (4; 0.7%), and Sharpe's grysbok (*Raphicerus sharpei*) (2; 0.4%) (Fig 4). A total of 13 hair fragments were unidentified.

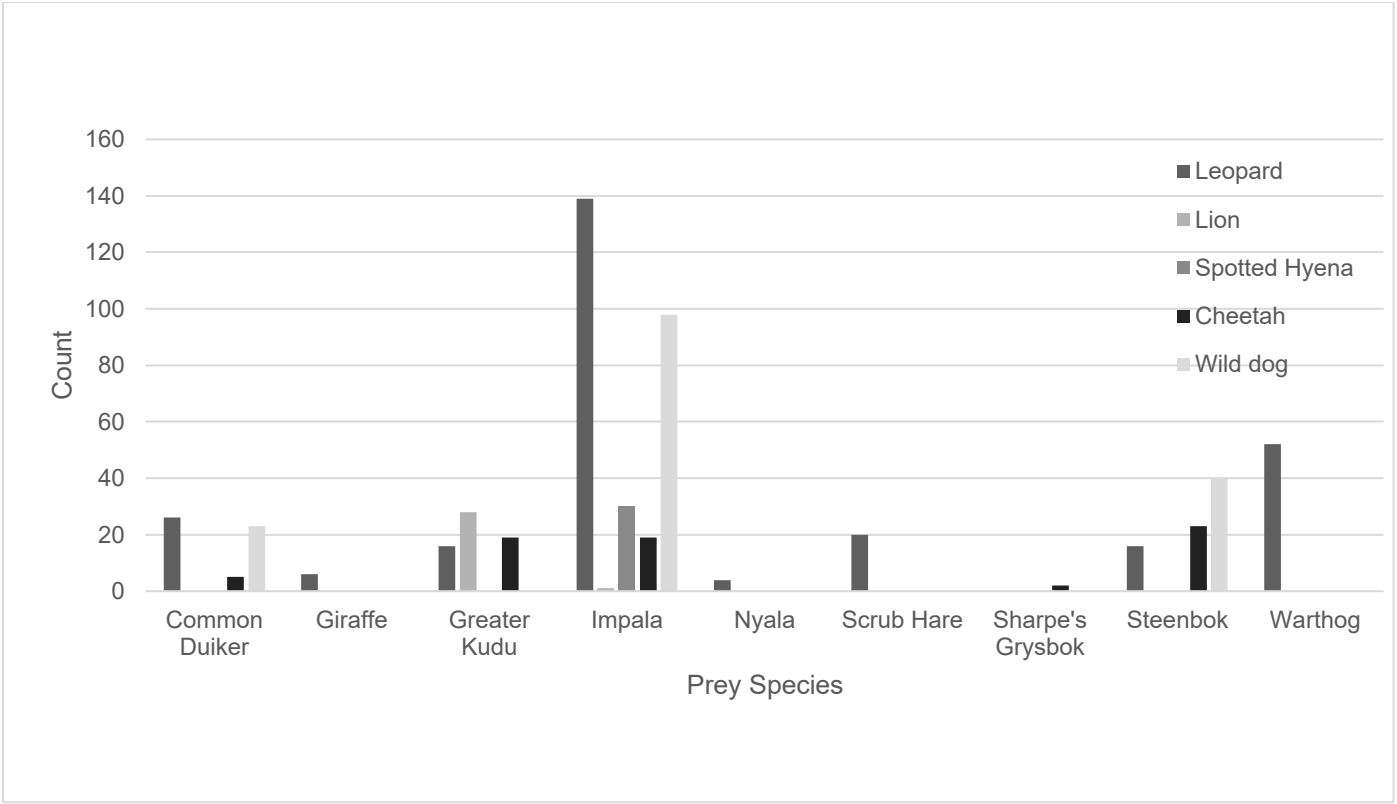

Figure 5:The number of occurrences of different prey species identified in the scats of large carnivores at Selati Game Reserve, showing the different dietary variation among the predators.

