Factors Influencing Cheetah (*Acinonyx jubatus*) Distribution in Kafue National Park, Zambia

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ABSTRACT

Globally, effective management of large carnivores, particularly threatened and endangered species like cheetah (*Acinonyx jubatus*), hinges upon a comprehensive understanding of their spatial distribution and conservation status. Despite being among the most threatened species within the Felid family, cheetah are data deficient throughout much of their known range, including within protected areas of Zambia, a potential stronghold for the species. In this study, existing camera trap data collected between 2018 and 2023, were used to assess cheetah occupancy estimates within Kafue National Park. These camera trap surveys were designed and run by the NGO Panthera Wildcat Conservation, in collaboration with Department of National Parks and Wildlife (DNPW) to estimate leopard density across the north, central, and southern regions of the park. To adapt this survey for use in cheetah occupancy analyses, I overlaid a 6 x 6 km grid cell onto the surveyed area (KNP), where each grid subsumed multiple camera traps stations, and was treated as an independent site. All subsequent analyses were conducted at this site level. Due to low detection of cheetah, I used a stacked occupancy model to analyse cheetah spatial distribution in relation to landscape/site covariates within KNP, interpreting the results as probability of site use rather than the true occupancy. Data on cheetah detection histories (presence and absence) were analysed against nine covariates, including closed versus open habitat types (namely open forest, closed forest and grassland), the relative abundance of both prey and other large predators (lion [*Panthera leo*] and spotted hyena [*Crocuta Crocuta*]), distance to water, anti–poaching patrol effort and distance to legal camps (lodges, NGO and DNPW bases). The results confirmed the presence of cheetah in KNP with 170 cheetah detections, 110 of which were independent. The detection probability for cheetah increased significantly with the sampling effort (total number of days cameras were active in a site) but the addition of other detection variables decreased the predictive performance of the models. The naïve occupancy varied from 28% in the south to 50% in the northern region. Similarly, cheetah detections were highest in the north and lowest in the south. Among the nine site covariates analysed, only prey RAI ($\beta = 2.08$), and proportion of open forest ($\beta = -3.55$) had a significant influence on cheetah probability of site use. Using cheetah by–catch data from a leopard survey provided a first estimate of cheetah occupancy in a Zambian National Park. These estimates could be improved through the addition of more sites and a longer survey duration (range: 80 –100 days) to improve estimates for this important carnivore species.

INTRODUCTION

1.1: Status of large carnivores

Since the late Pleistocene, large terrestrial carnivores have undergone substantial population declines and geographical range contractions (Beschta and Ripple, 2009; Prugh et al., 2009; Dirzo et al., 2014; Ripple et al., 2014; Galetti et al., 2018; Hoeks et al., 2020). Southeastern Asia and Africa have experienced the most pronounced geographical range contractions (Wolf and Ripple, 2017). Major threats to the persistence of large carnivores include habitat degradation, persecution by livestock managers, trophy hunting, disease, illegal commercial trade (Sillero–Zubiri and Laurenson, 2001), and the loss or reduced abundance of preferred prey species (Larsen and Ripple, 2003; Tittensor et al., 2014; Sandom et al., 2018; Enquist et al., 2020; Hoeks et al., 2020).

Globally, the decline in carnivore populations has been uneven, with some populations entirely extirpated while others have either persisted or are exhibiting gradual signs of recovery (Winterbach et al., 2013; Ripple et al., 2014; Chapron et al., 2014; Fernández–Sepúlveda and Martín, 2022). Within the carnivore order, the Felidae, which is the second largest family, has experienced the most significant declines with 18 out of the 38 species categorised as either Endangered or Vulnerable (Fernández–Sepúlveda and Martín, 2022). Examples of range contractions within this family include 92% for cheetah (*Acinonyx jubatus*), 94% for lion (*Panthera leo*), 95% for tiger (*Panthera tigris*), 79% for leopard (*Panthera pardus*), 78% for snow leopard (*Panthera uncia*), 64% for clouded leopard (*Neofelis nebulosa*), and 50% for sunda clouded leopard (*Neofelis diardii*) and Jaguar (*Panthera onca*) (Wolf and Ripple, 2017).

1.2: Cheetah distribution

The cheetah is among the most threatened species of Felidae and has seen precipitous declines across its wide historical range (Durant et al., 2017). Historical records indicate that over 100,000 cheetahs roamed across 44 countries in Africa and Asia (Durant et al., 2017). Cheetahs are categorised into four distinct subspecies — three of which are in Africa (*Acinonyx jubatus hecki* in Northwestern Africa, *Acinonyx jubatus soemmeringii* in Eastern Africa, and *Acinonyx jubatus jubatus* in southern Africa, and one in Asia (*Acinonyx jubatus venaticus*) (Prost et al., 2022). A fifth subspecies, *Acinonyx jubatus raineyi*, believed to inhabit East Africa, was proposed by Krausman and Morales (2005). However, its status remains contentious (Prost et al., 2022).

According to Durant et al. (2017) the extant global cheetah population is estimated to be around 7,100 adults and adolescents. However, a more recent assessment conducted by Weise et al. (2017) provided a slightly lower estimate of 6,517 mature individuals (IUCN, 2022). This population is distributed across 33 subpopulations in a vast area of approximately 3,100,000 km², with densities that rarely surpass two individuals per 100 km² (Durant et al., 2017; Figure 1). Out of the 33 subpopulations, Durant et al. (2017) found that 14 were experiencing a decline, three were classified as stable and only one population was classified as stable or increasing.

In Asia, cheetah have been eradicated from most of their historical range (IUCN, 2022). Presently, the critically endangered Asiatic cheetah (*A. j. venaticus*) (Farhadinia et al., 2017) is restricted to 36% (37,000 km²) of its historical range and is now found exclusively in Iran (Durant et al., 2017). This population represents 0.6% of the global cheetah population of which 44% reside in protected areas (Cristescu et al., 2018). There are estimated 50 mature individuals divided into three subpopulations: northeastern Iran, central Iran, and Kavir National Park (Khalatbari et al., 2017; Khalatbari et al., 2018).

In Africa, 30 fragmented cheetah subpopulations occur, confined to approximately 13% of their historical range (Durant et al., 2017). In east Africa, distinct subpopulations of cheetahs exist in Tanzania, Kenya, Ethiopia, South Sudan, and northern Uganda. Together these constitute approximately 11% of their historical range covering 615,000 km² (Durant et al., 2017). Notably, this population represents 32% of the cheetah global population (Cristescu et al., 2018). Their population is approximately 2,102 mature individuals spread across 14 subpopulations and only one subpopulation has > 200 individuals (Durant et al., 2017). Approximately 75% of this range occurs outside protected areas and overlaps with predominately traditional pastoralist communities (Durant et al., 2017). The status of cheetahs in Eritrea, Djibouti, Somalia, and Sudan remains unknown (IUCN, 2022).

In western, central, and northern Africa, cheetahs presently inhabit only 9% of their historical range, covering 1,037,000 km² (IUCN SSC, 2012; Belbachir et al., 2015; Durant et al., 2017). However, a significant portion of this range is situated within the Sahara where they exist at extremely low densities (Belbachir et al., 2015). Five distinct cheetah subpopulations have been identified in this region with an estimate of 419 mature individuals (IUCN SSC, 2012; Durant et al., 2017), 83% of which resides outside protected areas (IUCN SSC, 2012; Belbachir et al., 2015).

According to Cristescu et al. (2018), roughly 20% of these cheetahs reside within protected areas. Additionally, in west and central Africa, it has been estimated that among the 15 protected areas, 11 have recorded cheetah extinctions, representing 73% of site extinctions (Brugiere et al., 2015). According to Brugiere et al. (2015) and Durant et al. (2017), cheetahs have been extirpated from their historical range in several countries, including Western Sahara, Senegal, Nigeria, Mauritania, Tunisia, Guinea, Ivory Coast, Cameroon, the Democratic Republic of Congo (DRC), and Ghana. Comprehensive surveys conducted by Henschel et al. (2014) in well–protected areas across the Democratic Republic of the Congo, Côte d'Ivoire, Guinea, Senegal, Ghana, and Nigeria revealed an absence of cheetah. In Cameroon, the last reported sighting of cheetah dates back to the 1970s, and extensive research conducted in the Benoue Complex in 2007 and 2010 yielded no traces of cheetah tracks (Croes et al., 2011; IUCN, 2023).

Southern Africa serves as a crucial stronghold for cheetah with a population estimate of >1000 mature individuals distributed across 11 subpopulations (Durant et al., 2017; Weise et al., 2017). This region harbours a transboundary population extending across Namibia, Botswana, southern Angola, northern South Africa, southwestern Mozambique, and southern Zambia (Durant et al. 2017). In addition, small, isolated populations (each consisting of fewer than 100 mature individuals) exist in central Angola, Zambia, Zimbabwe, and Mozambique (IUCN SSC, 2015; Durant et al., 2015; Weise et al., 2017). Weise et al. (2017) estimated 3,577 adult and adolescent cheetahs in Zimbabwe, South Africa, Namibia, and Botswana. However, this contrasts with the 4,032 estimated by Durant et al. (2017) in the same countries. Weise et al. (2017) further showed that the largest cheetah population in southern Africa is potentially more fragmented than indicated by Durant et al. (2017). This population inhabits approximately 22% of their historical range encompassing an area of 1,325,000 km² (IUCN SSC, 2015), with a probable cheetah presence in an additional 424,000 km² (IUCN, 2022).

In Zambia, cheetahs previously occurred within the national parks, except for the Lower Zambezi National Park, where they are documented to either be absent or recorded sporadically (Skinner and Smithers, 1990; Purchase, 2007). In the late 1990s, three cheetahs were translocated from Namibia to the Lower Zambezi National Park, but none were able to survive (Purchase, 2007). Nevertheless, since 1990, tour operators have reported sighting one or two cheetahs in Jeki Plain in Lower Zambezi National Park (Marker, 2002a). Presently, their range has contracted, and extant populations are confined to three national parks — namely, Kafue National Park, Liuwa Plains, and Sioma Ngwezi National Park (Purchase, 2007). Cheetah sightings have been confirmed in Kafue National Park and Liuwa Plains (IUCN, 2023), as well as Sioma Ngwezi

National Park (Young et al., 2016, unpublished report), but they are largely absent outside of Zambia's protected areas (Purchase, 2007). Notably, no negative interactions between cheetahs and farmers have been recorded (Purchase, 2007).

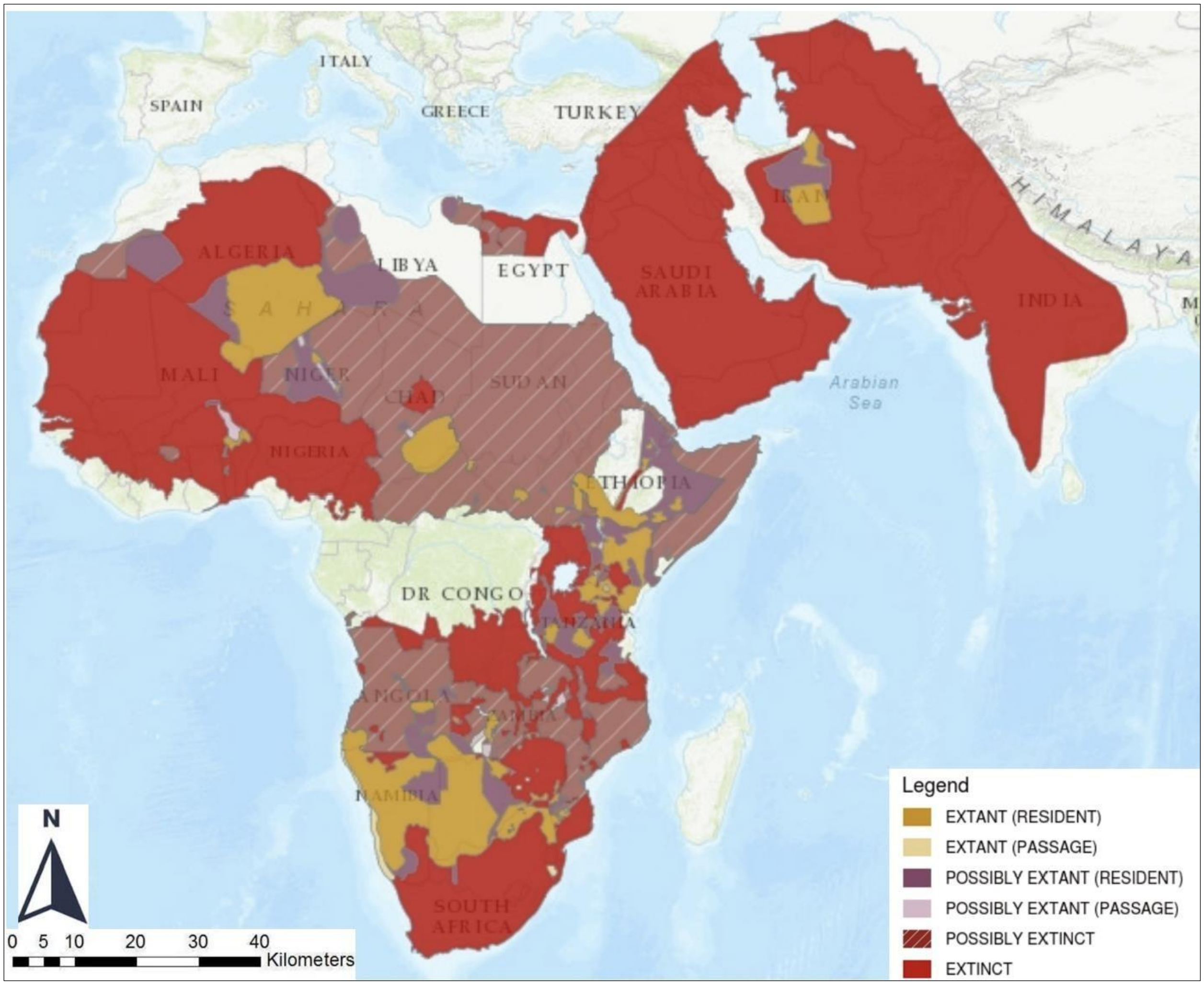

Figure 1: Geographical distribution for cheetah and their likely status, including whether they are possibly extinct or extinct, or possibly extant passage or resident, and extant, distinguished between resident populations and transient individuals using the area as a passage or corridor (Durant et al., 2023).

1.3: Threats

Cheetahs face several threats contributing to their significant decline across their geographic range. One of the primary threats is habitat loss and fragmentation which is particularly pronounced because of their low population density, requiring extensive land areas for survival compared to other carnivore species (IUCN SSC, 2007, 2012; Durant et al., 2017). According to Durant et al. (2017), 67% of the extant cheetah live outside of protected areas (encompassing 77% of their current known range). Cheetahs inhabiting areas outside protected areas often experience negative interactions with livestock (both subsistence and commercial) and game farmers because of the actual and perceived threat they pose to people's livelihoods (Marker et al., 2003; Dickman et al., 2014).

The combination of external threats faced by cheetahs outside protected areas, along with their extensive population decline, has led to their categorization as "protection reliant species" (Durant et al., 2017). While protected areas are meant to act as safe haven for wildlife, both illegal (e.g. bushmeat poaching) and legal (e.g. tourism) activities can have detrimental effects on cheetah populations (Lindsey et al., 2013a; Tablado and D'Amico, 2017; Soofi et al., 2018). Roe et al. (1997) demonstrated that unregulated tourism exerts adverse impacts on cheetah populations, including disruptions to hunting activities and the separation of mothers from cubs (IUCN, 2023). Instances of cub mortality resulting from such separations have been documented in the Serengeti National Park (IUCN, 2022), and Maasai Mara Reserve in southwest Kenya (Broekhuis et al., 2018).

A significant threat to small and isolated subpopulations are wire snares (IUCN, 2022). These are traps which are set for bushmeat purposes and inadvertently ensnare cheetahs (Marnewick et al., 2009; Lindsey et al., 2013a). Furthermore, substantial bushmeat extraction in areas where cheetahs still occur has had a profound impact on their population viability (Lindsey et al., 2013a; Ripple et al., 2016). In Kafue National Park for instance, illegal harvesting of bushmeat has impacted its herbivore communities, especially in the adjacent Game Management Areas (GMAs) which act as ecological buffer zones to the park (Lindsey et al., 2014). It is estimated that the overall wildlife population within the park has been reduced to approximately 25% of its carrying capacity (Lindsey et al., 2014). Some of the GMAs have witnessed even more pronounced declines in wildlife populations (Lindsey et al., 2014). Concurrently, habitat degradation within GMAs is exacerbated by anthropogenic activities, including shifting agriculture, charcoal production, fuelwood extraction associated with small-scale tobacco farming, and the establishment of mines in specific GMAs (Chemonics International Inc, 2011; Vinya et al., 2011; Lindsey et al., 2014).