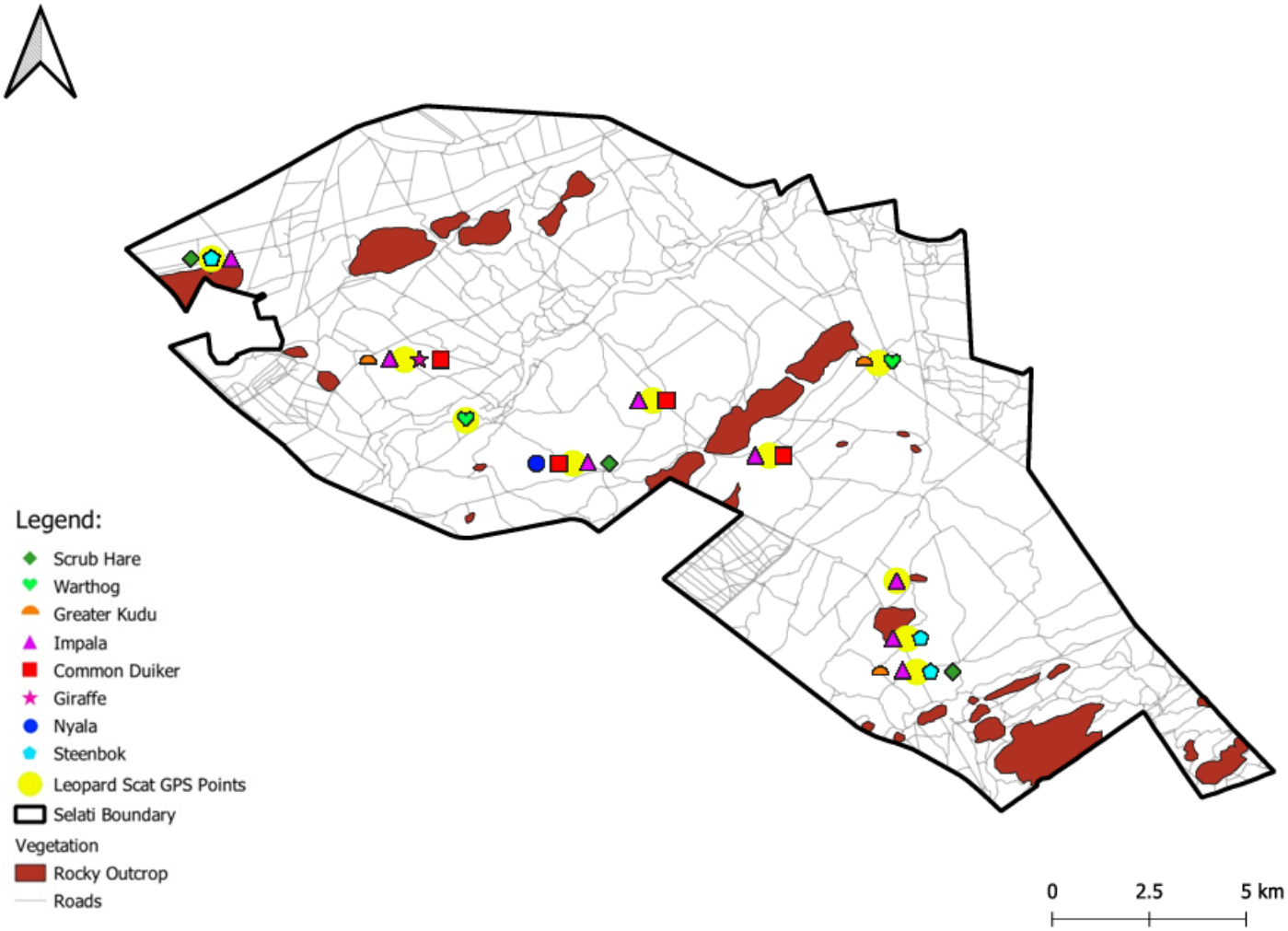

Figure 6: GPS locations of leopard scat samples collected around Selati Game Reserve, showing the different prey species found in each scat, represented by different shapes and colours. (For species, date of scat collection and scat coordinates, see Appendix 3.1)

A total of 10 leopard scat samples contained 279 hair fragments. Impala hair fragments were the most frequently detected (139 hairs; 49.8%), followed by warthog (52; 18.6%), common duiker (26; 9.3%), and scrub hare (207.2%). The least detected hair fragments were nyala (4; 1.4%) (Fig 5). There is notable clustering around the central and southern regions, especially near rocky outcrops (Fig 6).

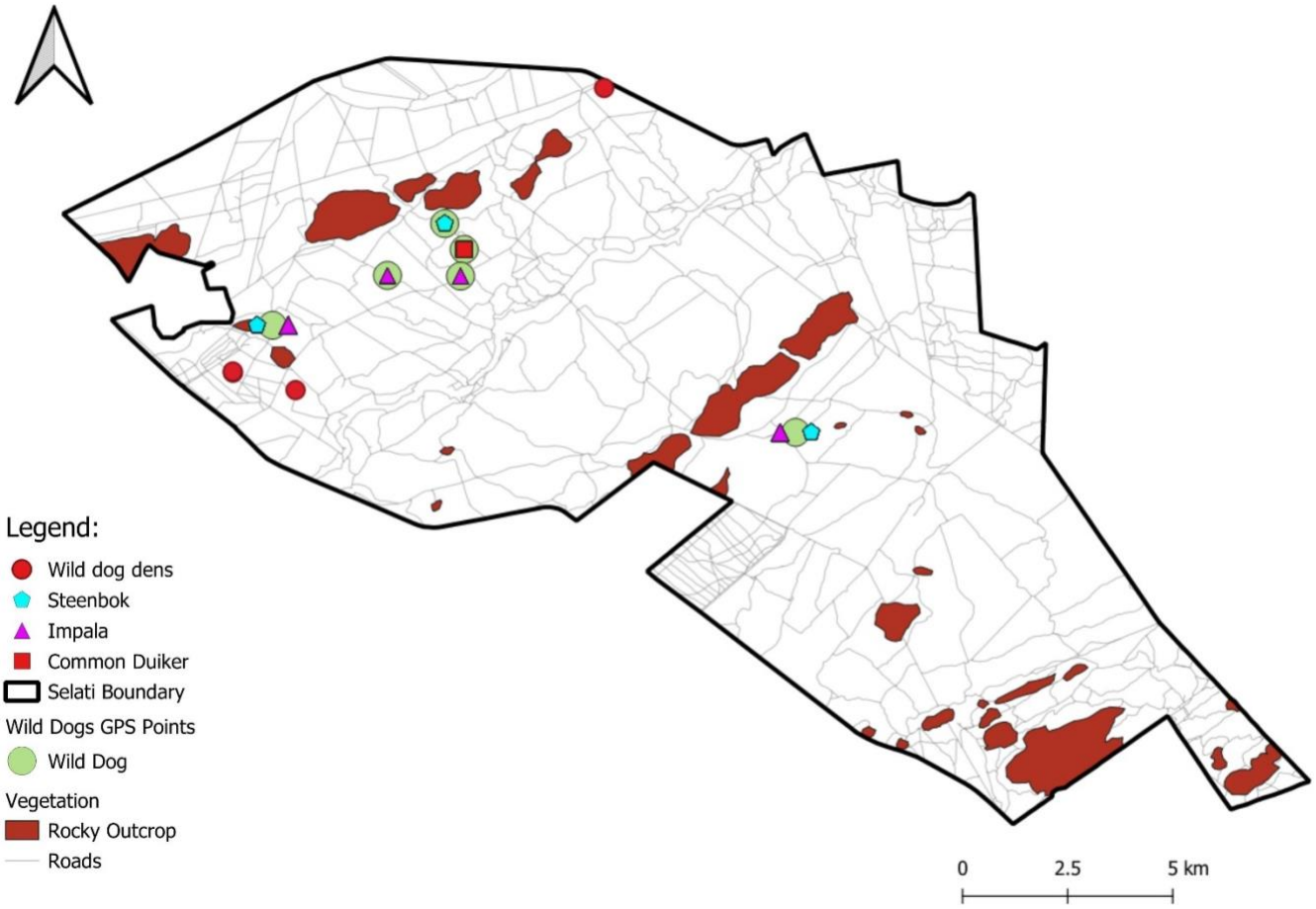

Figure 7: GPS locations of wild dog scat samples throughout Selati Game Reserve, showing the different prey species found in each scat, represented by different shapes and colours. (For species, date of scat collection and scat coordinates, see Appendix 3.1)

The scats of wild dogs (6 scats) contained a total of 161 hair fragments, with impala being the most frequent (98 hairs; 60.9%), followed by steenbok (40; 24.8%) and common duiker (23; 14.3%) (Fig 5). Most scat samples were collected from the western areas of the reserve, but 1 scat sample was collected near the centre, on the southern side of a rocky outcrop. The scat distribution appears to be near den sites and rocky outcrops (Fig 7).

Figure 8: GPS locations of scat samples collected from cheetah, spotted hyena and lion throughout Selati Game Reserve, showing the different prey species found in each scat, represented by different shapes and colours. (For species, date of scat collection and scat coordinates, see Appendix 3.1)

Cheetahs scat samples (3 scats) contained a total of 68 hair fragments, including steenbok (23 hairs; 33.8%), impala (19; 27.9%), greater kudu (19; 27.9%), common duiker (5; 7.4%), and Sharpe's grysbok (2;2.9%). Spotted hyena scat sample (1 scat) had a total of 30 hair fragments, with only impala being detected (30; 100%). Lion scat sample (1 scat) contained 29 hair fragments, with kudu (28; 96.6%) and impala (1;3.4%) being identified (Fig 5). All scat samples were collected near the western side of the reserve (Fig 8).