Road kills present a pronounced peril to cheetah populations, especially in regions with paved roads (IUCN, 2022). From 2001 to 2016, Iran documented 14 cheetahs killed along the highway traversing the Kalmand, Touran, Bafq, and Dareh Anjir protected areas (Iranian Cheetah Society, 2013; IUCN, 2022). In Serengeti National Park in Tanzania, six mature cheetahs were killed in a vehicle collision along the unpaved road from 2014 – 2019 (IUCN, 2022). Zambia, South Africa and Kenya have also recorded occurrences of cheetah fatalities linked to various roads (IUCN, 2022).

Cheetahs face an ominous prognosis in the wake of climate change (Khalatbari et al., 2018). The shifting dynamics of agricultural land conversion and concurrent reduction in available natural land exacerbate this challenge (IUCN, 2023). This is further compounded by rising sea levels, increasing human population movements, and heightened environmental variability (Khalatbari et al., 2018; IUCN, 2023). Modelled impacts, as described by Khalatbari et al. (2018), suggest that in Iran, cheetahs may find themselves compelled to undertake migrations toward more temperate regions in a bid to adapt to the transforming environmental conditions. Furthermore, this anticipated shift could potentially heighten negative interactions with local people and other large carnivores (Khalatbari et al., 2018).

Cheetahs are subject to a variety of illegal activities, including hunting for their skins as trophies, use of body parts for cultural purposes, and a significant illegal trade involving cheetah cubs being sold as pets in the Gulf states (Tricorache et al., 2021). The illegal trade, recognized as one of the foremost transnational crimes, poses a substantial threat to the survival of numerous species (Tricorache et al., 2018). Annually, the smuggling of approximately 300 cheetah cubs out of the African continent to meet the demands of the illegal pet trade raises significant concern (Tricorache et al., 2018; Schmidt-Küntzel et al., 2024). The unlawful capture of cheetahs is particularly prevalent in Ethiopia, Somalia, and northern Kenya, with a notable concentration of cases reported in Somaliland (Tricorache et al., 2018). Approximately 4,184 cheetahs were entangled in illegal wildlife trade between 2010 and 2019 (Tricorache et al., 2021; Schmidt-Küntzel et al., 2024). The *A. j. soemmeringii* has been identified as one of the cheetah populations that is susceptible to illegal live trade in Africa (Durant, 2022). In Somaliland, a genetic analysis conducted on 55 seized cheetahs revealed a uniform genetic composition exclusively attributed to the *A. j. soemmeringii.* This finding further underscores the prevalent illegal trade of cheetahs and exerts the substantial pressure on the population stability of the *A. j. soemmeringii* (Schmidt-

Küntzel et al., 2024). Despite regulatory efforts through both international and national laws governing the trade in wildlife species and their derivatives, the scale of the illegal wildlife trade remains high, with estimates ranging from U$50 billion to U$150 billion annually (Marker, 2019).

The low genetic diversity has also been identified as a potential threat to cheetah populations, as it is associated with impeding reproductive success and inadequate immune responses against pathogens (Melzheimer et al., 2018). However, it has been noted that free – ranging cheetahs exhibit proficient reproductive success and possess robust innate immune mechanisms to combat pathogens (Melzheimer et al., 2018). Therefore, the persistence of low genetic diversity raises concerns regarding the cheetah's capacity to adapt to swift environmental fluctuations or the emergence of novel diseases (Schmidt-Küntzel et al., 2018).

1.4: Hunting and diet

In their natural habitat, cheetah display a remarkable proficiency in hunting, attributed to their exceptional speed and agility, specialised anatomy and physiology, and hunting strategies (Hilborn et al., 2012; Wilson et al., 2013). Notably, they secure their prey in approximately 40% of their hunting attempts (Hilborn et al., 2012). Cheetahs usually engage in hunting during the early morning and early evening hours, employing a stalking technique to approach their prey (Caro, 1994; Hilborn et al., 2012; Marker, 2019). Various factors contribute to a successful cheetah hunt, these include, prey size, the response of the prey, the number of cheetahs involved in the hunt, and the distance covered by the cheetah during the pursuit (Caro, 1994; Hilborn et al., 2012; Wachter et al., 2018).

Cheetahs have the remarkable ability to endure extended periods without water, as they derive the necessary hydration from the blood of their prey (Caro, 1994; IUCN, 2022). They typically feast on a substantial kill and subsequently abstain from eating for 2 to 5 days (Caro, 1994, IUCN, 2022). Nevertheless, they will seize the opportunity to hunt daily if it presents itself (Caro, 1994; IUCN, 2022). Pettorelli et al. (2009) observed that cheetahs exhibit a propensity to avoid prominent water features due to the co–occurrence of other predators in these areas. This behaviour persists despite the tendency of prey species to aggregate around water points (Durant et al., 1988; Pettorelli et al., 2009). Conversely, other studies have suggested that cheetahs often prefer for areas adjacent to water points due to the abundance of prey species (Broekhuis, 2007; Tagwireyi et al., 2020). The dietary preferences of cheetahs vary based on their habitat type (Caro, 1994; Mungoma Kuloba et al., 2015). In contrast to other African predators, cheetahs rarely scavenge, and due to intense competition, they tend to lose approximately 10 – 15 % of their kills to kleptoparasitism, notably from lions and spotted hyenas (hereafter called hyenas) (Hunter et al., 2007; Marker et al., 2018; Marker, 2019). Cheetahs abandon their carcass once satiated and thus seldom spend much time at their kill sites (Hunter et al., 2007; Marker, 2019). They are known to be diurnal, a strategy aimed at reducing competition from other larger carnivores that are primarily nocturnal (Caro, 1994; Broekhuis et al., 2014; Belbachir et al., 2015). In areas that have less competition, such as South African farmlands and the Sahara, cheetahs have been observed to be more nocturnal (Marnewick et al., 2006; Belbachir et al., 2015). Additionally, other factors such as human persecution and extreme heat (e.g., deserts), have also been reported to contribute to the shift of cheetahs to nocturnal behaviour (Belbachir et al., 2015).

Cheetahs are strictly carnivorous (Andresen and Somers, 2013), preying mostly on small–medium–sized animals usually in the 23–56–kilogram range (Hayward et al., 2006; Bissett and Bernard, 2007; Andresen and Somers, 2013; Mutoro et al., 2022). Species such as small antelopes, gazelles, hares, and the young of larger antelope species like wildebeest (*Connochaetes sp.*), kudu (*Tragelaphus sp*.), oryx (*Oryx sp.),* and small warthogs (*Phacochoerus*) being the primary targets (Marker et al., 2018). Male cheetahs, particularly those in coalitions, may occasionally take down larger prey species such as zebra (*Equus hippotigiris, E. dolichohippus*), and ostrich (*Struthionidae*) (Mills et al., 2004; Clements et al., 2014; Clements et al., 2016; Marker et al., 2018). In both protected and unprotected areas, cheetahs occasionally prey on domestic livestock, as evidenced by the presence of livestock remains in their scat (Nyerembe, 2020; Mutoro et al., 2022). For instance, in the Ngorongoro Conservation Area (NCA), where Maasai pastoralists co–exist with wildlife while maintaining their own livestock, cheetahs were reported to be responsible for approximately 4.3% of livestock attacks.

In Kafue National Park (KNP), a shift in the dietary preferences of large carnivores towards medium–small prey has been observed over the past half-century, as evidenced by historical records dating back to 1960 – 1963 (Creel et al., 2018). This shift can be attributed primarily to changes in the availability of different prey species (Creel et al., 2018). Mitchell et al. (1965) and Creel et al. (2018) both documented patterns of predation in KNP, providing valuable insights into changes in carnivore diets. Cheetahs, for instance, were found to primarily prey on bushbuck (*Tragelaphus scriptus*), duiker (*Cephalophinae* spp.), hartebeest (*Alcelaphus lichtensteinii*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), oribi (*Ourebia ourebi*), puku (*Kobus vardonii*), reedbuck (*Redunca arundinum*), warthog (*Phacochoerus africanus*), wildebeest

(*Connochaetes sp.*), and zebra (*Equus quagga*), with puku accounting for the highest proportion of kills (45.4%) (Mitchell et al., 1965). Reedbuck was second (12%), followed by hartebeest (9%), wildebeest, warthog, and impala (6%) and the least frequently consumed were bushbuck, duiker, kudu, oribi, and zebra (all 3%). Similarly, Creel et al. (2018) observed a decline in the consumption of larger prey species such as hartebeest, wildebeest, kudu, roan (*Hippotragus equinus*), sable (*Hippotragus niger),* and zebra among the large carnivores, including cheetahs.

Both studies highlight the significant role of medium–small prey, particularly puku, in the diets of carnivores within KNP. This preference for medium–small prey is partly attributed to their relative abundance in the ecosystem (Creel et al., 2018). Presently, the most common herbivores in KNP include puku (13 individuals per km^2), impala (9.6 individuals per km^2) and warthog (1.7 individuals per km^2), as supported by data from distance sampling conducted by the Department of National Parks and Wildlife (DNPW) and anti-poaching foot patrols which included common duiker (Creel et al., 2018).

1.5: Habitat preference

Cheetahs inhabit a wide range of habitats and ecoregions, encompassing dry forests, dense scrublands, open grasslands, and even hyper–arid deserts like the Sahara (IUCN SSC, 2007; 2012, 2015; Durant et al., 2014, 2017). Young and Evans (1993) noted that cheetahs are not found in montane forests, however, there are occasional sightings of cheetahs in high altitudes areas in Mt Kenya (IUCN, 2022). Durant et al. (2010a) suggested that cheetahs, in comparison to other carnivores, appear to display relatively low habitat selectivity, a behaviour known to be influenced by the sex and social dynamics of the species (Bissett and Bernard, 2007).

Male cheetahs select habitats based on hunting needs, with coalitions choosing ranges that include both open areas for hunting and dense vegetation for cover (Bissett and Bernard, 2007). Meanwhile, females, particularly those with cubs, prefer heavily wooded areas or thickets to increase cub survival and minimize kleptoparasitism (Bissett and Bernard, 2007). Bissett and Bernard, (2007) further indicated that cheetahs can adapt to various habitats, challenging previous assumptions that suggested that cheetah prefer open areas (Hunter, 1998; Purchase and du Toit, 2000; Broomhall et al., 2003; Mills et al., 2004). This assumption could be attributed to the fact that most previous studies on cheetah ecology were conducted in open grassland savannas, with a specific emphasis on the Serengeti Plains in East Africa (Schaller,1972; Frame and Frame, 1980; Caro and Collins, 1986,1987; Durant et al., 1988; Fitzgibbon, 1990; Caro, 1994; Laurenson, 1994, 1995; Laurenson et al., 1995; Kelly et al., 1998, Durant, 1998, 2000a, b; Bissett and Bernard, 2007).

Myers (1975) observed that cheetahs are relatively rare within the expansive miombo woodlands of southern Tanzania and Mozambique (IUCN, 2022). The limited presence of cheetahs in Zambia has also been attributed to the predominance of the miombo woodland, which dominates the region (Purchase et al., 2007a). However, a recent study by Strampelli et al. (2021) conducted in the Ruaha-Rungwa ecosystem, characterized by central Zambezian and Eastern miombo woodlands, highlights the significance of these habitats for cheetahs. These contrasting perspectives raises questions of whether cheetahs can thrive in some miombo woodlands depending on the region. Confirming, this suggestion is essential for informing effective conservation strategies and management practices tailored to the specific ecological dynamics of cheetah populations in regions characterized by miombo woodland dominance.

Cheetahs often use trees as strategic lookouts or vantage points and for territorial markings (Nghikembua et al., 2016; Marker et al., 2018; Marker, 2019). When discretion is needed, such as during the stalking phase of hunting, they utilize the natural cover afforded by shrubs and tall grasses (Caro, 1994; Durant; 1998, 2000b; Hilborn et al., 2012). Pettorelli et al. (2009) reported that cheetahs demonstrate avoidance tendencies towards roads, likely due to their frequent use by tourists and the higher presence of other predators such as lions and hyenas.

1.6: Reproduction and mortality

Cheetahs are non–seasonal breeders, and their gestation period lasts approximately 90 to 95 days, with a litter size usually of three to five cubs (Caro, 1994, IUCN, 2022). The cubs face significant challenges to their survival, with mortality rates reaching 95% in the Serengeti. Approximately two–thirds of deaths in dens are attributed to predation (Laurenson, 1994; IUCN, 2022). Laurenson et al. (1992) noted that the mothers exhibit rapid re–conception following cub loss (IUCN, 2022). In Kgalagadi Transfrontier National Park, the survival rate of cubs is only 35.7%, with predation being the primary cause of mortality, including predation by lions, hyenas, and leopards, as well as smaller predators like honey badgers (*Mellivora capensis*), jackals (*Canis spp.*), and secretary birds (*Sagittarius serpentarius*) (Mills and Mills 2014). Adult cheetahs also face mortality risks, with annual rates varying by gender and age, and influenced by predation and hunting-related injuries (Durant et al., 2010b). Coalitions of males aid in territorial defence and mating, contrasting with the solitary nature of females when they are without sub–adult cubs. These social dynamics, along with predation pressures, shape cheetah distribution and behaviour in ecosystems such as the Serengeti and Namibian farmlands (Marker et al., 2003, Durant et al., 2004, 2010b).

1.7: Home range size and density estimates

Cheetahs are known to have large home ranges of (>1500 km^2; Marker, 2019) relative to other large cats, with factors such as vegetation, prey density, sex, and social grouping being major contributors (Caro, 1994; Marker, 2002b, Broomhall et al., 2003). The age of accompanying cubs, however, influences the daily movement patterns of female cheetahs, until the cubs become independent (Laurenson, 1994; IUCN, 2023). The influence of the cubs is largely attributed to the need for their safety, with mothers adjusting their hunting locations and movements accordingly. Cheetah home ranges in protected areas are believed to be influenced by factors such as prey migration, low rainfall, and predation avoidance (Caro, 1994; Durant, 2000a, b; Broomhall, 2001). On the Serengeti plains for instance, female cheetahs, and non–territorial males exhibit nomadic behaviour because of the migratory movements of prey with home ranges of approximately 800 km² (Durant et al.,1988; Caro, 1994; IUCN, 2022). In contrast, territorial males maintain smaller territories with an average home range of 30 km² which are mostly located in areas that are of heightened attractiveness to females (Durant et al.,1988; Caro, 1994; IUCN, 2022).

A study on Namibian farmlands showed a similar trend: territorial males maintained smaller territories, averaging 379 km², while non–territorial males had larger home ranges, with an average of 1,595 km² (Melzheimer et al., 2018). In the same study, the female cheetah home range was estimated to be 650 km² (Melzheimer et al., 2018). Data from Kruger National Park indicate a negligible difference between male and female cheetah home ranges (Broomhall et al., 2003). Cheetah density estimates within well–managed and productive protected areas (PAs) like the Serengeti and Kruger National Park are estimated to be one individual per 100 km². A figure derived from the lower spectrum of the 1.3 to 2.5 individuals per 100 km² typically observed in such PAs (Durant et al., 2011; Marnewick et al., 2014; Broekhuis and Gopalaswamy, 2016). In contrast, less protected areas, such as Namibian farmlands, show a lower density of 0.25 individuals per 100 km², aligning with observed ranges between 0.25 and 0.83 individuals per 100 km² (Marker, 2002a). In the Sahara, density is as low as 0.025 individuals per 100 km², based on Algerian Sahara studies (Belbachir et al., 2015), while in West and Central Africa, densities are slightly higher at 0.1 individuals per 100 km², reflecting the intermediate pressures from habitat encroachment and illegal activities (IUCN, 2022).

1.8: Conservation status

According to the International Union for Conservation of Nature (IUCN), cheetahs are currently listed as vulnerable (IUCN, 2023), with two subspecies, *Acinonyx jubatus hecki*, and *Acinonyx jubatus venaticus*, classified as critically endangered (Belbachir, 2008; Durant et al., 2023). Presently, ongoing assessments for the status of *Acinonyx jubatus soemmeringii* suggests that the species is likely to be classified as endangered (Durant et al., 2023). The substantial decline in mature individuals of *Acinonyx jubatus soemmeringii*, from 260 to 590, warrants the classification of this subspecies as endangered (Schmidt-Küntzel et al., 2024).