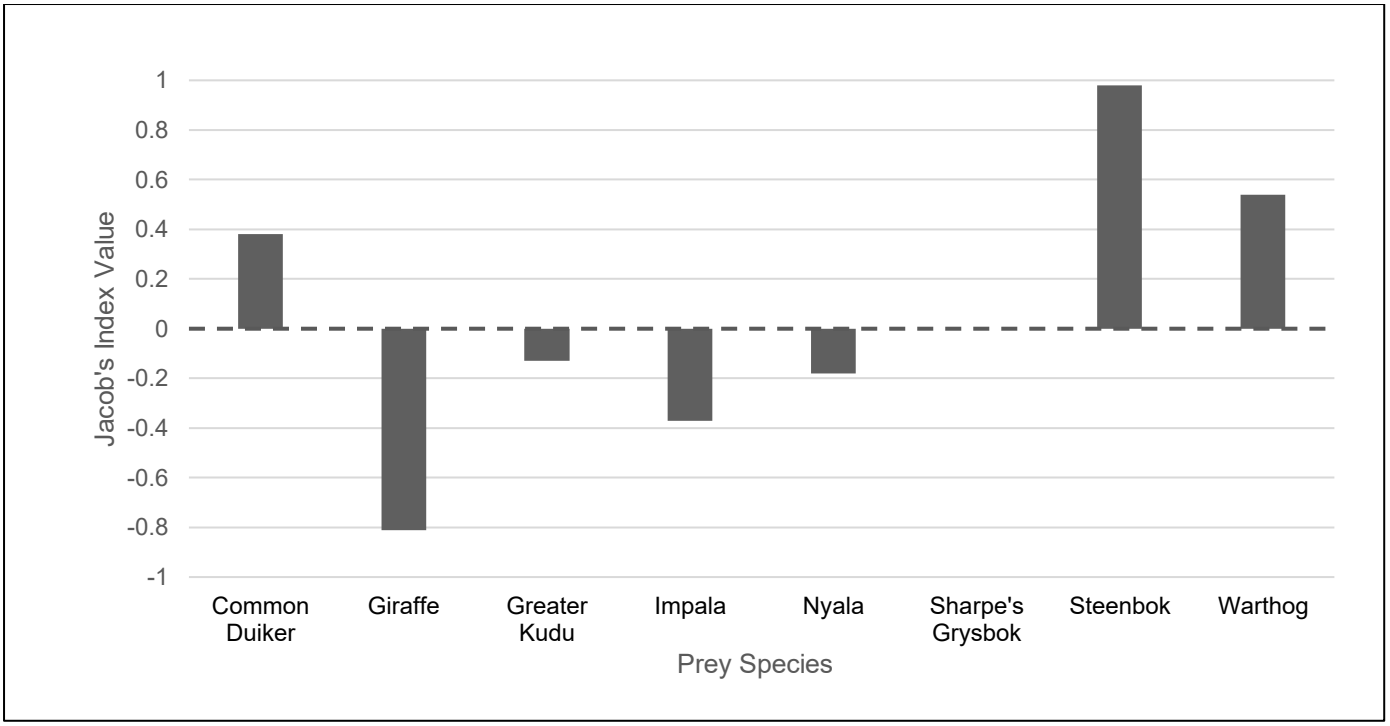

Figure 9: Jacob's Index values for five carnivore species, showing prey selection preferences. values range from -1 (strong scarcity) to +1 (strong frequency), with 0 indicating neutral selection. Data is based on observed vs expected prey use. Scrub hare was not included as there was no aerial count data (For aerial data, see Appendix 4.2)

Jacob's Index values showed distinct prey frequencies among five carnivore species, leopards, lions, cheetahs, spotted hyena and wild dogs (Fig 9). Steenbok and duiker showed high frequency of depredation across several carnivores, with Jacob's Index values approaching +1.0. Warthog was also frequently depredated upon, with a value around +0.50. in contrast, giraffe exhibited the strongest scarcity, with a Jacob's Index value close to -0.81. Impala was also scarce, though less strongly, with a Jacob's Index value of -0.36, while kudu and nyala showed mild scarcity with values of -0.16 and -0.12. Sharpe's grysbok appeared neutral with a value of 0.

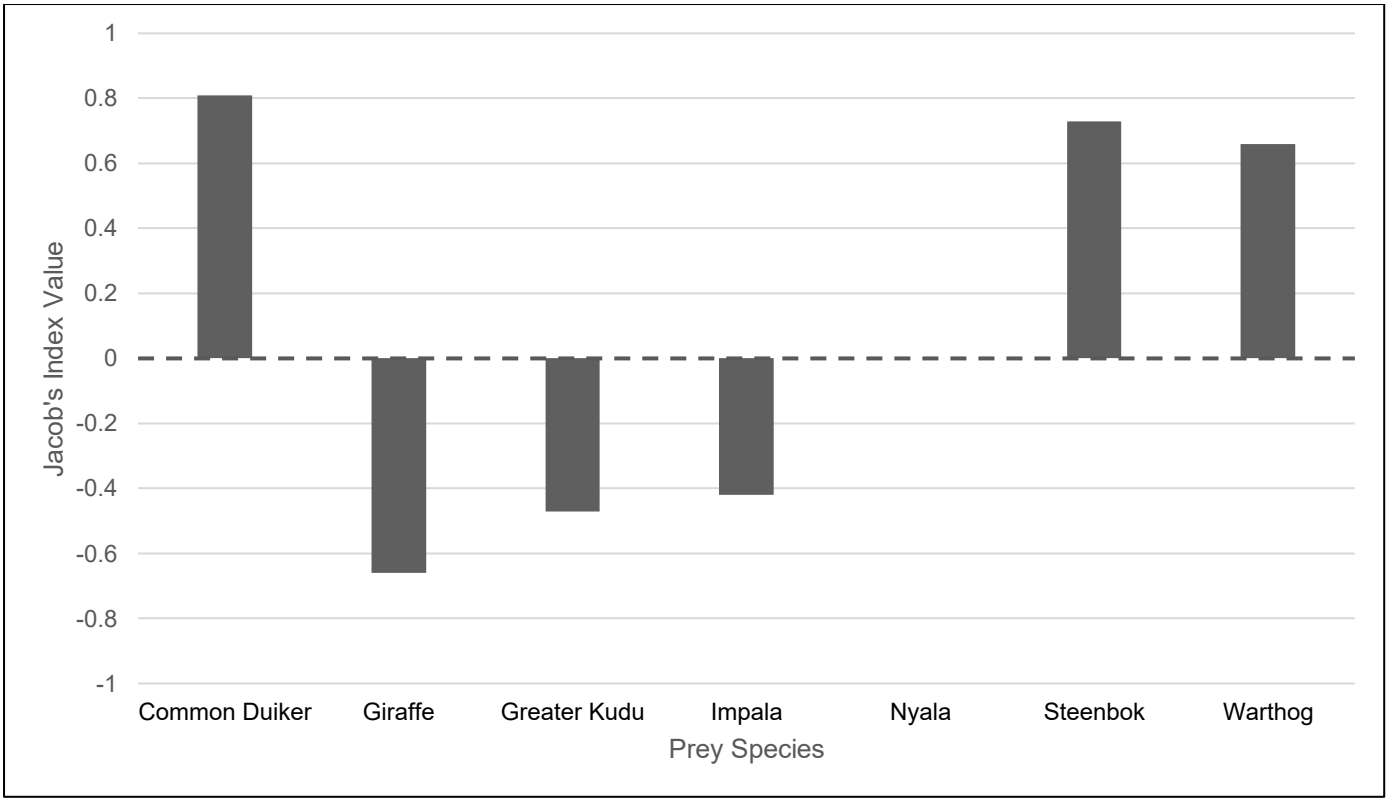

Figure 10: Figure 10: Jacob's Index values indicating prey preference of leopards. the index ranges from -1 (strong scarcity) to +1 (strong frequency), with 0 representing neutral selection. Data is based on observed vs expected prey use. Scrub hare was not included as there was no aerial count data (For aerial data see Appendix 4.2).

Jacob's Index values suggest that leopards exhibit strong prey preference patterns among the available species (Fig 10). The highest frequency was observed for duiker with a Jacob's Index value of +0.80, followed closely by steenbok and warthog, with Jacob's Index values of +0.73 and +0.66. Leopards showed a scarce depredation on giraffe with a value of -0.66 and moderate scarcity on kudu and impala with values of -0.47 and -0.42. Nyala was neutrally selected, with a value of 0.

A chi-square test revealed that there were significant differences in the number of prey species-specific hairs recorded for each predator ($\chi^2 = 471.48$, $P < 0.0001$). Notable differences include warthog (52 observed in leopard scat vs 26 expected), impala (1 observed in lion vs 15 expected), steenbok should have appeared more frequently in leopard, lion and spotted hyena scat (16, 0, 0 observed vs 39, 4 and 4 expected). Kudu was overrepresented in lion scat (28 observed vs 3 expected).

4.0 Discussion

This study aimed to evaluate the dietary habits and frequency of prey within the scats of leopards, lions, wild dogs, cheetahs and spotted hyenas within Selati Game Reserve through scat analysis. By analysing 580 hair fragments from 21 scats, cumulative and species-specific dietary data was gathered. The findings showed both convergence and divergences in dietary patterns, which could be shaped by different hunting strategies, social groups, and habitat use (Owen-Smith and Mills, 2008).

4.1 Cumulative Prey Composition

Impala was the most frequent prey species found within the scats which is consistent with other findings as they are one of the most abundant antelope in many savanna ecosystems (Mramba, 2022). Their high abundance means that they are frequently encountered by predators, making them a common occurrence in dietary studies, and game count data (Deventer and Shrader, 2021). Selati's game count data supports this as they have 2852 impala individuals, but only 40 common duiker and 50 steenboks, showing a huge difference in abundance (See appendix 4.2 for aerial count data). Furthermore, impalas have a medium body size and tend to form open herd structures making them an easy target, especially for pack or ambush predators (Radloff and Du Toit, 2004). However, despite their high frequency in scat, the Jacobs Index indicates that impala was scarce relative to their abundance. This suggests that while impala is consumed, their selection is lower than expected, which could be due to the energy required to capture them compared to other prey that is easily subdued, especially for solitary species like leopards (Stein *et al*., 2015). Similarly, there was a high frequency of common duiker and steenbok hair in the carnivores' diets which supports the theory that smaller prey offers advantages in terms of catchability and reduced handling risk, especially for solitary predators such as leopards and cheetahs (Quinn and Cresswell, 2004). This is corroborated by Jacob's Index results, where both common duiker and steenbok had strong frequencies. This could be because these species are solitary, meaning they are easily depredated upon and become easy targets for predators due to their small size and lack of vigilance (Furstenburg, 2008; Baker, 2025).