The re–classification of the cheetahs as an endangered species under the IUCN red list is being advocated due to the rapid contraction of their range, rendering them more vulnerable to population declines (Durant et al., 2017; Weise et al., 2017; IUCN, 2023). Currently they are classified as a species under watch requiring regular assessment every three years (Durant, 2022). Additionally, cheetahs are categorised under Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) as well as the Convention on the Conservation of Migratory Species on Wild Animals (CMS) (IUCN, 2023).

The species holds a protected status under the national legislation across the majority of its current range, as well as in some areas it previously occupied (IUCN, 2023). However, in several countries, the killing of cheetah is permissible aimed at mitigating threats to human life and livestock, as delineated in animal control regulations (e.g., Botswana, Namibia, and Zambia) (Marker et al., 2003; Purchase et al., 2007a). Systematic monitoring of such killings is seldom conducted (IUCN, 2022), leading to a lack of comprehensive data on the extent of these operations. Furthermore, authorization for the retention of cheetah–derived parts, such as skins, may occur within these operations in certain countries, potentially amplifying incentives for cheetah removal to occur (IUCN, 2022).

1.9: Occupancy modelling

Occupancy models have become a popular method to study species distribution in conservation biology (MacKenzie et al., 2006), as they account for imperfect detection when estimating species' true occupancy within a given area (MacKenzie et al., 2006; Zeller et al., 2011). Factors influencing species' occupancy (ψ) and detection (p) probabilities, such as habitat characteristics and environmental conditions, can be incorporated into occupancy models with associated linear terms (MacKenzie et al., 2006). Several fundamental assumptions must be met for accurate estimation using occupancy models. Firstly, that the surveyed population remains closed (i.e., no births/deaths/emigration) with no false detections, sites are independent and finally, that there is no unexplained variation (heterogeneity) in ψ and p (MacKenzie et al., 2006). Emerging approaches, both statistical and practical, allow researchers to relax model assumptions and evaluate novel drivers of ψ and p, such as potential species interactions (Gerber et al., n.d). These approaches can also account for sources of bias, such as 'false–positive' errors linked to species misidentification (Gerber et al., n.d). The versatility of occupancy models is such that several different data sources can be used in occupancy models, including the identification of spoor, interviews with local communities, hair traps, and camera traps (Midlane et al., 2014). Occupancy can be interpreted in various ways, including as the proportion of area occupied (PAO) within a study region (Midlane et al., 2014). PAO estimation requires point–based sampling methods like camera traps (Efford and Dawson, 2012).

Alternatively, it can also be interpreted as the probability of site use, particularly for animals with expansive home ranges (Mackenzie and Royle, 2005).

1.10: Aims and objectives of the study

The lack of data on the population status of cheetah throughout much of their current range makes it difficult to understand anthropogenic and environmental drivers of their occurrence. The aim of this study, therefore, was to investigate the spatial distribution of cheetah, and how landscape/site covariates influence their occupancy in Kafue National Park. In this regard I used data from six years of camera trap surveys, designed to monitor leopard density, in the north, central, and south regions of the park (Figure 5). By modifying the camera trap array to meet the assumptions of an occupancy study, I was able to explore how cheetah occupancy varies: 1) across the surveyed regions of the park, 2) in closed versus open habitats, 3) in relation to prey availability, 4) in relation to competition (lion and hyena), 5) in relation to distance to water, 5), in response to anti– poaching patrol effort, and 6) in relation to distance to legal camps (lodges, NGO and DNPW bases)

Study predictions

I predicted that cheetah occupancy would positively correlate with prey availability and abundance, regardless of potential risks posed by predators (Vanak et al., 2013). This prediction stemmed from the observed contrast in prey dynamics across different geographical regions. Durant's (1998) research in the Serengeti plain of Tanzania unveiled cheetahs' preference for areas with low prey densities, likely to reduce encounters with predators such as lions and hyenas. Conversely, research by Purchase and Du Toit (2000) in Matusadona National Park in Zimbabwe revealed a divergent pattern, with cheetahs favouring areas rich in prey and experiencing reduced predator risk, primarily from lions and hyenas. However, Vanak et al. (2013) demonstrated that despite the overlap in the home ranges of cheetahs and predators, particularly lions, cheetahs actively sought out prey-rich areas, regardless of potential risks posed by lions.

Considering the relationship between cheetah and other predators – particularly lion and hyena, I predicted that the presence of these competitors would negatively influence the probability of cheetah occupancy, as they are known to engage in kleptoparasitism by stealing cheetah kills and occasionally preying on cheetah cubs (Durant 1998; Durant, 2000a; Pettorelli et al., 2009; Tagwireyi et al., 2020, IUCN, 2022). Finally, despite the cheetah not being water dependent, studies have shown that they tend to prefer areas that are near to water points due to the high densities of prey such as puku and impala (cheetahs preferred prey) (Broekhuis, 2007; Tagwireyi et al., 2020). I therefore hypothesised that water availability would play a significant role in determining cheetah occupancy patterns in Kafue National Park.

METHODS AND MATERIALS

2.1: Kafue National Park

Kafue National Park (KNP) is Zambia's largest and oldest national park and was proclaimed in 1950 (Mwima, 2001; Midlane et al., 2014; Kafue National Park, 2022). It is unfenced and covers an expansive area of approximately 22,319 km^2 (Midlane et al., 2014; Kafue National Park, 2022) and it is surrounded by nine Game Management Areas (GMAs) (Figure, 2) which serve as buffer zones, which together with the core park, results in ~66,000 km^2 of unfenced protected area known as the Greater Kafue Ecosystem (GKE) (Vinks et al., 2020; Kafue National Park, 2022). While the park itself receives strict protection, the GMAs are managed as 'controlled zones', aiming to balance ecological preservation with economic benefits for both the park and the neighbouring communities (Watson et al., 2015; Dietz et al., 2023). According to the Zambia Wildlife Act No. 12 of 1998, GMAs play a critical role in conserving ecologically significant areas while addressing local development needs (Mkanda et al., 2018), thus mitigating the negative impacts of human activities on adjacent national parks. GMAs also serve as spaces for both consumptive (mainly trophy hunting) and non–consumptive (tourism) (Lindsey et al., 2013b). Over the last fifty years, GMAs have faced significant challenges from poaching and human encroachment, adversely affecting the herbivore populations in the park (Lewis and Phiri, 1998; Becker et al., 2013; Overton et al., 2017). This decline in the prey species has negatively impacted the large carnivore populations (Midlane et al., 2014; Schuette et al., 2018; Vinks et al., 2020, 2021). KNP and its surrounding GMAs are part of the Kavango–Zambezi Transfrontier Conservation Area (KAZA TFCA), which covers a landmass of 520,000 km^2 (Vinks et al., 2021). This transboundary conservation area comprises 5 countries including Angola, Botswana, Namibia, Zambia and Zimbabwe of which KNP and its surrounding GMAs contribute 13% of the total transboundary conservation area (Vinks et al., 2021).

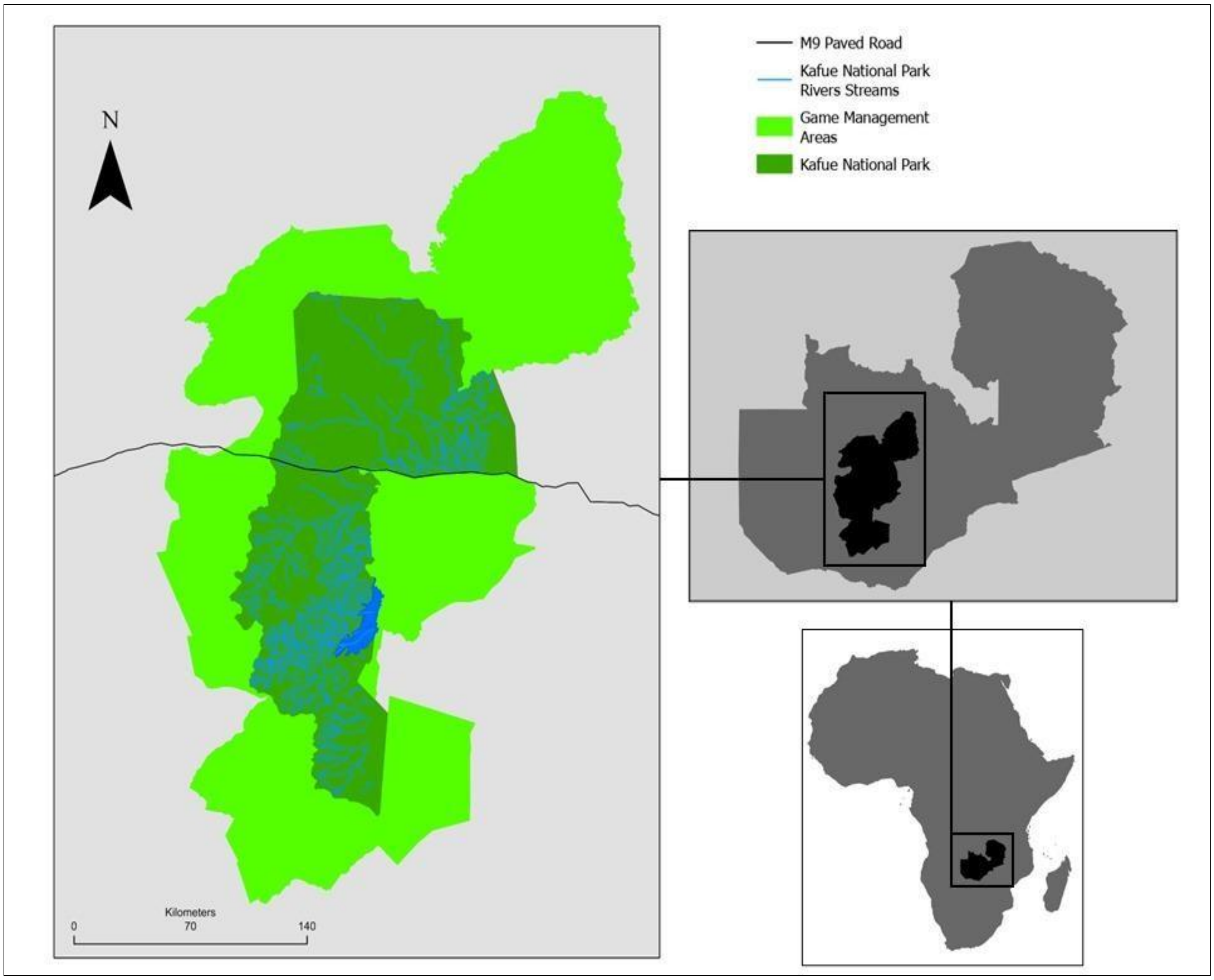

Figure 2: Location of Kafue National Park and the surrounding Game Management Areas within Africa and Zambia, including all the major streams, rivers and the main road system M9.

Climate and drainage systems

KNP experiences two distinct seasons that define its climate: the wet season, spanning from October to April, and the dry season, extending from April/May to September/October (Mwima, 2001). July typically marks the coldest period, with a maximum temperature of 28°C, while mean minimum temperatures range from 5°C to 7°C (Mwima, 2001). In contrast, October stands out as the hottest month, with maximum temperatures reaching 35°C (range: 31°C – 35°C), while minimum temperatures typically range between 15°C and 18°C (Mwima, 2001). The annual average rainfall varies from 600mm to 1200mm, which falls in a gradient of least rainfall in the southern region (< 800mm) to the much wetter northern region (> 1000mm) (Mwima, 2001; Mbewe, 2015).

The Kafue River serves as the primary drainage system within the park and stands as one of its key features (Mwima, 2001). Several other rivers, including the Lufupa, Mushingashi, Lunga, Shishamba, Musa, Nkala, Nanzhila, and various seasonal tributaries, flow through the park and into the Kafue River (Mwima, 2001). The Kafue River meets with Lake Itezhi tezhi, a humanmade reservoir, which lies on the park's boundary in the south (Mbewe, 2015). The park features two flood plains: the Busanga flood plains which borders the Lufupa river is located in the north and the Nanzhila flats in the south (Fanshawe et al., 2010; Mbewe, 2015). Dambos, which are natural troughs and depressions that collect run-off, are found in various parts of the park (Zambia Wildlife Authority Fire Management Plan for Kafue National Park and Its Surrounding Game Management Areas, 2007). These serve as crucial water sources for the park's wildlife.

Vegetation

KNP has a diverse vegetative landscape (Figure 3). The majority of the park is covered by the forest, with closed forests including dry deciduous and riparian forest types, while the predominant open forests (Figure 3) comprise of the Kalahari, mopane, miombo, and munga woodlands (Fanshawe et al., 2010). Within the open forests, the miombo woodland dominates and is characterised by *Brachystegia* and *Julbernardia* species (Vinks et al., 2020, 2021). Notably, the specific subtype present in the park is the central Zambezian miombo (Mbewe, 2015). This woodland serves as crucial habitat for several large herbivores such as the sable antelope and hartebeest (Frost, 1996; Vinks et al., 2020). The northern boundary of the park is bordered by Kalahari woodland, while the central region hosts a mixture of miombo and Kalahari woodlands. The southern part has a combination of evergreen teak (Zambian teak) forests and degraded munga and mopane woodlands (Fanshawe et al., 2010). Additionally, substantial termite mounds within the forest nurture unique evergreen plant life, including the candelabra tree (*Euphorbia ingens*) and the jackal berry (*Diospyros mespiliformis*) (Fanshawe et al., 2010). The park also features both extensive grasslands (namely – Busanga Plains [north region] and Nanzhila flats [south region]) and smaller open plains characterized by termite mounds (Fanshawe et al., 2010).

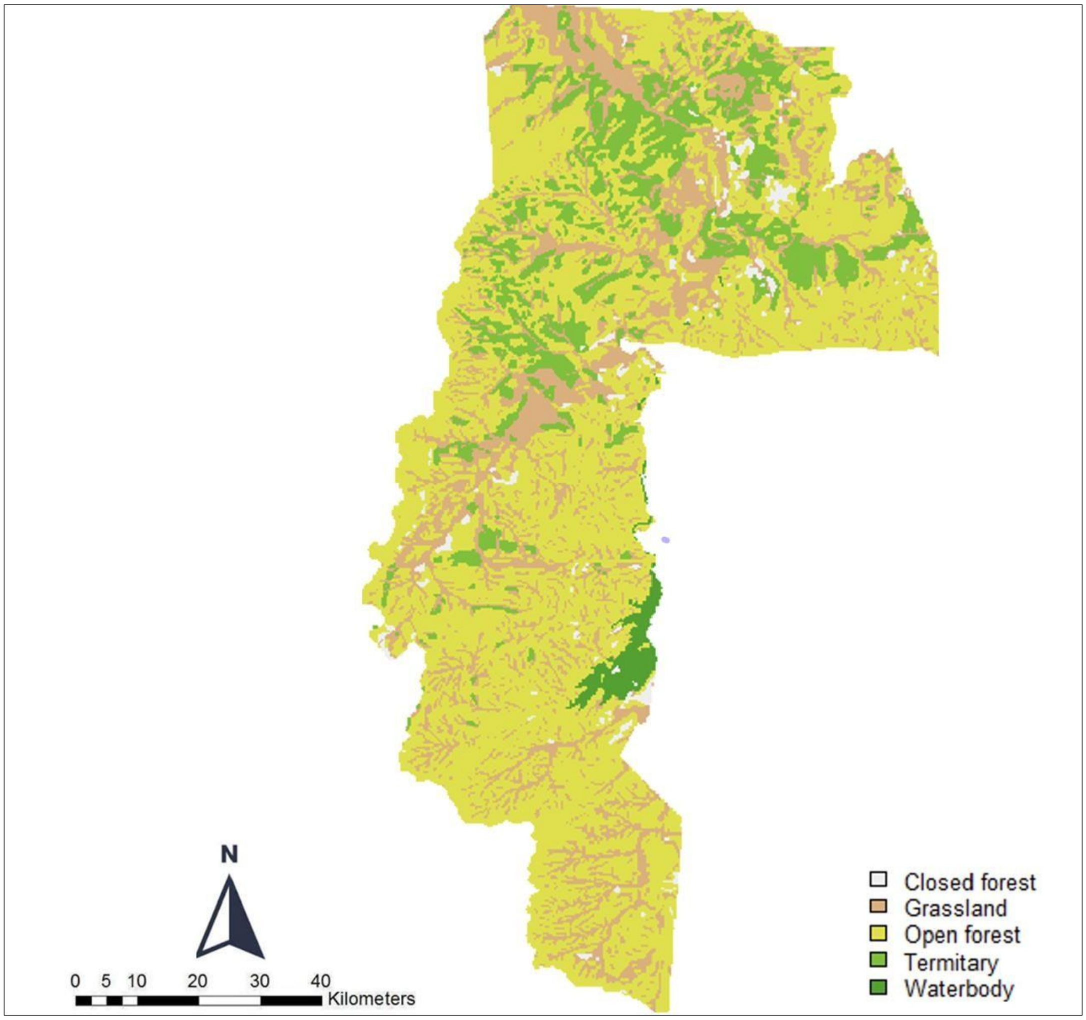

Figure 3: Kafue National Park vegetation map showing the proportion of the different vegetation types – closed forest (white), grassland (brown), open forest (yellow), termitary (light green) and lake Itezhi-tezhi – waterbody (dark green).