Greater kudu hair fragments were identified multiple times and whilst they are a large antelope which requires group hunting, they may be taken down by lions, leopards or scavenged by other predators (Tilahun, 2018). Furthermore, previous studies have shown that leopards may occasionally prey on juvenile kudu, who are more susceptible and easier to subdue (Mills, 1984). Additionally, studies have found that greater kudu favour following game paths, which makes them more predictable in their movements and potentially more vulnerable to predators such as leopards, especially in densely vegetated areas where visibility is limited, and cover is abundant

for the predator (Wichatitsky *et al*., 2004). Scrub hare was identified, particularly in the scat of leopards. This could be due to their crepuscular activity patterns, which overlap with the hunting times of leopards (Puls *et al*., 2021). In addition, they occupy a range of open and shrub dominant environments, making them available across a range of microhabitats. Although aerial counts do not estimate scrub hare abundance, their consistent presence in carnivore scats may indicate opportunistic predation when more energetically rewarding prey is unavailable (Hayward *et al*., 2006). The lower frequency of large prey species such as giraffe suggests predators avoid high risk species unless an opportunity arises, for example if a species is injured or a young individual (Muller *et al*., 2018). This is supported as studies state that carnivores typically avoid high risk prey unless the balance of cost and reward is altered by vulnerability, therefore, such prey is normally consumed by lions or scavenged by spotted hyenas after natural deaths or failed hunts (Owen-Smith and Mills, 2008; Muller *et al*., 2018).

4.2 Species-Specific Prey Composition

When looking at the prey composition broken down by carnivore species, it reveals significant dietary partitioning among five predators. Leopards displayed the most diverse diet, including impala, common duiker, steenbok, greater kudu, warthog and scrub hare. This generalist feeding behaviour is consistent with their solitary and adaptable hunting strategy, which allows them to exploit a wide variety of prey depending on habitat type, prey availability, and competition (Hayward *et al*., 2006). Furthermore, smaller prey such as duiker and scrub hare were found in leopards scat reflecting the leopard's ability to stalk and depredate in dense vegetation and open areas (Bothma and Walker, 1999). This ecological plasticity may reduce competition with more specialised or social predators and supports the leopard's persistence across varied environments (Abrams and Cortz, 2015; Kshettry *et al*., 2018). In contrast to leopards, lions showed a higher frequency of larger prey species such as kudu which aligns with studies that state how lions hunt using cooperative predation (Stander, 1992). This social hunting behaviour enables them to target larger prey or species that rely on herd structures for defence, as coordinated group attacks allow lions to isolate and depredate on individuals more efficiently than solitary predators (Funston *et al*.,1998). Other studies found that lion's prey on a wide variety of species, including zebra, wildebeest, and buffalo, which suggests that the detection of only kudu and impala in the Selati scat samples may be due to prey availability, recent kills or sampling bias (Hayward and Kerley, 2005).

Wild dogs had a high amount of medium sized antelopes such as impala within their scat, which supports findings from other reserves where wild dogs have been observed favouring prey between 20-60kg (Creel and Creel, 2002). Moreover, wild dogs prefer to hunt medium sized antelope such as impala as these prey species offer a good balance between energetic trade-offs

and manageable risks. Their cooperative hunting strategy allows them to execute high speed chases with coordinated teamwork, which increases their overall hunting success and reduces the risk of kleptoparasitism from larger predators such as lions and spotted hyenas as they can consume the prey quickly (Fanshawe and Fitzgibbon, 1993; Carbone *et al*., 2005). Cheetahs predominately consumed small to medium prey species such as duiker and steenbok, which reflects their use of speed and visual hunting strategy. These prey species have been found in previous studies on the diets of cheetah and fall within the optimal weight range between 15 to 40 kg (Mutoro *et al*., 2022). This optimal weight range balances the energy gained from the prey with the energy spent depredating on it, whilst reducing the risk of injury and the likelihood of kleptoparasitism from larger carnivores (Scantlebury *et* al., 2014). The absence of larger prey in the cheetah's diets is to be expected given their limited strength and inability to defend kills from scavengers. However, greater kudu was found in their diets, which is atypical given the species larger size of 200kg. Therefore, the cheetah may have preyed upon a juvenile or subadult, which would be closer to their preferred prey weight class (Annear *et al*., 2023). Furthermore, coalitions of males have been known to hunt prey outside their usual range for solitary individuals which may explain the presence of greater kudu in the scat sample (Cornhill and Kerley, 2020). Spotted hyenas exhibited a limited dietary profile, consuming only impala. This is uncommon as they normally have dietary flexibility as they have different roles as hunters or scavengers (Fouche *et al*., 2022). Most hyenas have been seen to shift their behaviour to scavenging if competition from lions is highly likely, therefore they will capitalise on the left-over prey from lion kills or other naturally deceased species (M'soka *et al*., 2016). Moreover, hyenas have strong jaws and digestive systems that are capable of consuming and digesting a wide variety of animal matter, including bones and teeth, which many other predators can not digest effectively (Valkenburgh and Ruff, 2009). This ability to exploit both fresh kills and carcasses enables them to thrive in fluctuating environments (Lehmann *et al*., 2016).