Fauna

Overall, the park harbours 158 mammals, 515 birds, 70 reptiles, 36 amphibians, and 58 fish species (Mbewe, 2015). A diverse array of antelope species (21 species; Kafue National Park, 2022) are present, including oribi, hartebeest, sable, roan, impala, grysbok (*Raphicerus melanotis*), duiker, red lechwe (*Kobus leche leche*), sitatunga (*Tragelaphus spekii*) and puku (Mbewe, 2015). Other mammalian inhabitants include elephants (*Loxodonta africana*), buffalo (*Syncerus caffer*), aardvark (*Orycteropus afer*), pangolin (*Manis temmincki*) bushpig (*Potamochoerus larvatus*), warthog, spring hare (*Pedetes capensis*), zebra and bushbaby

(*Galago spp.*). Importantly, KNP is also home to an intact carnivore guild, including both large species (cheetah, leopard, hyena, African wild dog (*Lycaon pictus*), and lion) (Creel et al., 2018) and smaller species (e.g., caracal (*Caracal caracal*), African wild cat (*Felis silvestris*), spotted–necked otter (*Hydrictis maculicollis*), serval (*Leptailurus serval*), African clawless otter (*Aonyx capensis*), honey badger, marsh mongoose (*Atilax paludinosus*), large grey mongoose (*Herpestes ichneumon)* and the white–tailed mongoose (*Ichneumia albicauda*)) (Purchase et al., 2007b). Notably, the cheetah population in KNP is the largest in Zambia (Purchase, 2007). Hippopotamus (*Hippopotamus amphibius*), Nile crocodile (*Crocodylus niloticus*), and monitor lizard (*Varanus niloticus)* frequent the Kafue River and its tributaries.

2.2: Camera traps

Camera traps are valuable for monitoring the abundance and distribution of wildlife, especially elusive and rare species (Marnewick et al., 2008; Brassine and Parker, 2015; Rocha et al., 2016; Cordier et al., 2022). Compared to alternative methods (e.g., line transects, live traps, and track plots), camera traps have been deemed more efficient and accurate in meeting a wide variety of study objectives, such as estimating species richness or density (Rovero and Marshall, 2009; Paull et al., 2012; Glen et al., 2014; Dupuis–Desormeaux et al., 2016). They are cost–effective, require less labour, and they can be deployed over large areas for extended periods (Buxton et al., 2018; Palencia et al., 2021), making them indispensable in wildlife research and conservation efforts (Green et al., 2020).

A review of camera–trapping studies conducted from 2008 to 2013 showed that most studies explored population parameters such as relative abundance and density (Burton et al., 2015). In particular, camera traps are a popular way to estimate population densities of individually recognisable species through capture–recapture analyses (Karanth, 1995; Karanth and Nichols, 1998; Alonso et al., 2015; Green et al., 2020). However, the application of camera traps spans from individual-level studies, e.g., animal movements (Royle et al., 2014), to broader population and community-level analyses e.g., occupancy, local abundance, species inventories and community ecology (Karanth, 1995; Nicholson and Van Manen, 2009; Sollmann et al., 2012; Wilting et al., 2012; Mohamed et al., 2013; Sollmann et al., 2017).

A systematic literature review conducted in Africa, revealed a focus on terrestrial wildlife in camera trap publications, with South Africa having the highest number of studies (28.9%) (Cordier et al., 2022). Most of these studies assessed species occupancy (41.4%), with mammals being the most studied taxa (Cordier et al., 2022) and most studies (43.9%) focusing on a single species. Large carnivores were the most popular study animal (24.8%), with leopards (*Panthera pardus*) being the focal species in 60 studies (Cordier et al., 2022). Habitats under investigation included forests (42.6% of studies) and savannah/bushveld (35.5% of studies), with a notable preference for conducting camera trap studies in protected areas (68.9%) (Cordier et al., 2022).

In Kafue National Park, Panthera, a non–governmental organization (namely Panthera Wild Cat Conservation, hereafter called Panthera) conducts camera trapping surveys across the park and five adjacent GMAs to monitor populations of leopards. These surveys, which operate annually or biennially, occur at twelve localities, of which three (north, central and south) are located within the park itself.

2.3: Panthera camera trap survey design based on the spatial capture–recapture method (SECR)

Panthera's survey design is tailored for the detection of leopards, with each survey covering 200 – 600km^2 and comprising of 36 – 51 camera trap stations spaced 2 – 5 km apart. The variation in the number of camera trap stations deployed across the survey years (2018 – 2023) is due to camera traps being damaged, removed or malfunctioning (Table 1). Camera stations were placed along animal movement pathways, such as roads, drainage lines, and water bodies. Each station consists of two cameras, enabling the identification of the target species (leopards) by providing images of both flanks, which have unique pelage patterns (Wilting et al., 2012; Alonso et al., 2015; Rogan, 2021; Smyth et al., 2022). The variation in the number of operational days was largely due to environmental factors, such as rainfall, which impeded accessibility to certain camera trap stations. Consequently, surveys extended beyond or before the anticipated 45 days (i.e., the suggested survey length required for accurate SECR modelling; Rogan, 2021).

In 2018, camera traps were deployed only in the central region, and these cameras were not rotated across different sites within the survey season (Figure 4). In 2019, the camera traps were deployed in the northern region (specifically in the Busanga plains) and the southern region, and again, there was no rotation between sites within the survey period (Figure 4). From 2020 to 2023, the camera traps were deployed annually across the north, central, and southern regions, and the cameras traps were set in the same locations each year. Over this period (2018 – 2023), a total of 592 camera trap stations were deployed, yielding a total of 34,928 camera trap nights.

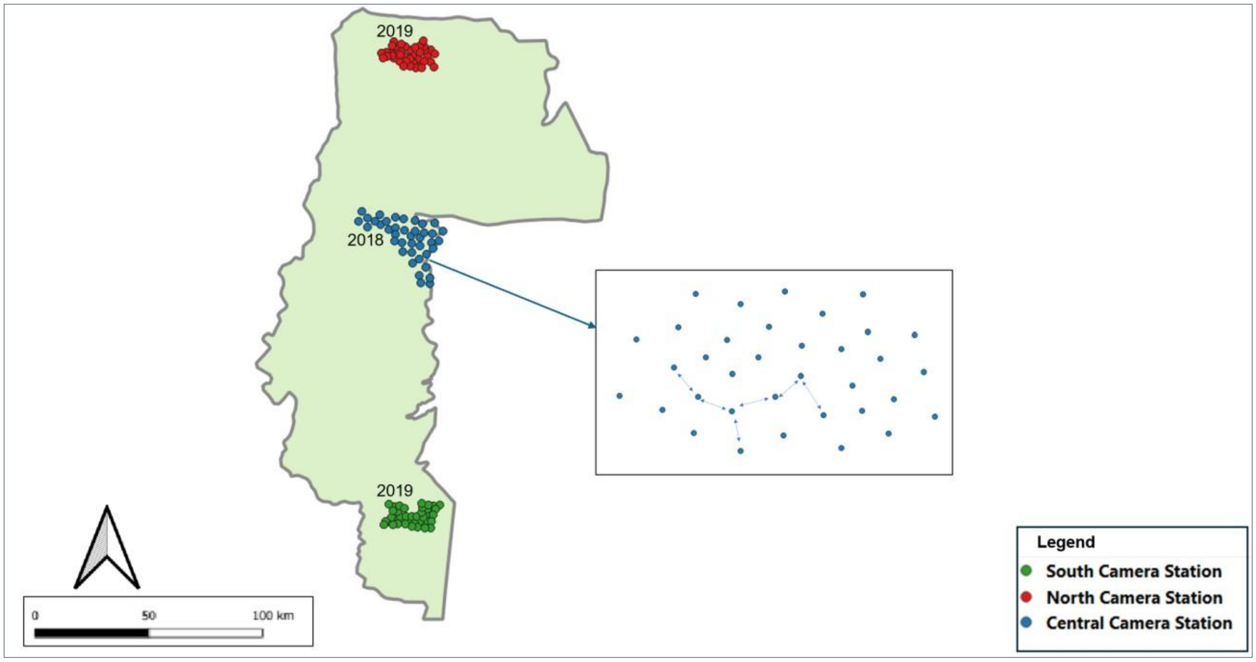

Figure 4: Camera trap stations and year of first deployment across the three distinct regions within KNP. The stations are colour – coded to indicate deployment location: red – north, blue – central and green – south. The inserted square (black border with blue dots) is a zoomed in view of the central site with a camera station spacing of 2 – 3 km^2. The dashed line with arrows indicates possible movement paths of an identified leopard.

2.4: Occupancy survey design for cheetahs

While the survey design was optimized to obtain leopard density estimates using SECR modeling, thus maximising the number of cameras within a leopard's home range, my objective was to estimate cheetah occupancy. To achieve site independence, a key assumption of occupancy models, I superimposed a 6 x 6 km grid over the surveyed area and treated multiple camera trap stations within each grid cell as a single independent site (Harmsen et al., 2024). Furthermore, the 100 km² home range was used because there's no literature available on cheetah home ranges in Kafue National Park. Additionally, when I initially used a 10 x 10 km grid, there were not enough sites to calculate the probability of site use for cheetahs. Hereafter, "site" refers to the aggregated camera trap stations within each grid cell (Harmsen et al., 2024).

All the camera data were pooled and analysed at site level, which served as the sampling unit (Harmsen et al., 2024). This resulted in a total of 61 sites (north = 18, central = 22, south = 21), with an average of 3 cameras (range: 1 – 7) per site. The total number of sites surveyed across all survey years (2018 – 2023) in each region was calculated by multiplying the number of sites per region by the number of survey years (n = 5) (Table 1). This yielded a total of 305 surveyed sites, comprising 90 sites in the northern region, 110 in the central region, and 105 in the southern region (Table 1). Out of the total 305 surveyed sites, wildlife was recorded at only 212 sites (69.5%). Considering the extensive movement patterns for cheetah it is highly likely that the assumption of spatial independence of sites was still violated (MacKenzie et al., 2002; Mkonyi et al., 2018). Consequently, data interpretation focused on discerning the influence of the covariates on the probability of site use for cheetah rather than estimating the true cheetah occupancy. The survey period of 36 – 79 days exceeded the 30 days (range: 30 – 100 days) recommended to obtain reasonably precise occupancy estimates for species like cheetah with low detection rates (Mackenzie and Royle, 2005; Guillera–Arroita et al., 2010; Shannon et al., 2014) and also satisfied the assumption of population closure (O'Brien, 2010; Shannon et al., 2014).

Predictor variables

Incorporating relevant covariates into the probability of site use analysis satisfied the heterogeneity assumption, which states that there is no unexplained variation in the probability of site use (ψ) (Royle and Nichols, 2003; MacKenzie et al., 2006; MacKenzie et al., 2017). I therefore, included covariates influencing cheetah site use based on prior studies on cheetah distribution (Caro, 1994; Broomhall et al., 2003; Muntifering et al., 2006; Bissett and Bernard, 2007; Mungoma Kuloba et al., 2015). Specifically, I included habitat type, prey availability (relative abundance index [RAI]), RAI of competitors (lions and hyenas), distance (km) to open water (main drainage lines), anti–poaching patrol effort (total patrol distance in each site) and distance to legal camp (lodges, NGO and DNPW bases) in my analyses.

Broad habitat type — namely grassland, open, and closed forest — is thought to influence prey availability, which varies significantly across habitats, and thus directly influence cheetah distribution (Pettorelli et al., 2009; Tagwireyi et al., 2020). Furthermore, different habitats offer cheetahs varying degrees of visibility and escape routes from larger predators (e.g., lion). For example, female cheetahs prefer thickets to protect cubs (Durant, 1998; Bissett and Bernard, 2007). The RAI for prey, lions, and hyenas were included to account for the influence of prey availability and predator competition on cheetah spatial distribution (Durant, 2000a; Hunter et al., 2007; Pettorelli et al., 2009; Vanak et al., 2013). The selection of lions and hyenas as focal predator covariates in this study is based on their confirmed status as primary competitors for cheetah (Hayward and Kerley, 2008; Pettorelli et al., 2009; Belbachir et al., 2015). Eleven prey species were selected based on previous research on the diet of cheetah within Kafue National Park, and included; bushbuck, duiker, hartebeest, impala, kudu, oribi, puku, reedbuck, warthog, wildebeest, and zebra (Mitchell et al., 1965; Creel et al., 2018).

The main drainage lines included were permanent water sources that are unaffected by seasonal fluctuations, namely the Kafue River, Lufupa, Lunga, Shishamba, Musa, Nanzhila, Lubunji, Lwansanda, Mukombo, Ntemwa and lake Itezhi tezhi. Proximity to water was included based on prior studies that have recorded that the distance to water has an influence on cheetah habitat use (Tagwireyi et al., 2020). The inclusion of the distance to legal camps such as lodges, NGOs and DNPW bases was to represent ‘habitat safety’, given wildlife often prefer locations near legal camps due to a perceived decrease in poaching risks (Davis et al., 2023). This reasoning aligns with the findings of Beale et al. (2018), which suggested that areas around ranger posts experienced lower rates of elephant mortality. Similarly, the decision to incorporate the anti–poaching patrol effort (i.e., total patrol distance in each site) covariate was informed by research demonstrating a negative correlation between wildlife abundance and areas with limited protection (Vinks et al., 2020).

To minimise the effect of season, camera traps were only deployed within a single season (namely, the dry season). To address potential biases in the detection due to camera trap placement, I incorporated the presence of roads to the detection probability (Cusack et al., 2015). The inclusion of the road covariate was driven by the fact that most of the cameras across the surveyed regions in KNP were deployed along roads, and roads are known to influence species detectability (Cusack et al., 2015). Additionally, roads enhance the frequency of photographic captures for large carnivores, as they are known to frequently utilize roads (Davis et al., 2023) due to their large home ranges and high movement rates. Roads offer efficient travel, energy conservation, and potential prey encounters (Kautz et al., 2021).

I therefore included two measures of road presence– firstly, proportion of sites on the road (whereby sites within a 100 – meter radius from the road were considered to be ‘on’ the road, or ‘not’ otherwise), and secondly the distance of the sites to the nearest road. Furthermore, given the variation in the number of camera trap stations and sampling effort (total number of days all camera traps were active in a site), I also included these variables as covariates when modeling the detection probability (Harmsen et al., 2024). Prior studies have also shown that an increase in both the number of camera trap stations within a site and sampling occasions is positively linked to species' detection probability (Gálvez et al., 2016; MacKenzie et al., 2017).

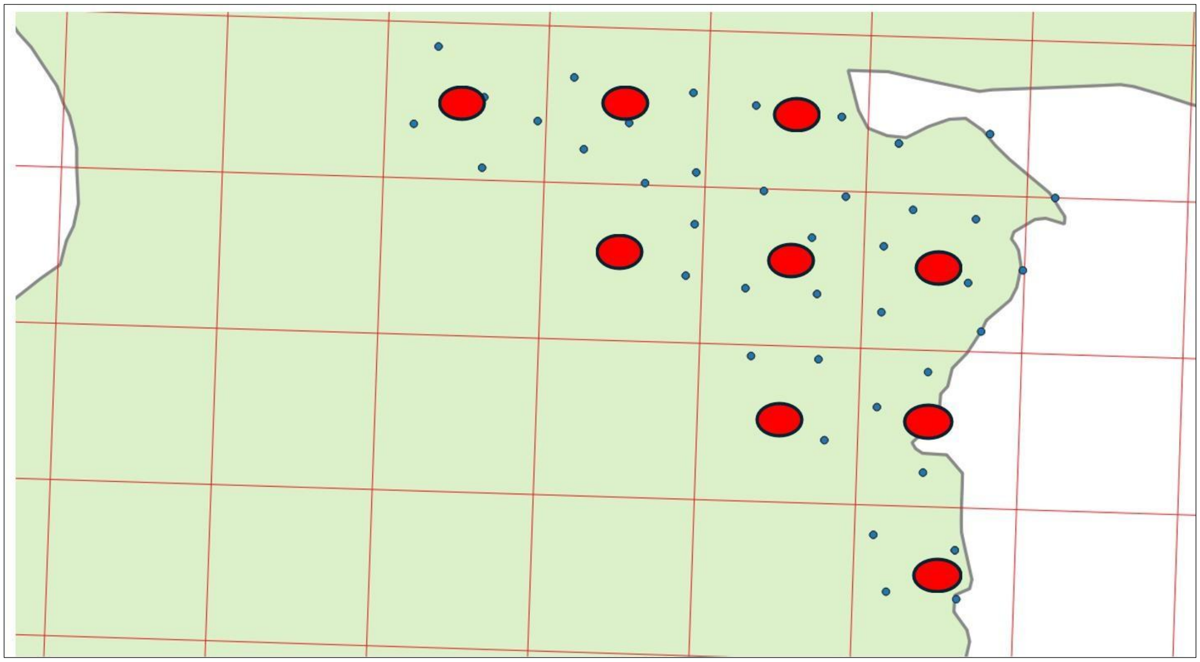

Figure 5: Camera trap locations for 2018 (blue dots) in the central region within KNP showing the centroid (large red circle) for each of the 6 x 6 km grid cells. Cheetah detections from all the camera traps in each grid cell were combined to represent a single site.

2.5: Data analysis

2.5.1: Data preparation

Camera trap data were initially processed to ensure that only the days when camera traps were functional were considered in further analyses. Detections of cheetah at each station were classified as independent if they were recorded more than 30–minutes apart (Cornhill et al., 2023). Due to the limited number of cheetah detections, a 'stacked' occupancy model was used, in which data from multi–year surveys (2018 – 2023) were incorporated into a single–season model (Bates et al., 2015; Harmsen et al., 2024). This model uses the combination of site–year as the sampling unit for estimating occupancy probability (Harmsen et al., 2024). The cheetah encounter history was formulated as a binary matrix, with rows corresponding to the encounter histories at a specific site–year, and columns delineating captures during each sampling occasion (Otis et al., 1978; Davis et al., 2023). If a cheetah was detected at a site, for a specific sampling occasion, it was assigned a value “1” (Davis et al., 2023). If no cheetah was detected, it was assigned the value “0” (Davis et al., 2023). Each sampling occasion consisted of 15 days. This period was selected to mitigate any issues that might arise from the inflation of zeros in the encounter history data (O’Connell et al., 2006). When the models were run with 10–day sampling periods, they failed to achieve reliable convergence.

The vegetation layer for Kafue National Park, initially in vector format (i.e., a shapefile) (Figure 3), was extracted from the global map of land use/land cover (LULC), generated by the Impact Observatory’s deep learning AI land classification model in collaboration with Esri (Zanaga et al., 2021). I rasterized the layer, resulting in a 250m x 250m raster grid, where each raster cell (or pixel) represented a vegetation type at a 10m resolution. From the rasterized vegetation layer, I created a raster stack, which contained three raster layers, one for each vegetation type, with binary values (0/1) indicating the presence or absence of the respective vegetation type within each raster cell. Using the R programming software (R Development Core Team, 2023), I calculated the total number of raster cells within each site. Subsequently, the proportion of each vegetation type within a particular site was calculated by dividing the summed number of raster cells representing each vegetation type by the total number of raster cells within that site (Figure 13 and 14). Additionally, the distance (km) from the centroid of each site (Figure 5) to the nearest main drainage lines or water sources, legal camps, and roads were calculated using R. The drainage lines, legal camps and roads were also extracted from shapefiles derived from global map of land use/land cover (LULC) (Zanaga et al., 2021).

The anti–poaching patrol effort data from 2018 to 2023 were sourced from the Spatial Monitoring and Reporting Tool (SMART) software, which functions as a repository for law enforcement information pertaining to anti–poaching activities conducted within the park (Kafue National Park, 2022). These data were then used to quantify the total patrol distance in each site. This process enabled the assessment of total patrol distances as a measure of law enforcement activity.

Detections of eleven prey species were aggregated to create a single prey covariate (prey RAI) for each site. Prey RAI was estimated by firstly summing the total number of independent captures for each prey species at each site across all the survey years, then dividing this by the total sampling effort and then multiplying by 100 to produce an index (MacKenzie et al., 2017). Predator

RAI was similarly calculated for lion and hyena. All continuous covariates (both on occupancy and detection) were standardised to have a mean of 0 and standard deviation of 1 (Oksanen et al., 2020; Harmsen et al., 2024), to improve model convergence and fit, and to make the coefficients more interpretable (especially when comparing effect sizes).

2.5.2: Occupancy model construction

I implemented all my occupancy models within a Bayesian framework using Stan (Carpenter et al., 2017), through the R package 'ubms' (Unmarked Bayesian model) version 1.2.6 (Kellner et al., 2022; Harmsen et al., 2024). This allowed for the incorporation of random effects – a measure that is implemented to prevent the artificial reduction in the variance (Bates et al., 2015). I therefore included 'site' as a random effect in all the occupancy models, to account for non– independence between repeated surveys (different years [2018 – 2023]) conducted at the same site (Kellner et al., 2022; Harmsen et al., 2024).

2.5.3: Model selection and assessment of model fit

My model ranking procedure consisted of a two–step approach. The first step was detection probability (p) model selection, where the top–ranked detection model was selected by comparing Expected Log Pointwise Predictive Density (ELPD) (Sivula et al., 2020; Sivula et al., 2023) values for selected combinations of fixed effects on p, while keeping the probability of site use (ψ) constant. The ELPD is a metric used to assess the goodness of fit of each model, whereby models with higher ELPD values indicate a better fit to the data (Sivula et al., 2020; Sivula et al., 2023; Harmsen et al., 2024). When comparing models, ELPD differences (Δ ELPD) of 4 are considered to be significant (Sivula et al., 2020; Harmsen et al., 2024). If the Δ ELPD exceeds 4, it is compared to the standard error (SE), which measures the uncertainty or variability associated with the estimated Δ ELPD (Vehtari et al., 2017; Sivula et al., 2020). Larger SE values indicated greater uncertainty in the Δ ELPD. Consequently, given the small ELPD differences (Δ ELPD) observed in my results, the selection of the best and top–ranked model was based on the model with the highest predictive power (ELPD) and the weight (likelihood of each model being the best model [Vehtari et al., 2017]).

In step 2, I adopted the best–fit detection from step 1, and ran models for each site use (ψ) covariate individually (single covariate models). As in step 1, the best and top–ranked covariates were selected by comparing the ELPD for the various combinations of fixed effects on ψ, while maintaining p constant. The significance of effect for individual covariates was determined by assessing the β–coefficient estimates using their 95% confidence intervals (Midlane et al., 2014). Covariates exhibiting intervals that overlapped with zero were considered as non– significant and the non–overlaps were considered significant.

Model selection procedure

In step one, I assumed that all the sites have the same probability of being occupied by cheetah and, the cheetah's probability of being detected during surveys at any of the sites was the same (i.e., the null model 'dm0'). In model dm1, I included the covariate 'sampling effort' (total number of days camera trap stations were active in a site). In model dm2, in addition to the scaled effort, I added the camera stations in each site as an additional covariate. In model dm3a, and dm3b I included the road covariate, with model dm3a assessing the influence of the proportion of sites located on the roads. In model dm3b I explored the distance of the sites from the roads, thereby evaluating how proximity to roads impacts cheetah detection. With the last model, dm4, I incorporated all the above covariates.

For step 2, the null model M0 represented the baseline ψ where all the other covariates were held constant. Models M1 — M9 represented the nine individual covariates that were added to each model (single covariate models) while the top ranked detection probability (p) covariate was held constant.

2.3:4: Model fitting and evaluation

I ran the models using three Markov Chain Monte Carlo (MCMC) chains, each consisting of 50,000 iterations. A warm–up period of 4,000 iterations was applied, and these iterations were subsequently discarded before assessing the model summaries (Vehtari et al., 2021). I assessed model convergence using the Brooks–Gelman–Rubin convergence diagnostic (R–hat < 1.1) and visual examination of the posterior distributions via trace plots (Vehtari et al., 2021; Kellner et al., 2022; Harmsen et al., 2024). R–hat values close to, or below, 1.1 implies minimal discrepancy between the chains, suggesting sufficient convergence (Vehtari et al., 2021)

RESULTS

3.1: Descriptive results

A total of 17,995 camera trap nights were recorded, which was calculated by multiplying the average number of days per survey (n = 59) by the total number of sites surveyed across all the years (n = 305) (Table 1). The number of independent captures of wildlife for each survey at each site ranged from 9787 – 28,469, with a total of 55,782 independent captures (Table 1). On average, 48 species were detected across all the survey years and sites. The highest number of species detected in a single survey was 55 for the northern region during the 2023 survey, while the lowest was 44 recorded in 2020 in the same region (Supplementary information – Table 5). The most frequently captured specie across all the survey years was impala (n = 32,636 captures), with the most captures recorded in 2023 (> 12,000) (Supplementary information – Table 7).

Out of the 61 sites, across the study area (KNP), cheetah was detected at 25 sites. The central region had the highest number of sites (n = 10) where cheetah was detected, followed by the northern region (n = 9) and then the southern region (n = 6) (Table 1). A total of 170 cheetah detections were recorded across all sites, with the northern region exhibiting the highest number of detections (n = 122), followed by the central region with 34 detections, and the south had the lowest cheetah detections (n = 14) (Table 1). A total of 112 independent cheetah detections were recorded across all the sites and survey years. The northern region had the highest number of independent cheetah detections (n = 79), followed by the central region (n = 24), and then the southern region (n = 9). On average the naïve occupancy across all survey years (2018 – 2023) for the three regions was 41%. The northern region had the highest naïve occupancy (50%) followed by central (45%), and the southern region was the lowest (28%) (Table 1).

The combined total of prey species captured across all sites and survey years was 72,043. The year with the highest number of prey captures was 2023 (n = 28,361) (Supplementary information – Table 7). The prey RAI ranged from 0 – 101.67, with a mean value of 16.3. The highest prey RAI was recorded in the northern region (Supplementary information – Table 9). The number of independent captures for lion and hyena were 982 and 1,294 respectively (Supplementary information – Table 6). Lion RAI ranged from 0 – 31, with a mean of 1.67 while hyena RAI ranged from 0 – 15 with a mean of 2.12. The highest lion RAI was recorded in the central region, whereas the highest hyena RAI was recorded in the northern region (Supplementary information – Table 9).

Proximity of sites to legal camps varied from 0.46 – 13.2 km with the mean distance between sites and legal camps being approximately 3.8 km. The distance between sites and the nearest main drainage lines ranged from 0 to 21 km. On average the sites were approximately 3.3 km away from the main drainage lines. The anti–poaching patrol distances varied from 0 – 5,769.8 km across the surveyed sites, with an average distance of 185.1 km.

Table 1: General summary of all camera trap surveys conducted in three regions (North, Central and South) within Kafue National Park from 2018 – 2023. Data include the number of camera stations, number of sites surveyed, number of sites with wildlife captures, survey length (days), total independent captures of all wildlife, Total number of cheetah detections, independent cheetah detections per site, number of sites with cheetah detections, and naïve occupancy of cheetah in each region averaged over all surveys. The asterisk (*) in the table denotes the total number of sites where cheetahs were detected across all the survey years. It should be noted that this figure does not represent the sum of individual sites where cheetah detections occurred for each year independently.

Region	Year	Number of stations	Number of sites surveyed	Number of sites with wildlife captures	Survey length (days)	Total number of independent captures of all wildlife	Total number of cheetah detections	Number of independent cheetah detections per site	Number of sites with cheetah detections	Naïve occupancy (%)
North	2019	36	18	11	64 [Aug 21-Oct 24]	2,774	20	14	5	
	2020	39	18	13	55 [Aug 17-Oct 11]	2,273	16	13	5	
	2021	40	18	12	52 [Sep 6-Oct 28]	3,060	12	9	3	
	2022	40	18	12	66 [Aug 28-Nov 2]	4,121	26	18	7	
	2023	49	18	17	72 [Aug 5-Oct 16]	5,298	48	25	6	
Across all survey years			***90***	***65***		***17,526***	***122***	***79***	***9 ****	***50%***

Central	2018	40	22	14	57 [Oct 13-Dec 8]	6,135	3	2	1	
	2020	40	22	14	64 [Jun 8-Aug 11]	4,681	17	12	8	
	2021	51	22	20	48 [Jun 8-Jul 26]	5,147	2	2	2	
	2022	40	22	14	53 [May 24-Jul 16]	4,169	8	5	4	
	2023	51	22	22	62 [May 15-Jul 16]	8,337	4	3	3	
Across all survey years			**110**	**84**		***28,469***	***34***	***24***	***10 ****	***45%***
South	2019	40	21	14	36 [Nov 8-Dec 14]	859	0	0	0	
	2020	40	21	14	56 [Oct 21-Dec 16]	1,751	1	1	1	
	2021	38	21	14	59 [Sep 23-Nov 21]	1,465	0	0	0	
	2022	40	21	14	79 [Sep 13-Dec 1]	1,781	0	0	0	
	2023	48	21	21	63 [Jun 15-Aug 17]	3,931	13	8	6	
Across all survey years			***103***	***63***		***9787***	***14***	***9***	***6 ****	***28%***
Grand total		**592**	**305**	**212**		**55,782**	**170**	**112**	**25**	**41%**

3.2: Occupancy Modeling

Detection models

The best detection model included only sampling effort as a predictor variable (ELPD= – 231.83). The model had the most substantial weight (0.59), indicating a strong balance between predictive power (ELPD) and weight (the relative likelihood of each model being the best model). The addition of the road predictor variable (proportion of sites on the road) slightly decreased the ELPD to –232.26, with a Δ ELPD of –0.433 and a weight of 0.34, indicating a slightly lower predictive power but still having substantial support relative to the weight. Incorporating the number of camera stations in a site, and total distance of sites to the nearest road, resulted in a weight of 0 – indicating minimal support for these models. The null model, with the least parameters (2.76), had a significantly lower ELPD (–261.55) than the top ranked model, with a weight of 0.06, showing it's the least supported model.

Table 2: Model selection for the detection predictors based on their Expected Log Pointwise Predictive Density **(ELPD),** Including the number of parameters **(nparam),** the difference in ELPD relative to the top model **(Δ ELPD),** the standard error **(SE),** and relative weights **(Weight).**

Model	ELPD	nparam	Δ ELPD	SE	Weight
effort	–231.83	3.67	0	0	0.59
effort + prop. sites on road	–232.26	5.10	–0.43	1.76	0.34
effort + num. stations in a site	–232.49	4.61	–0.67	0.44	0.00
effort + total distance of sites to the nearest road	–233.09	5.25	–1.26	1.25	0.00
effort + prop. sites on road + num. stations in a site + total distance of sites to nearest road	–234.24	7.48	–2.41	2.17	0.00
null	–261.55	2.76	–29.71	9.29	0.06

There was a strong positive relationship (β = 0.82, 95% CI [0.71, 0.92]) between the sampling effort (i.e., total number of days cameras were active in a site) and the detection probability of cheetah (Figure 6).