Many of the carnivore species within this study, feed on the same prey species, particularly impala, which was found in all species scat. This overlap in prey selection can intensify interspecific competition, as multiple carnivores are relying on the same primary prey, which can lead to direct confrontations over kills or carcasses or indirect effects such as altered hunting times, increased stress, or forced shifts in diet (Tarjuelo *et al*., 2017). For example, cheetahs who are more fragile and susceptible to kleptoparasitism, may start to avoid preferred hunting areas if lions or spotted hyenas are present. This dietary overlap underscores the importance of niche partitioning in predator guilds (Rabe *et al*., 2025). As most species seem to target impala, which could be due to their abundance and catchability, small differences in hunting strategies, group structure, and habitat use can help prevent competition (Martins and Harris, 2013; Hintz and Lonzarich, 2018). For instance, wild dogs cooperative hunting allows them to consume prey

quickly and avoid scavengers, whereas leopards may rely on stealth and cover to target less vigilant species (Hubel *et al*., 2016). These differences within a shared ecosystem allows a balance between overlapping dietary needs, which in turn reduces direct competition and promotes co-existence (Hayward and Kerley, 2008; Schmitz, 2017).

4.3 Spatial Distribution of Scats

The spatial distribution of scats varied according to the different predator species. Understanding where each scat was found and collected has given insights into the habitat preferences and inter specific interactions among the five large carnivores within Selati Game Reserve. Most scat samples were concentrated in the western and central regions of the reserve, often near rocky outcrops and den sites. However, leopard scats were found to use the southern part of the reserve, indicating a wider use of the ecosystem and potential avoidance of areas that could be dominated by larger predators (Mann *et al*., 2020). The observed distribution patterns suggest that rocky outcrops and den sites significantly influence spatial use, which could be because these features offer concealment, elevated vantage points for hunting, protection from high temperatures, and a safe location to rest or raise young (Fitzsimons and Michael, 2017).

Leopards demonstrated a strong spatial association with rocky outcrops which could be because these features offer secluded cervices that serve as ideal denning and resting sites (Fitzsimons and Michael, 2017). Furthermore, these rocky outcrops not only offer a space for the leopards to rest but also, they serve as important thermoregulatory features as the rock faces are shaded and cause a cooler microclimate from the heat (Gubbi *et al*.,2020; Makuya and Schradin, 2024). Moreover, the rocky outcrops offer safety for cub rearing females by reducing the risk of detection by dominant competitors or scavengers and provide a climate buffer which enhances the cub's survival (Balme *et al*., 2017). Moreover, leopards often cache kills around rocky outcrops to avoid kleptoparasitism by lions and spotted hyenas, which shows the importance that these rocky outcrops serve to certain species. By dragging their kills into these rock crevices, leopards can feed on kill for several days without losing their kill, which minimises energy expenditure associated with repeated hunts (Balme *et al*., 2017). Unlike lions and spotted hyenas, who tend to prefer open plains or lowland areas, leopards utilise these elevated areas to reduce direct encounters (Swanson *et al*., 2016). This habitat partitioning helps facilitate coexistence among carnivores with overlapping dietary needs. Therefore, when leopards use areas that are underutilised by the dominant species, they can reduce conflict, whilst maintaining access to the required prey populations (Martins and Harris, 2013; Hintz and Lonzarich, 2018).

Similarly to leopards, wild dogs showed a habitat influenced spatial pattern, with scat samples clustered around known den sites, particularly in the western part of the reserve. This distribution

reflects their foraging strategy during the denning period, where adults hunt within a certain radius around the dens to provision the pups (Alting *et al*., 2020). Studies have found that these dens are often near dense vegetation, as they provide physical protection from predators and environmental factors, whilst allowing access to prey (van der Meer *et al*., 2013). However, one wild dog scat was found in the southern part of the reserve, which is an area predominately used by lions. This rare observation could suggest long distance foraging movements or dispersal behaviour which are common in wild dog ecology (Jordan *et al*., 2023). Studies state that wild dogs are known for their large home ranges and nomadic tendencies outside the denning period and often cover vast area in search of prey (Woodroffe, 2010). The presence of scat in the lion dominated southern territory could reflect an exploratory search by a subordinate pack or dispersing individuals seeking new territory or resources (Jackson *et al*., 2017). It may also suggest opportunistic hunting behaviour, as wild dogs can occasionally exploit less familiar areas, if prey availability or reduced competition allows it (Creel *et al*., 2024). Alternatively, this observation could show temporary avoidance of the main denning area due to a disturbance, shifts in prey movements or pressure from predators (Jackson *et al*., 2014). Studies have documented wild dogs adjusting their spatial use in response to competition or habitat changes, therefore the scat being isolated may show how the species has a flexible movement ecology within a competitive carnivore guild (Baker *et al*., 2014).