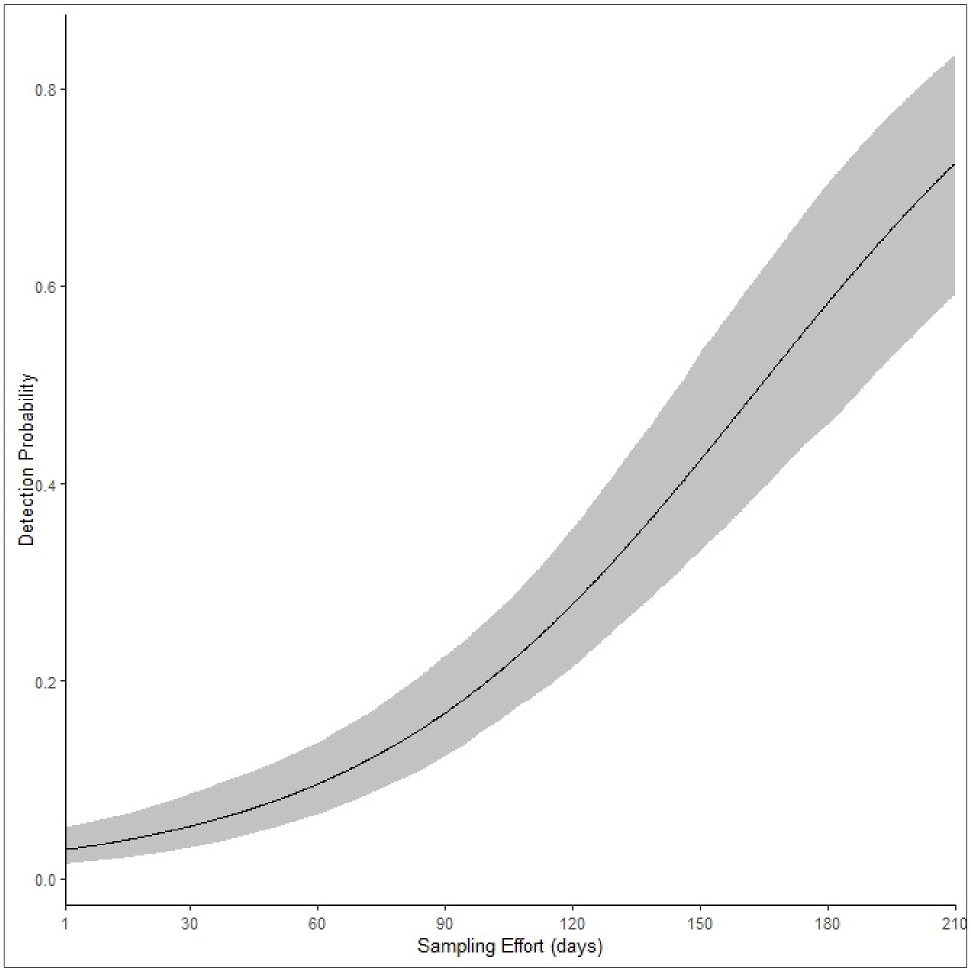

Figure 6: Predicted relationship between sampling effort and the probability of cheetah detection within the Kafue National Park. 95% Confidence interval (CI) is shown by shaded regions.

Model ranking for site covariates

Model ranking using ELPD showed that Prey RAI had the highest ELPD value (–216.09) and a significant weight (0.53), indicating the best predictive power (ELPD) and support (weight) among all the models evaluated. The second–best model included the proportion of open forest with an ELPD value of –218.21, 12.9 as the number of parameters and a weight of 0.33. The proportion of closed forest, grassland, and null models all had slightly lower ELPD values compared to the Prey RAI and the proportion of open forest, indicating slightly lower predictive accuracy. Among them proportion of closed forest had the highest ELPD (–219.72), while the proportion of grassland had the lowest ELPD value (–219.83). Lion RAI, distance to legal camps (km), distance to water (km), hyena RAI and anti–poaching patrol effort models had even lower ELPD values compared to the two best models (Prey RAI and proportion of open forest), indicating poorer predictive accuracy. They also had higher ELPD differences (Δ ELPD), indicating greater differences in predictive performance compared to the best model (Prey RAI). These results are summarised in Table 3 below.

Table 3: Model selection for the nine occupancy covariates based on their Expected Log Pointwise Predictive Density **(ELPD),** Including the number of parameters **(nparam),** the difference in ELPD relative to the top model **(Δ ELPD),** the standard error **(SE),** and relative weights **(Weight).**

Model	**ELPD**	**nparam**	**Δ ELPD**	**SE**	**Weight**
Prey RAI	–216.09	19.44	0.00	0.00	0.53
Proportion of open forest	–218.21	12.95	–2.12	3.21	0.33
	–219.72	20.58	–3.63	3.30	0.12
Proportion of closed forest					
Null	–219.76	20.52	–3.67	3.31	0.02
Proportion of grassland	–219.83	18.61	–3.7	3.36	0.00
Lion RAI	–220.22	21.29	–4.1	3.26	0.00
Distance to camp (km)	–220.44	21.59	–4.35	3.26	0.00
Distance to water (km)	–220.63	20.49	–4.54	3.29	0.00
Hyena RAI	–220.94	20.50	–4.85	3.31	0.00
Anti–poaching patrol effort	–221.32	21.19	–5.23	3.72	0.00

Single covariate occupancy model

Only prey RAI and proportion of open forest had a significant impact on cheetah probability of site use, with cheetah more likely to occur at sites with higher prey abundance (β = 2.08, 95% CI [0.53, 4.40]), and less likely to occur at sites with a higher proportion of open forest (β = – 3.55, 95% CI [–6.06, –1.11]) (Figure 7). The relationship between cheetah probability of site use and prey RAI followed a logistic trend, with a sharp increase in cheetah site use as prey RAI increases before beginning to plateau at ~0.75 prey RAI (Figure 7, left graph). In contrast, as the proportion of open forest increased, cheetah site use decreased sharply.

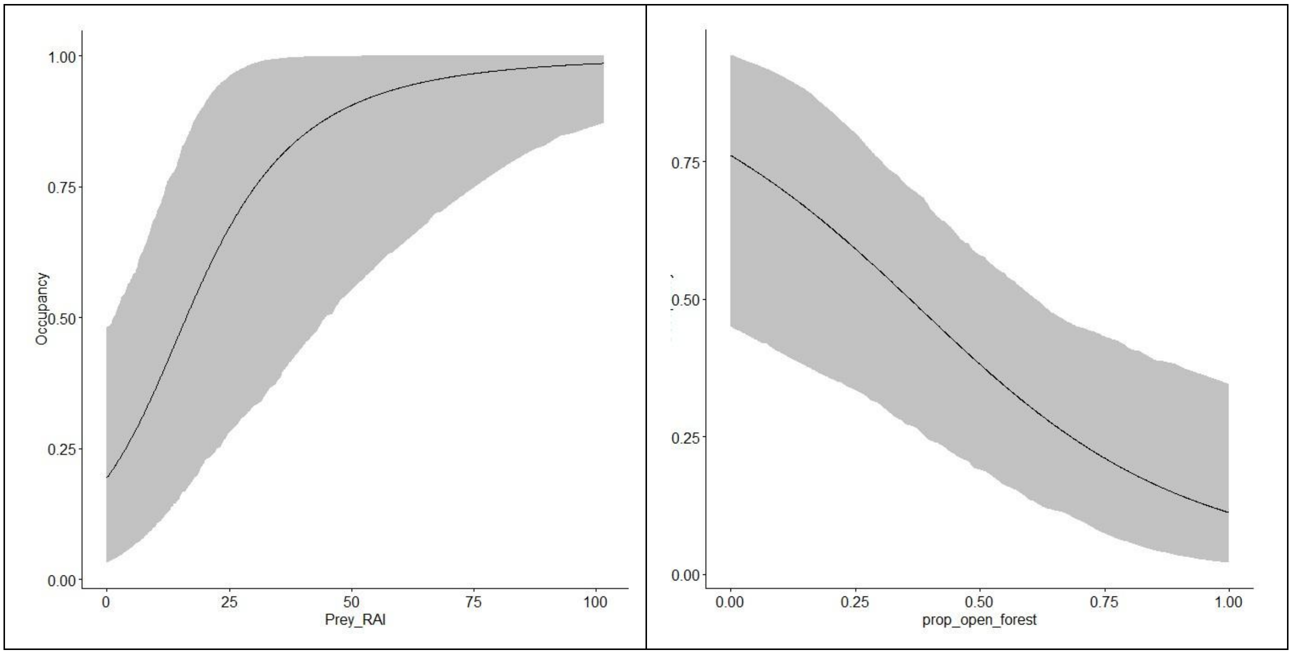

Figure 7: Variation in cheetah probability of site use with Prey RAI (left graph) and proportion of open forest (right graph) within the Kafue National Park. 95% Confidence intervals (CI) are shown by shaded regions. The Y-axis labelled 'occupancy' on the graph denotes the 'probability of site use'.

Of the nine–covariates assessed in my study, seven had no significant impact on cheetah probability of site use, as indicated by confidence intervals all overlapping zero (Figure 8). These covariates included the proportion of closed forest, the proportion of grassland, lion RAI, hyena RAI, anti–poaching patrol effort (total patrol distance in each site), distance to water, and distance to legal camps.

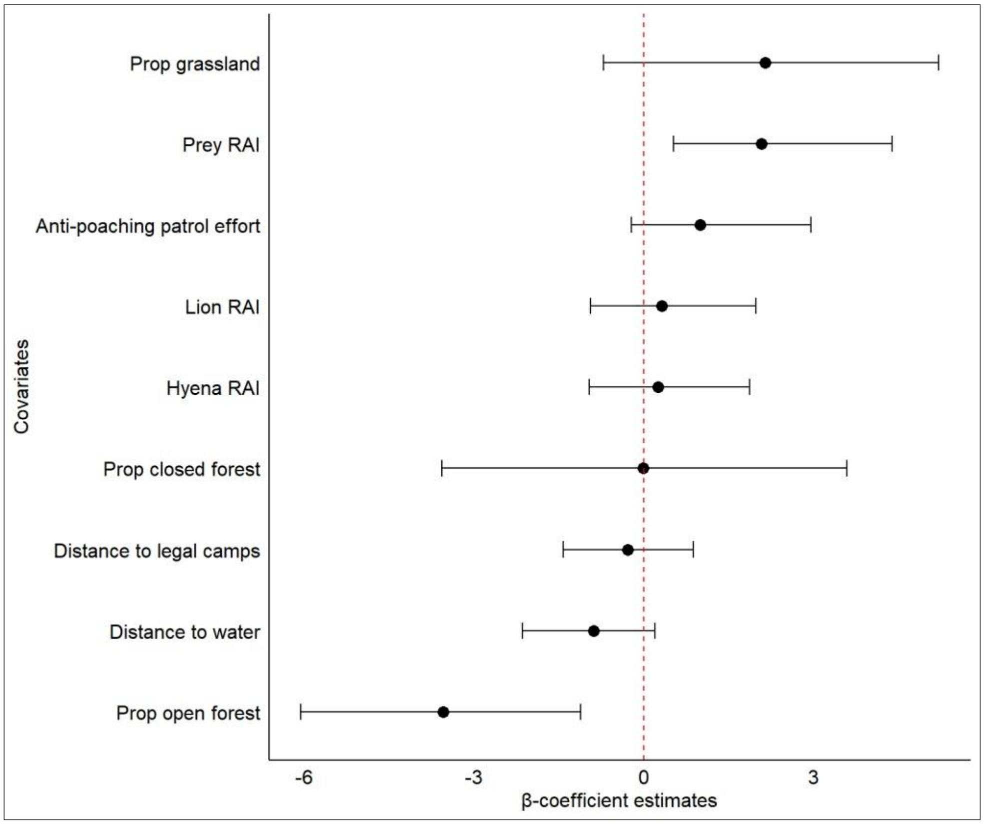

Figure 8: β–coefficient estimates (black circles), and associated 95% confidence intervals for the site–specific covariates explaining cheetah probability of site use (Ψ) in Kafue National Park. Significant β–coefficient estimates are indicated by the non–overlap of the confidence intervals with zero and the overlaps indicates non–significance. The direction of the effect is represented by the sign of the coefficients, with positive and negative values indicating the respective directions of influence.

The proportion of grassland and anti–poaching patrol effort (total patrol distance in a site) had a positive relationship with cheetah probability of site use, although their wide confidence intervals indicated a lack of support based on the goodness of fit metric. This may further reflect that cheetahs are found across a wide range of values. The estimates include (β = 2.15, 95% CI [–0.71, 5.22]) and (β = 1.00, 95% CI [–0.22, 2.96]), for proportion of grassland and anti–poaching patrol effort (total patrol distance in a site). Proportion of closed forest (β = –,.01, 95% CI [–3.57, 3.59]), distance to legal camps (km) (β = –0.28, 95% CI [–1.42, 0.88]) and both lion (β = 0.32, 95% CI [–0.93, 1.98]) and hyena (0.26, 95% CI [–0.96, 1.88]) RAI, had β–estimates close to zero, indicating that they have a weak relationship whether positive or negative with cheetah probability of site use (Table 4, Figure 8). Similarly, the distance to water and cheetah probability of site use showed a negative relationship with a wide confidence interval (β = –0.88, 95% CI [–2.14, 0.20]) (Table 4, Figure 8).

Table 4: Coefficient estimates **(β),** standard deviation **(SD),** 95% confidence interval **(LCI and UCI**), and **R-hat (*R^*)** values for all nine site covariates. The *R^* value was used to assess the convergence Markov Chain Monte Carlo (MCMC) chains. *R^* values <1.1 indicated good convergence and reliable estimates (Vehtari et al., 2021).

Covariate	**β–estimate**	**SD**	**95%CL (LCI and UCI)**		**R–hat**
Distance to water	–0.88	0.58	–2.14	0.20	1.00
Distance to legal camps	–0.28	0.57	– 1.42	0.88	1.00
Prey RAI	2.08	1.00	0.53	4.40	1.00
Lion RAI	0.32	0.73	–0.93	1.98	1.00
Hyena RAI	0.26	0.71	–0.96	1.88	1.00
Anti–poaching patrol effort	1.00	0.81	–0.22	2.96	1.00
Proportion of closed forest	–0.01	1.78	–3.57	3.59	1.00
Proportion of open forest	–3.55	1.24	–6.06	–1.11	1.00
Proportion of grassland	2.15	1.50	–0.71	5.22	1.00

DISCUSSION

4.1: Overview

The cheetah (*Acinonyx jubatus*) is currently experiencing a precipitous decline towards potential extinction, with extirpations reported in nearly twenty countries and a reduction to merely 9% of its original geographic range (Durant et al., 2017). Compared to other large carnivores, cheetahs are understudied, leading to a significant gap in our knowledge regarding their distribution and the status of various population, particularly in regions such as Zambia (Durant et al., 2015; Cristescu et al., 2018). This paucity of data on cheetah distribution highlights the urgent need for comprehensive studies on its current range. Leveraging techniques such as camera trapping and occupancy modelling offers an opportunity for estimating the distribution of cheetah across vast areas, while accounting for the inherent imperfections in detection (MacKenzie et al., 2006; Zeller et al., 2011). In this study, I used data collected from three large–scale camera trap arrays active between 2018 – 2023 to assess the probability of site use by cheetah across the surveyed regions of Kafue National Park (KNP) in Zambia. The explanatory variables used to elucidate cheetah probability of site use included both environmental and anthropogenic factors. Environmental covariates consisted of habitat types (namely closed forest, open forest and grassland), relative abundance of prey species, competitive interactions (indexed by the relative abundance of lions and hyenas), distance to water. Anthropogenic covariates included anti–poaching patrol effort (total patrol distance in each site), and the distance to legal camps (lodges, NGO and DNPW bases).

4.2: Capture histories and occurrences

A comprehensive capture history was obtained from 305 sites. Among these, wildlife captures were recorded from 212 sites, accounting for 69.5% of the total surveyed sites. There was a total of 112 independent cheetah detections with the highest number recorded in the north (Table 1) which encompasses the Busanga plains, characterized by expansive grasslands that support abundant herbivore diversity and abundance, including key prey species such as puku, wildebeest, and zebra (Vinks et al., 2020). Importantly the northern region also had the highest prey RAI.

Based on the model comparison for the detection probability, the model including only the covariate "sampling effort" (i.e., total number of days cameras were active in a site) performed best in describing the probability of detecting cheetah site use (Table 2). From a practical point of view, this indicates that increasing the duration of the camera trap survey would significantly increase the probability of detecting their presence. This is consistent with a study by Shannon et al. (2014) which indicated that survey duration for rare species (characterised by low detection probabilities), often entails conducting surveys for an extended period to increase the chances of adequate detection. The proportion of sites on the road also improved cheetah detection (Table 2), consistent with a study by Davis et al. (2023), which suggests that camera trap survey designs for monitoring carnivores often involve placing cameras along roads. However, this is contrary to Durant's observation of cheetah's exhibiting avoidance behaviour towards roads, presumably because they are frequented by tourists and other predators such as lions and hyenas (Pettorelli et al., 2009). Therefore, Brassine and Parker's (2015) recommendations to customize array designs tailored specifically for cheetahs, with an emphasis on using scent marking posts should be highly considered as this will increase the effective monitoring of the cheetah.

Only two of the nine covariates considered, namely prey RAI and the proportion of open forest, had a strong influence on cheetah probability of site use within KNP. Prey RAI was the top ranked covariate among the nine other covariates evaluated, as determined by Expected Log Pointwise Predictive Density (ELPD) metrics (Table 3). The positive estimate ($\beta = 2.08$) (Table 4) and narrow confidence intervals for prey RAI suggests that areas with higher prey abundance are more likely to attract cheetah, aligning with findings from other studies (Mitchell and Hebblewhite, 2012; Andresen and Somers, 2013; Vanak et al., 2013; Tagwireyi et al., 2020) and supporting my first prediction. Notably, more prey species were captured in the northern region which was characterised by the grasslands followed by the central region and the least number of captures was in the southern region. There has been a discernible dietary shift among large carnivores, including cheetah, towards medium–small prey species over the past five decades in KNP (Creel et al., 2018). The estimated densities for the three most abundant prey species include 9.6 per km² for impala, 13 per km² for puku, and 1.7 per km² for warthog (Creel et al., 2018). Furthermore, Vinks et al. (2020) also acknowledged the high densities and abundance of impala, puku and warthog within KNP. However, he noted that their densities were low compared to historical records from undisturbed miombo herbivore guilds (Vinks et al., 2020).

The negative coefficient (β = –3.55) and narrow confidence intervals for the proportion of open forest suggested that cheetah actively avoided forested areas. This aligns with existing literature suggesting cheetahs prefer expansive grassland plains (Caro, 1994; Broomhall et al., 2003; Mills et al., 2004), despite their documented adaptability to various ecosystems including woodlands (Purchase and du Toit, 2000; Mills et al., 2004; Andresen and Somers, 2013). However, it is possible that open forest areas are less attractive to cheetah, likely due to limited visibility and manoeuvrability which are crucial for successful hunts (Caro,1994; Durant et al., 2004; Mills et al., 2004; Hilborn et al., 2012). Open forest, primarily composed of central Zambezian miombo woodlands, are distributed across various regions within KNP (Fanshawe et al., 2010; Mbewe, 2015). Additionally, other woodland types such as Kalahari, munga, and mopane are also present (Fanshawe et al., 2010). Previous research has linked the sparse distribution of cheetahs in Zambia with the predominance of miombo woodlands (Purchase et al., 2007a). In stark contradiction, a recent study conducted in the Ruaha-Rungwa ecosystem of Tanzania challenges this notion, suggesting that miombo woodlands might serve as a crucial habitat for cheetahs (Strampelli et al., 2021). Strampelli et al., (2021) further indicated that eleven out of the seventeen independent cheetah detections captured by camera traps originated from the two surveyed miombo sites. Moreover, despite the predominant focus of cheetah studies in Southern Africa in mopane habitat, the significance of woodlands for the species throughout its range cannot be overlooked (Strampelli et al., 2021).

Out of the nine covariates evaluated, seven did not show statistically significant associations with cheetah site use. Despite the absence of statistical significance, consistent trends were observed in the beta estimates for each covariate. These trends provided valuable insights into how these covariates may influence the distribution of cheetahs within KNP, therefore, prompting further exploration and interpretation as outlined below.

The β–estimate for the proportion of closed forest (β = –0.01) was close to zero, suggesting that closed forests are likely to have a neutral effect on cheetah probability of site use. This observation could be linked to the minor extent of closed forest within KNP, which covers only 1.77% of the entire park (Figure 3 and Supplementary information – Figure 14). On the other hand, a positive trend was observed for the proportion of grassland, indicating a weak positive association between increased grassland cover and the likelihood of cheetah site use. This trend is consistent with previous studies, which posit that grasslands, by virtue of their open landscapes, offer enhanced visibility for hunting and may be indicative of the presence of preferred prey species, thereby potentially increasing cheetah site use (Caro, 1994; Broomhall et al., 2003; Mills et al., 2004; Durant et al., 2004). The combination of abundant herbivores and expansive grassland terrain is likely to enhance both prey visibility and accessibility for cheetahs, which have been identified to be important variables influencing cheetah presence and abundance (Caro,1994, Broomhall et al., 2003; Mills et al., 2004; Durant et al., 2004). This could explain why the northern region of KNP which is characterised by extensive grasslands had the highest numbers of cheetah detections and naïve occupancy (Table 1).

Although my study did not specifically assess individual prey species density across various habitat types, recent research Vinks et al. (2020) indicates that puku density in KNP was notably higher in regions with low proportions of closed forest habitats compared to other habitat types. The density of warthogs was highest in areas characterized by a low proportion of open forest. Conversely, impala and zebra densities exhibited a positive correlation with the prevalence of open forest habitats, with zebra density peaking in areas where approximately half of the vegetation composition comprised open forest (Vinks et al., 2020). This underscores the variability in the distribution and abundance of prey species across different habitat types and regions, as supported by the independent captures of prey species in my study (Supplementary information – Table 8). Notably, the north and central regions of KNP have higher independent captures of most prey species, including puku, impala, and warthog compared to the south region (Supplementary information – Table 8), a pattern that aligns with the independent detections and naïve occupancy of cheetahs (Table 1). When comparing the findings of Vinks et al. (2020) with my results, it becomes evident that the distribution of cheetahs is likely influenced by a complex interplay between habitat selection and prey availability.

Contrary to my second prediction, the presence of lions and hyenas did not significantly influence the probability of cheetah site use. This suggests co–existence, as previously reported for cheetah and other large predators (Cristescu et al., 2018), with possible fine scale spatial– temporal avoidance (Durant, 1998, 2000a) and differences in prey preferences (Hayward et al., 2006). While hyenas are present in Kafue National Park (KNP) and have been described as occurring in low numbers—a trend that has persisted for several decades (Creel et al., 2018)—the similarity in their detection rates to those of lions suggests that their numbers may not be as low as initially perceived. This indicates that their presence might be underestimated or that their activity patterns make them equally likely to be detected.

The RAI for hyenas ranged from 0 – 15, with the highest recorded in the northern region (Supplementary Information – Table 9). Notably, independent captures of hyenas were highest in the central region (Supplementary Information – Table 6). Furthermore, there was a weak positive relationship between hyenas and the probability of cheetah site use, which could be attributed to factors such as direct avoidance by cheetahs upon encountering hyenas, either by sight or sound. Compared to lions, hyenas are perceived as a lesser threat (Durant, 2000a; Webster et al., 2012; Swanson et al., 2014; Swanson et al., 2016).

Lions are estimated to occur at a density of 3 – 4 individuals per 100 km^2, a figure lower than reported densities in comparable ecosystems with less prey depletion (Vinks et al., 2021). This corroborates my findings, which revealed low lion RAI values ranging from 0 – 31, with a mean of 1.67, with the highest in the central region (Supplementary information – Table 9). Independent captures of lions were also highest in the central region (Supplementary information – Table 6). Creel et al. (2018) have shown that larger carnivores exhibit overlapping prey preferences in KNP, suggesting a shared reliance on similar resources, particularly when prey availability is limited. Cheetahs prefer open areas with high prey RAI, while lions prefer habitats that provide concealment for improved prey capture (Midlane et al., 2014). Cheetahs have been observed to exhibit a direct avoidance of lions more frequently in open habitats than in woodlands, by maintaining an average distance of 110 meters from lions (Broekhuis et al., 2013; Vanak et al., 2013). The low RAI of larger predators could be an advantage to cheetahs as this could reduce the threat of kleptoparasitism, which has been shown to have a negative impact on their abundance (Hunter et al., 2007; Broekhuis et al., 2013) and reproductive success (Kelly et al., 1998; Mills and Mills, 2014).

Water serves as a crucial resource for most wildlife as a feature around which many animals, particularly prey species for carnivores, tend to aggregate (Durant et al., 1988; Hopcraft et al., 2005; Pettorelli et al., 2009; Tagwireyi et al., 2020). Despite not being water-dependent, cheetahs exhibit a preference for habitats near water sources (Tagwireyi et al., 2020). This aligns with my findings, with the probability of cheetah site use decreasing as the distance to water increases, supporting my third prediction (Table 3). In Gonarezhou National Park (GNP) and Matusadona National Park in Zimbabwe, cheetah hunting behaviour was more likely in areas near water sources, which was attributed to higher densities of preferred prey species, particularly impala (Hayward et al., 2006; Tagwireyi et al., 2020; Van Der Meer et al., 2020). Observations from the Serengeti landscape also support this preference, but here it was argued that cheetah tend to favour habitats near water with relatively lower prey densities to reduce interspecific competition with lions and hyenas (Durant, 1998; Tagwireyi et al., 2020).

Neither proximity to a legal camp nor anti–poaching patrol effort had a significant influence on cheetah site use. Cheetahs were more likely to use sites with higher anti–poaching patrol effort ($\beta = 1.00$). Substantial research has shown that low wildlife densities are often correlated with limited protection measures (Caro et al., 1998; Stoner et al., 2007; Ogutu et al., 2009, 2011; Schuette et al., 2016; Rosenblatt et al., 2019; Vinks et al., 2020). Thus, it seems cheetah may benefit from higher anti–poaching effort which may prevent the depletion of preferred prey but avoid areas of permanent human habitation, which are perceived as a threat.

In KNP, the illegal harvesting of bushmeat through poaching has been detrimental to herbivore populations (Lindsey et al., 2014), particularly large herbivores (Overton et al., 2017). This phenomenon may explain the observed shift in large carnivore’s prey preference towards medium– small species, and a reliance on available alternatives (Creel et al. 2018). This shift in prey preferences has led to an increase in competition for food resources among large carnivores. Such competition likely did not exist before the reduction of the large herbivores, as large carnivores such as lions are known prefer larger prey species such as buffalo (Hayward and Kerley, 2005), while cheetahs prefer medium–small species (Hayward et al., 2006; Bissett and Bernard, 2007; Andresen and Somers, 2013; Mutoro et al., 2022). Watson et al. (2013, 2015) further highlights the pronounced correlation between bushmeat poaching and human encroachment, a trend that has been observed to increase within the buffer zones (GMAs) surrounding KNP. In some instances, cheetahs have become inadvertently ensnared in traps set for bushmeat extraction, highlighting the risks posed by illegal hunting activities (Marnewick et al., 2009). The combination of external threats faced by cheetahs outside protected areas, along with their extensive population decline, has led to their categorization as "protection reliant” (Durant et al., 2017). Therefore, law enforcement through anti–poaching patrol efforts not only safeguards herbivore populations but also helps protect cheetahs and other wildlife from becoming unintended victims of snaring activities.

4.3: Limitations and recommendations

Adapting camera trap surveys designed specifically for leopard density estimates, to calculate cheetah occupancy, comes with clear limitations, the most obvious of which is a lack of independence between sampling sites. To overcome this limitation, I subsumed multiple camera stations into 6 x 6km grid cells. However, even after doing so, with the extensive movement patterns for cheetah, it is highly likely that the site independence was not attained, thus violating an assumption of occupancy modeling (MacKenzie et al., 2002; Mkonyi et al., 2018).

Furthermore, low detection rates of cheetah limited the model's ability to detect potential changes in cheetah occupancy over time. I therefore used a stacked occupancy model, which allowed for the integration of presence/absence data from multiple years into a single–season occupancy model (Harmsen et al., 2024). As a result, I emphasise that my study focused solely on evaluating the influence of site covariates on the probability of cheetah occurrence and site use, rather than providing comprehensive insights into temporal occupancy dynamics and the true occupancy measures.

Given the current knowledge gap regarding cheetah ecology and distribution, I recommend designing cheetah specific surveys with the addition of more sites to increase the statistical power for predicting cheetah distribution patterns as suggested by Shannon et al. (2014) and Brassine and Parker (2015). Due to the limited number of cheetah detections, and thus the need to reduce model complexity, I did not specifically examine the individual influence of each of the eleven prey species on the probability of cheetah site use. Therefore, I recommend that future assessments should investigate the impact of each individual prey species on cheetah site use and consider how these prey species are affected by various habitat types. Adopting such an approach will facilitate a more comprehensive understanding of cheetah site use in relation to prey availability and habitat dynamics, thereby enhancing conservation efforts and management strategies. Additionally, there is a clear need to acquire both spatial and temporal movement data through existing collaring studies to verify and further inform some of the findings in this dissertation—namely, the overdispersion of cheetahs in areas with high prey (RAI), their avoidance of open forests, and their interactions with other large predators—despite the known welfare impacts that collars may have on the cheetahs (Arhant et al., 2022). Analysing these movement patterns of cheetahs will elucidate the critical habitat requirements, predator interactions, and the need for protection within the highly seasonal environment of Kafue National Park, characterized by frequent flooding and fires due to anthropogenic activities (Midlane et al., 2014).

4.4: Conclusion

This study leverages existing camera trap data collected by the Panthera a non–governmental organisation (NGO) as part of their long–term monitoring of leopards within protected areas of Southern Africa, including Kafue National Park (KNP) in Zambia. These data also provide information on the distribution and abundance of other species including cheetah within the KNP landscape. Using the occupancy modeling approach, I assessed factors that influence the probability of site use for cheetah in three different regions of the park. The naïve occupancy of cheetah was highest in the north, followed by the central region and lowest in the south (Table 1). Similarly, cheetah detections were highest in the north and lowest in the south. Prey RAI and proportion of open forest emerged as significant covariates influencing site use, with cheetahs preferring areas with high prey abundance and avoiding open forests. Importantly, cheetah occupancy was not strongly influenced by the RAI of other large predators—namely lions and hyenas—or by anthropogenic factors. Therefore, their persistence in KNP seems largely reliant on adequate prey persisting in open habitat types. Limiting illegal bushmeat harvesting through routine anti–poaching patrols may suffice for ensuring the persistence of cheetah in KNP, with northern and central regions being the areas of highest priority.

These findings provide valuable insights into the ecological factors driving cheetah distribution in KNP. By prioritizing regions with high prey abundance and implementing effective protection strategies, such as anti-poaching patrols, conservation efforts can be more targeted and effective. This approach can significantly enhance the long-term viability of cheetah populations in KNP. The results of this study can assist the Department of National Parks and Wildlife (DNPW), Panthera, and African Parks (AP) in refining their management strategies and ensuring the sustainability of cheetah populations. This research underscores the importance of incorporating ecological data into adaptive conservation planning, which is critical for supporting sustainable cheetah populations not only in KNP but also in other similar landscapes across Southern Africa.