In contrast to leopards and wild dogs, cheetahs showed a more dispersed scat distribution, with samples mostly located in the central areas of the reserve. Studies have found that they will normally avoid areas that lions typically occupy, such as densely vegetated habitats due to the risk of predation and kleptoparasitism (Durant, 2000). Therefore, they are constrained in where they move and tend to prefer open habitats that reduce the likelihood of encounters with larger carnivores (Swanson *et al*., 2016). This spatial displacement may force cheetahs into areas where prey availability is reduced, but the reduced risk of meeting other carnivores outweighs this trade off (Cornhill *et al*., 2023). However, lions prefer areas where they can use their group hunting strategies, therefore they tend to concentrate near areas where prey species often aggregate such as waterholes (Loarie *et al*.,2013). These environments allow them to have good visibility and the ability to work as a group to ambush their prey, which increases their hunting success (Scheel and Packer, 1991). As an apex predator, they are less constrained by the presence of other carnivores and tend to exert a top-down influence, therefore mediating the spatial dynamics of other carnivores, whilst exploiting a range of different areas (Swanson *et al.*, 2016; Everatt *et al*., 2019). The spotted hyena scat was found near the central areas of the reserve, spatially overlapping with multiple carnivores. The proximity of spotted hyena scat to lion and leopard suggests that they may have been capitalising on the kill of these larger carnivores, which supports their role as opportunistic feeders (M’soka *et al*., 2016).

5.0 Limitations and Future Directions

There are several limitations to this study that should be considered. To start, the overall sample size was very small, with only 21 scat samples in total, and the number of scats samples varied between carnivore species, potentially causing the frequency data to be biased towards more heavily sampled species such as leopards. These sample imbalances limit the reliability of the comparative analysis across carnivore species and may cause the results to show perceived importance of certain prey species in a carnivore's diet, when it is not an accurate representation. Moreover, the scats were collected over different years and seasons, which can cause a temporal variation in both predator diet and prey availability that was not standardised. Seasonal shifts in ecosystems such as Selati have been known to influence herbivore movements and abundance, as well as the hunting behaviours of carnivores (Gorini *et al*., 2012; Gil *et al*., 2025). Therefore, the collection of scat samples from different periods of time could have obscured the ecological patterns in prey selection. Another key limitation to mention is the methodology used to identify hair fragments. Hair samples were examined under a microscope and compared to a reference key for identification. However, the reference list was missing a few species, and 13 hair fragments were unidentified, meaning that the results might be uncertain as the unidentified hairs could have represented common or rare prey types, which may have changed the overall interpretation of prey frequency found within the different carnivore diets. Microscopic hair analysis also relies heavily on the quality of the reference list, which can increase the risk of misidentification (De Marinis, 2006).

Future directions should aim to address these limitations through several different approaches. Firstly, increasing the sample size and making sure the scat collection of each carnivore is balanced. This would allow for a more comparative analysis of dietary preferences. Furthermore, scat samples should be collected within the same year and season to control temporal variation in both prey availability and predator behaviour and movements. This would help to understand the potential shifts in diet linked to changes in resource availability or interspecific competition (Symondson, 2002). Furthermore, future studies would benefit from combining kill site analysis with scat sampling, as it provides complementary insights into prey size, prey age, and predator hunting strategies (Klare *et al*., 2011). Additionally, the use of genetic analysis of scats would help reduce the number of uncertainties associated with microscopic hair identification, especially when the hair fragments are damaged from digestion. Genetic techniques such as DNA metabarcoding allows for a precise identification of both predator and prey species, which further enhances the accuracy of dietary analysis (Davison *et al*., 2002; Thuo *et al*., 2019; Buzan *et al*., 2024). Moreover, hair analysis could improve by utilising advanced imaging tools such as Scanning Electron Microscopy (SEM), which could improve the visualisation and classification of hair

fragments, particularly those that lack certain structures such as the medulla. This would reduce identification errors and improve consistency within the results (Davis *et al*., 2020).

6.0 Conclusion

In conclusion, this study confirms there are observable differences in the prey composition of scat samples across large carnivore species at Selati Game Reserve, supporting the main hypothesis. A total of 21 scat samples, with 580 hair fragments were analysed, revealing some dietary trends such as leopards and wild dogs frequently consuming smaller prey like common duiker, impala and steenbok, while lion consumed larger prey species such as greater kudu. Furthermore, spatial patterns of scat distribution showed clustering near key features such as rocky outcrops and den sites, with leopards and wild dogs showing strong associations with these features, which could be due to fact they provide cover from other predators and thermoregulatory benefits. These dietary and spatial differences show how niche partitioning helps to reduce interspecific competition among large carnivores sharing an ecosystem, and how variations in prey selection, size of prey, habitat preferences and hunting strategies for example ambush by leopards or pursuit by wild dogs, all contribute to minimising direct competition. Understanding the diets of the large carnivores within Selati Game Reserve can inform management strategies that will help support both predator and prey populations.

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