SUPPLEMENTARY INFORMATION

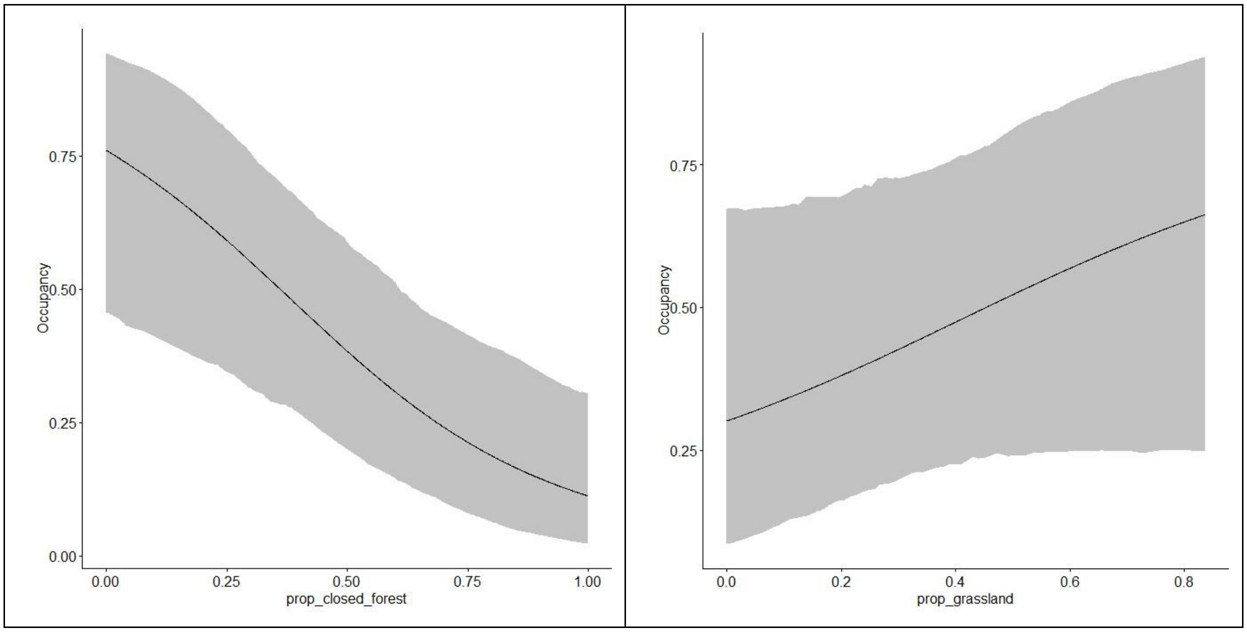

Figure 9: Estimated effect of proportion of closed forest (left graph) and proportion of grassland (right graph) on predicted cheetah site use within the Kafue National Park. 95% Confidence intervals (CI) are shown by shaded regions. The Y-axis labelled 'occupancy' on the graph denotes the ‘probability of site use’

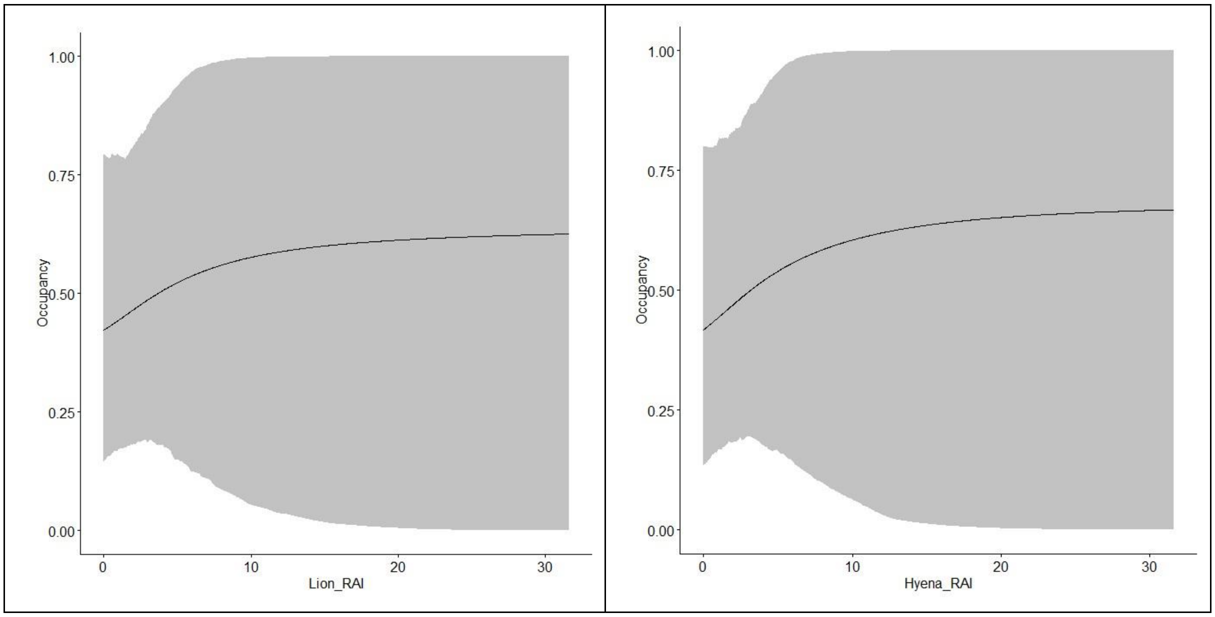

Figure 10: Estimated effect of lion RAI (left graph) and hyena RAI (right graph) on predicted cheetah site use within the Kafue National Park. 95% Confidence intervals (CI) are shown by shaded regions. The Y-axis labelled 'occupancy' on the graph denotes the ‘probability of site use’

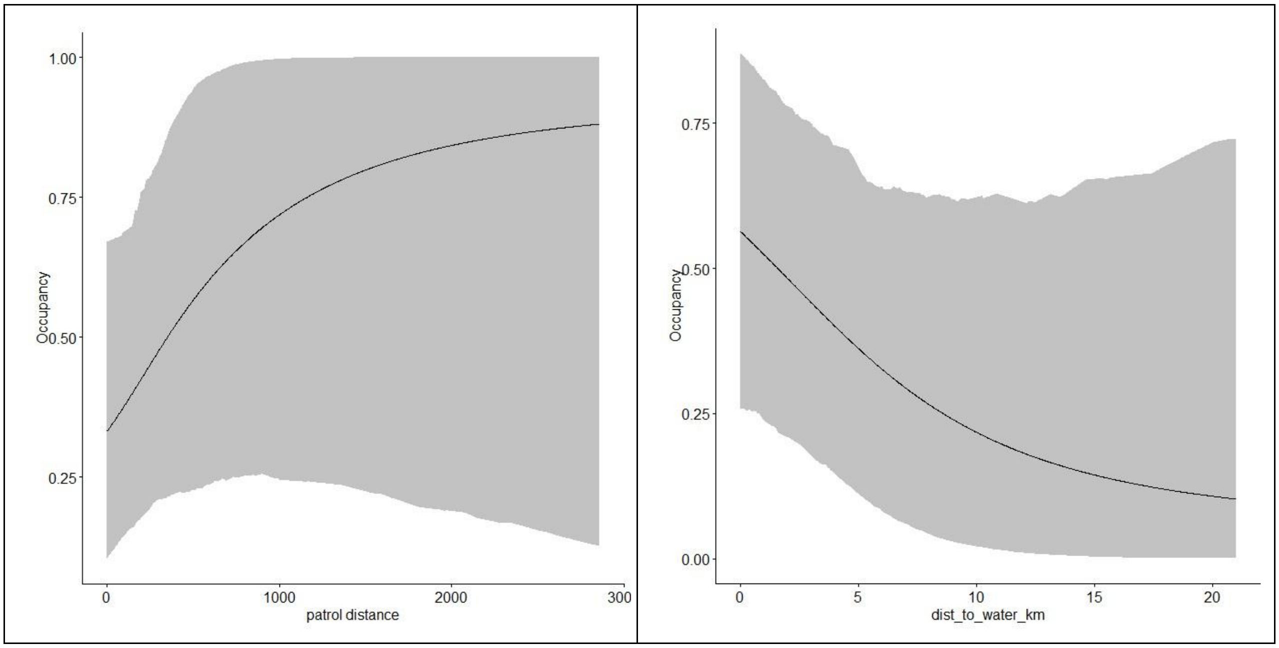

Figure 11: Estimated effect of anti–poaching patrol effort (total patrol distance in each site) (left graph) distance to water (right graph) on predicted probability of cheetah site use within the Kafue National Park. 95% Confidence intervals (CI) are shown by shaded regions. The Y-axis labelled 'occupancy' on the graph denotes the ‘probability of site use’

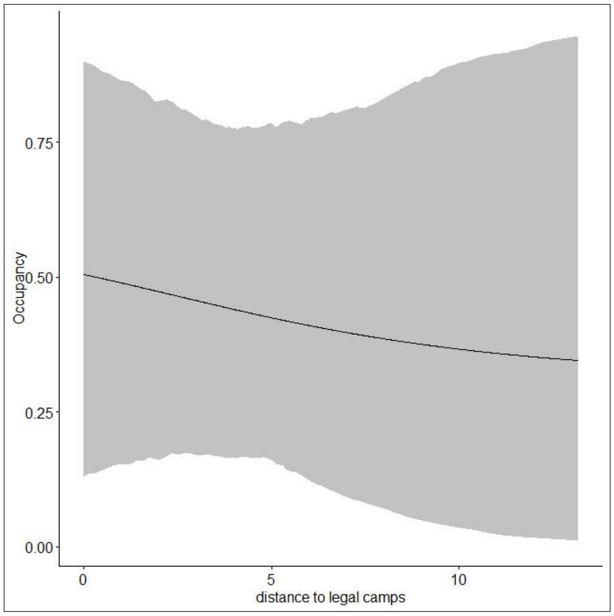

Figure 12: Estimated effect of the distance to legal camps on predicted probability of cheetah site use within the Kafue National Park. 95% Confidence intervals (CI) are shown by shaded regions. The Y-axis labelled 'occupancy' on the graph denotes the ‘probability of site use’

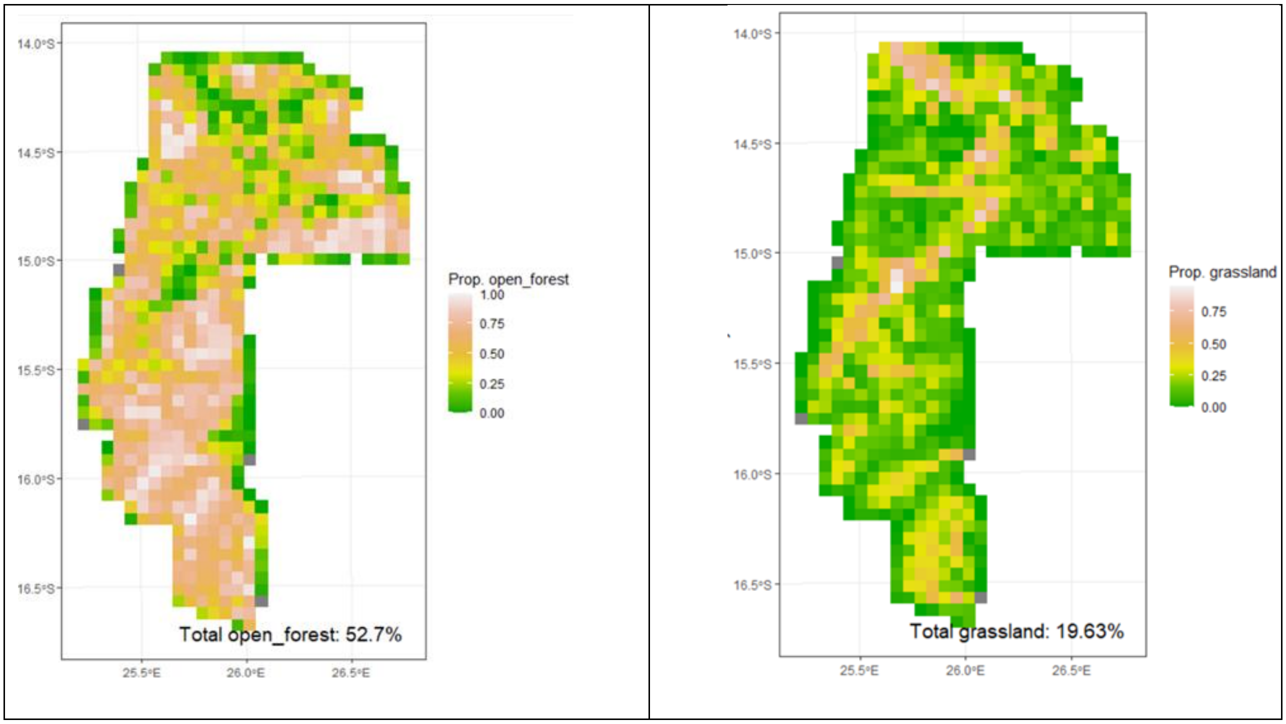

Figure 13: Proportion of open forest (left map) and grassland (right map), with legends indicating the percentage distribution across the study area.

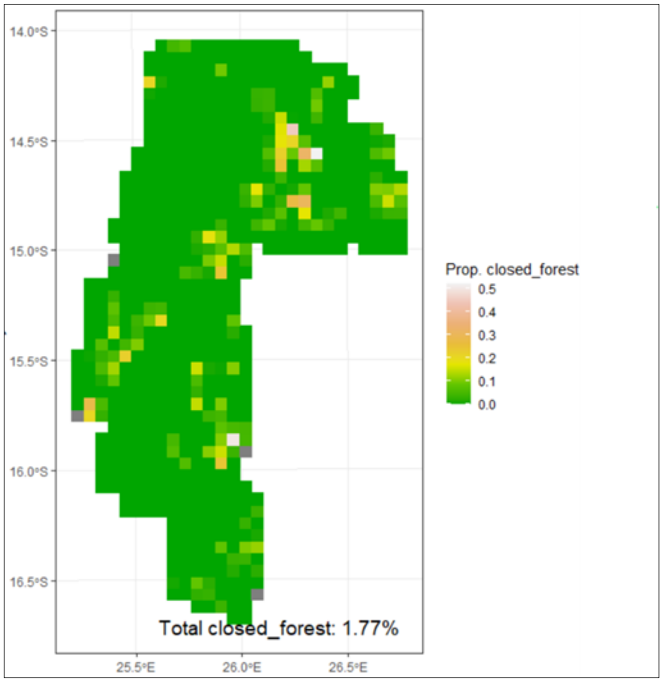

Figure 14: Proportion of closed forest, with the legend indicating the percentage distribution across the study area.

Table 5: Total number of species captures per year across the three regions (north, central and south).

Region	Year	Total species captured
Kafue Central	2018	51
Kafue Central	2020	46
Kafue Central	2021	46
Kafue Central	2022	47
Kafue Central	2023	54
Kafue North	2019	45
Kafue North	2020	41
Kafue North	2021	48
Kafue North	2022	43
Kafue North	2023	55
Kafue South	2019	40
Kafue South	2020	51
Kafue South	2021	47
Kafue South	2022	52
Kafue South	2023	54
Average number of species captured		**48**

Table 6: Independent captures of hyenas and lions per year and region

Region	Year	Independent Captures (Hyena)	Independent Capture (Lion)
Kafue Central	2018	79	29
	2020	132	105
	2021	103	127
	2022	69	91
	2023	166	255
Total		***549***	***607***
Kafue North	2019	116	14

	2020	92	21
	2021	108	62
	2022	37	48
	2023	155	66
Total		**508**	**211**
Kafue South	2019	44	13
	2020	35	24
	2021	36	51
	2022	46	27
	2023	76	49
Total		***237***	***164***
Grand Total		***1,294***	***982***

Table 7: Total number of prey captures tabulated across all the years (2018 – 2023) for each species. Species included are bushbuck, duiker, hartebeest, impala, kudu, oribi, puku, reedbuck, warthog, wildebeest, and zebra.

Species	**Year**						**Total number of captures per prey species**
	2018	***2019***	***2020***	***2021***	***2022***	***2023***	
Bushbuck	290	316	436	472	766	885	3165
Duiker	400	389	504	400	970	1211	3874
Hartebeest	218	175	293	475	429	656	2246
Impala	3179	668	3942	5329	5024	14494	32636
Kudu	190	24	162	185	181	628	1370
Oribi	0	57	185	59	250	177	728
Puku	1030	537	1744	4791	1429	6385	15916
Reedbuck	10	30	89	59	128	307	623
Warthog	692	485	917	1210	1125	2343	6772
Wildebeest	6	183	227	315	1777	753	3261
Zebra	58	134	101	333	304	522	1452

Total number of captures per year	**6073**	**2998**	**8600**	**13628**	**12383**	**28361**	**72043**

Table 8: Independent captures for eleven key prey species in each region. Species included bushbuck, duiker, hartebeest, impala, kudu, oribi, puku, reedbuck, warthog, wildebeest, and zebra.

Region	**Species**	**Independent captures**
Kafue Central	Bushbuck	582
Kafue Central	Duiker	399
Kafue Central	Hartebeest	164
Kafue Central	Impala	2012
Kafue Central	Kudu	242
Kafue Central	Oribi	3
Kafue Central	Puku	1625
Kafue Central	Reedbuck	27
Kafue Central	Warthog	967
Kafue Central	Wildebeest	5
Kafue Central	Zebra	28
Kafue North	Bushbuck	756
Kafue North	Duiker	719
Kafue North	Hartebeest	226
Kafue North	Impala	711
Kafue North	Kudu	30
Kafue North	Oribi	213
Kafue North	Puku	1167
Kafue North	Reedbuck	92

Kafue North	Warthog	772
Kafue North	Wildebeest	281
Kafue North	Zebra	158
Kafue South	Bushbuck	60
Region	**Species**	**Independent captures**
Kafue South	Duiker	537
Kafue South	Hartebeest	214
Kafue South	Impala	671
Kafue South	Kudu	138
Kafue South	Oribi	118
Kafue South	Puku	27
Kafue South	Reedbuck	140
Kafue South	Warthog	274
Kafue South	Wildebeest	45
Kafue South	Zebra	

Table 9: The range for the relative abundance index (RAI) for prey, lion and hyena per region

Species	Region	Minimum RAI	Maximum RAI
Prey	North	0	101.67
Prey	Central	0	96.72
Prey	South	0	51.33
Lion	North	0	6.45
Lion	Central	0	31
Lion	South	0	2.7
Hyena	North	0	15

Hyena	Central	0	13
Hyena	South	0	6.89

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